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Original Research Article

Environmental representativity in marine protected area networks over large and partly unexplored seascapes

Yorgos Stratoudakis^{a,*}, Ana Hilário^b, Cláudia Ribeiro^{c,d}, David Abecasis^d, Emanuel J. Gonçalves^{e,f}, Francisco Andrade^g, Gilberto P. Carreira^h, Jorge M.S. Gonçalves^d, Luis Freitasⁱ, Luis Menezes Pinheiro^j, Marisa I. Batista^k, Miguel Henriques^l, Paulo B. Oliveira^a, Paulo Oliveira^m, Pedro Afonsoⁿ, Pedro Ivo Arriegas^o, Sofia Henriques^p

^a Instituto Português do Mar e da Atmosfera, IP (IPMA), Rua Alfredo Magalhães Ramalho 6, 1449-006, Lisboa, Portugal

^b Biology Department and CESAM, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal

^c Observatório Oceânico da Madeira (OOM), Edifício Madeira Tecnopolo, 9020-105, Funchal, Madeira, Portugal

^d Centre of Marine Sciences (CCMAR), University of the Algarve, Campus de Gambelas, 8005-139, Faro, Portugal

^e MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041, Lisboa, Portugal

^f Oceano Azul Foundation, Oceanário de Lisboa, Esplanada D. Carlos I, 1990-005, Lisboa, Portugal

^g MARE - Marine and Environmental Sciences Centre, FCUL, Laboratório Marítimo da Guia, 2750-374, Cascais, Portugal

^h Direção de Serviços de Biodiversidade e Política do Mar, Direção Regional dos Assuntos do Mar (SRMCT), Rua D. Pedro IV, 29, 9900-111, Horta, Açores, Portugal

ⁱ Madeira Whale Museum, Rua Garcia Moniz 1, 9200-031, Caniçal, Madeira, Portugal

^j Geosciences Department and CESAM, University of Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal

^k LPN – Liga para a Protecção da Natureza, Estrada do Calhariz de Benfica 187, 1500-124, Lisboa, Portugal

^l Instituto da Conservação da Natureza e das Florestas, IP (ICNF), Parque Natural de Arrábida, Praça da República, 2900-587, Setúbal, Portugal

^m Instituto das Florestas e Conservação da Natureza, IP-RAM (IFCN), Quinta Vila Passos, Rua Alferes Veiga Pestana 15, Funchal, Madeira, Portugal

ⁿ Institute of Marine Research (IMAR) and MARE, University of the Azores, 9901-862, Horta, Azores, Portugal

^o Instituto da Conservação da Natureza e das Florestas, IP (ICNF), Divisão de Conservação da Biodiversidade, Avenida da República, 16-16B, 1050-191, Lisboa, Portugal

^p MARE - Marine and Environmental Sciences Centre, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016, Lisboa, Portugal

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ABSTRACT

Converting assemblages of marine protected areas (MPAs) into functional MPA networks requires political will, multidisciplinary information, coordinated action and time. We developed a new framework to assist planning environmental representativity in a network across the marine space of Portugal, responding to a political commitment to protect 14% of its area by 2020. An aggregate conservation value was estimated for each of the 27 habitats identified, from intertidal waters to the deep sea. This value was based on expert-judgment scoring for environmental properties and features relevant for conservation, chosen to reflect the strategic objectives of the network, thus providing an objective link between conservation commitments and habitat representativity in space.

* Corresponding author. IPMA, Rua Alfredo Magalhães Ramalho 6, 1449-006, Lisboa, Portugal.

E-mail addresses: yorgos@ipma.pt (Y. Stratoudakis), ahilario@ua.pt (A. Hilário), claudia.ribeiro@oom.arditi.pt (C. Ribeiro), dabecassis@ualg.pt (D. Abecasis), emanuel@ispa.pt (E.J. Gonçalves), faandrade@fc.ul.pt (F. Andrade), gilberto.mp.carreira@azores.gov.pt (G.P. Carreira), jgoncal@ualg.pt (J.M.S. Gonçalves), luisfreitas@museudabaleia.org (L. Freitas), imp@ua.pt (L.M. Pinheiro), marisa.batista@lpn.pt (M.I. Batista), miguel.henriques@icnf.pt (M. Henriques), pboliveira@ipma.pt (P.B. Oliveira), paulo.oliveira@madeira.gov.pt (P. Oliveira), pafonsopim@gmail.com (P. Afonso), Pedro.Arriegas@icnf.pt (P.I. Arriegas), snpires@fc.ul.pt (S. Henriques).

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Portugal

Additionally, habitats' vulnerability to existing anthropogenic pressures and sensitivity to climate change were also scored. The area coverage of each habitat in Portugal and within existing MPAs (regionally and nationally) was assigned to a scale of five orders of magnitude (from <0.01% to >10%) to assess rarity and existing representation. Aggregate conservation value per habitat was negatively correlated with area coverage, positively correlated with vulnerability and was not correlated with sensitivity. The proposed framework offers a multi-dimensional support tool for MPA network development, in particular regarding the prioritization of new habitats to protect, when the goal is to achieve specific targets while ensuring representativity across large areas and complex habitat mosaics. It requires less information and computation effort in comparison to more quantitative approaches, while still providing an objective instrument to scrutinize progress on the implementation of politically set conservation targets.

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1. Introduction

Networks of Marine Protected Areas (MPAs) are nested structures, with emerging conservation properties at higher levels of organization (e.g., species range extensions or re-establishments are only discernible at the level of the network), that require substantial knowledge, planning and monitoring to become effective (Roff, 2014). They aim to assure adequate habitat representativity, connectivity, replication and redundancy so that individual MPAs can act synergistically towards nature conservation goals (Gorud-Colvert et al., 2014) and build resilience to current and anticipated anthropogenic impacts, including those of climate change (McLeod et al., 2009; Johnson et al., 2018). In theory, such networks should consist of multiple sites with replicates of all habitat types that 1) are designed to be functionally connected, 2) individually or in aggregate, are of sufficient size to sustain minimum viable populations of the largest species in a region (including seasonal migrants), and 3) their resident species can sustain their populations by recruitment from one MPA to another (Roff, 2005).

Many countries started designating MPAs to respond to local needs, often ignoring the bigger picture of guaranteeing the long-term sustainability of these areas through connectivity between populations, communities and ecosystems. Moving from ad-hoc sets of MPAs to a functional network can be a long process that requires baseline information, strategic planning, regular monitoring and adaptive decision-making (Olsen et al., 2013; Roff, 2014). For large spatial scales where ocean circulation and biological connectivity patterns are still poorly known, a first step is to create a coherent set of MPAs based on past efforts of spatial protection (Ardron, 2008). This requires sufficient environmental representation to protect the full range of biodiversity, from genes to species and higher taxa along with the communities, evolutionary patterns and ecological processes that sustain it (Spalding et al., 2007). In face of the customary data-limited situation, assessment of ecological coherence is usually based on heuristics, considering broad levels of spatial organization, biogeographic classification and inclusion of vulnerable or sensitive biota against reasonable, yet arbitrary thresholds (Ardron, 2008; Johnson et al., 2014). For example, a recent assessment for the Celtic Sea considered the spatial coverage of MPAs to exceed the established threshold value of 10% in total area but with uneven repartition among countries and underrepresentation of deep-water habitats (Foster et al., 2017).

Identifying an appropriate ocean classification system and the environmental attributes of relevance for conservation are prerequisites for any decision on what proportion of marine space to protect and how to select and manage specific areas. Conservation planning is even more challenging for large marine areas ($\sim 10^6$ km²) as a result of data limitations, scale mismatch (Roff, 2005), lack of clear understanding of the mechanisms structuring marine biodiversity (Zacharias and Roff, 2000) and connectivity (Hilário et al., 2015), multiple definitions for the concept of conservation value (Campourteres and Anand, 2016), region-specific threats to environmental attributes (Zacharias and Gregr, 2005) and shifting baselines (Johnson et al., 2018). Too broad biogeographic concepts (such as the delimitation of realms and provinces) or too narrow coastal habitat classifications (such as the biotopes defined by the lower levels of the EUNIS - European Nature Information System, <http://eunis.eea.europa.eu/habitats-code-browser.jsp> - classification system) are unable to guide conservation plans at this larger scale, requiring a hierarchical compromise between geological/geophysical and biological components of classification (Roff and Taylor, 2000) influenced by regional contingency.

The marine space of Portugal extends across a large part of the temperate North East Atlantic (NEA), comprising ecosystems and seascapes ranging from the intertidal to the hadal zone, with knowledge and surveying sharply decreasing with depth and distance to the coast (Vasquez et al., 2015). This vast marine space includes some habitats with major pressures and urgent conservation needs (e.g. Cunha et al., 2013) but where also a large fraction of seascapes remains essentially unexplored. Earliest designation of small MPAs in Portugal started in the 1970s-80s: Selvagens and Garajau (Madeira); Berlengas (mainland continental shelf); Caldeirinhas and Formigas bank (Azores). Designation of marine areas increased during the 1990s, initially through the extension of already existing protected areas on land to the inner shelf area (e.g., Arrábida, in the mainland). In the 2000s larger marine areas were delimited by the implementation of the EU Birds and Habitats Directives over the territorial waters of the mainland (e.g., Pereira et al., 2018) and the islands (e.g. Abecasis et al., 2015). More recently,

MPAs beyond territorial waters were also designated both within the Exclusive Economic Zone (EEZ, e.g., Gorringe – Ramos et al., 2016) and on the proposed Extended Continental Shelf area (ECS, e.g., the Rainbow – Chantal-Ribeiro, 2010) submitted by Portugal to the Commission on the Limits of the Continental Shelf. Currently, the marine space of Portugal contains over 140 designated areas according to various regional, national and international typologies, corresponding to 93 non-overlapping marine areas covering over $300 \times 10^3 \text{ km}^2$ (c.a. 76% in the submitted ECS - information compiled by the task force described below) and including all types of designations, independently of the degree of regulation, implementation and protection. The area covered by MPAs corresponds to c.a. 4% in the EEZ of Portugal, becoming c.a. 7% when the marine space of the submitted ECS is also considered (although only a very small fraction of this area corresponds to fully no-take or no-entry marine reserves in few coastal MPAs).

This work describes the framework that was developed in Portugal to assist the planning of a comprehensive national MPA network, extending across the entire marine space of the country, politically assumed to represent a target of 14% of its national area by 2020. Previous efforts to address Portuguese MPAs systematically focused on specific issues in coastal waters only, for instance: proposing a representative MPA network for mainland Portugal coastal habitats based on specific fish habitat use information (Abecasis et al., 2017); identifying priority areas for conservation based on the spatial distribution of species and habitats within the Natura 2000 EU Directive (Pereira et al., 2018) and the spatial distribution of anthropogenic impacts (Fernandes et al., 2018); comparing the effectiveness of coastal MPAs in the Azores (Afonso et al., 2018) or the Madeira/Selvagens (Ribeiro, 2008; Friedlander et al., 2017) archipelagos. The challenge here was to develop a tool adequate to inform decisions for new MPA designations under the expressed 14% target, given existing limitations in data availability. This challenge was presented to experts with distinct disciplinary, regional and environmental knowledge, asked by the government to work together for a year to provide scientifically robust and transparent advice to guide political conservation decisions in aspiring a national MPA network. The framework that resulted from this interaction is illustrated through its application to the Portuguese marine space but can be used in comparable scenarios to advise planning or to scrutinize the quality of decisions to protect a target fraction of the ocean under limited and uneven data.

2. Material and methods

2.1. The study system

The Portuguese EEZ covers $1.7 \times 10^6 \text{ km}^2$ across three regional sub-zone components separated by international waters: the mainland (western and southern Iberian margin and shelf: $3.28 \times 10^5 \text{ km}^2$), the Azores archipelago (crossing the Mid-Atlantic Ridge and bounded southwards by the East Azores Fracture Zone: $9.54 \times 10^5 \text{ km}^2$) and the Madeira archipelago (including the Selvagens archipelago: $4.46 \times 10^5 \text{ km}^2$). The three are united, as concerns the national jurisdiction for the protection and the exploration of resources of the seabed and subsoil, in the Portuguese proposal for the Extension of the Continental Shelf submitted in 2009, under Article 76 of the United Nation Convention on the Law of the Sea to the UN Commission on the Limits of the Continental Shelf, resulting in a contiguous area of c.a. $4 \times 10^6 \text{ km}^2$ of the temperate NEA (Fig. 1).

Plate boundary tectonic processes related to the Africa-Eurasia convergence since the end of the Cretaceous and intraplate volcanism shape, to a large extent, the complex present seabed topography that interrupts the vast areas of NEA abyssal plains (Quartau et al., 2018). Only a small fraction of this area has bottom depths between 200 and 2000 m, mostly associated with steep bathymetric gradients (e.g. Morato et al., 2008a). Its geomorphological complexity induces distinctive biogeochemical and oceanographic processes (e.g., upwelling and sedimentation at the head of the canyon of Nazaré that brings the oceanic margin within 1 km from the coast – Cunha et al., 2011; seaweed productivity at the Ormonde peak of the Gorringe seamount, 200 km SW of mainland Portugal – Ramos et al., 2016; formation of sedimentary contourite ridges by the effect the Mediterranean Outflow Water (MOW) – Garcia et al., 2009). These processes interact to create a puzzle of patchy, isolated habitats and communities (e.g., island shelf communities - Hawkins et al., 2000; hydrothermal vents – Cardigos et al., 2005; mud volcanoes – Pinheiro et al., 2003).

The pelagic oceanic domain spans over 2000 km in latitude, from homogeneous, sub-tropical oligotrophic oceanic waters in the south (off Selvagens and the Great Meteor seamount complex at around 28°N) to seasonally productive temperate oceanic waters of sharper horizontal gradients shaped by the eastward flow of the North Atlantic drift in the north (around 48°N). In between, a Gulf Stream branch links to the Azores Current south of 34°N , whose axis becomes remarkably zonal and attains highest mean speeds at the longitudes of the Azores archipelago (Fig. 1). Longitudinally, the system covers almost 3000 km, from the western edge of continental Europe to the western limit of Azorean sub-zone, where oceanic waters are already under the Northwest Atlantic subtropical gyre province (Longhurst, 1995). Coastal/shelf processes (e.g., coastal divergence, runoff) and larger scale currents lead to the formation of seasonally varying fronts, whose recurrence is higher at locations where the flow is bathymetrically controlled (e.g. SW of Gorringe, Fig. 1). In deeper layers (~1000 m), the Mediterranean outflow through the Strait of Gibraltar, and its subsequent spreading and entrainment, corresponds to a distinct water mass - the MOW – which is responsible for the relatively high salinities at these depths with implications on the ocean circulation at local and regional scales (Pinheiro et al., 2010; Sánchez-Leal et al., 2017).

The Iberian coast is at the eastern boundary of the NEA between 36 and 44°N , extending along the 9°W meridian, with a narrow continental shelf (10–40 km) punctuated by some large to medium-sized submarine canyons (Arzola et al., 2008). The Azores Current reaches this Iberian margin where it interacts with slope currents and other mesoscale processes (e.g. the

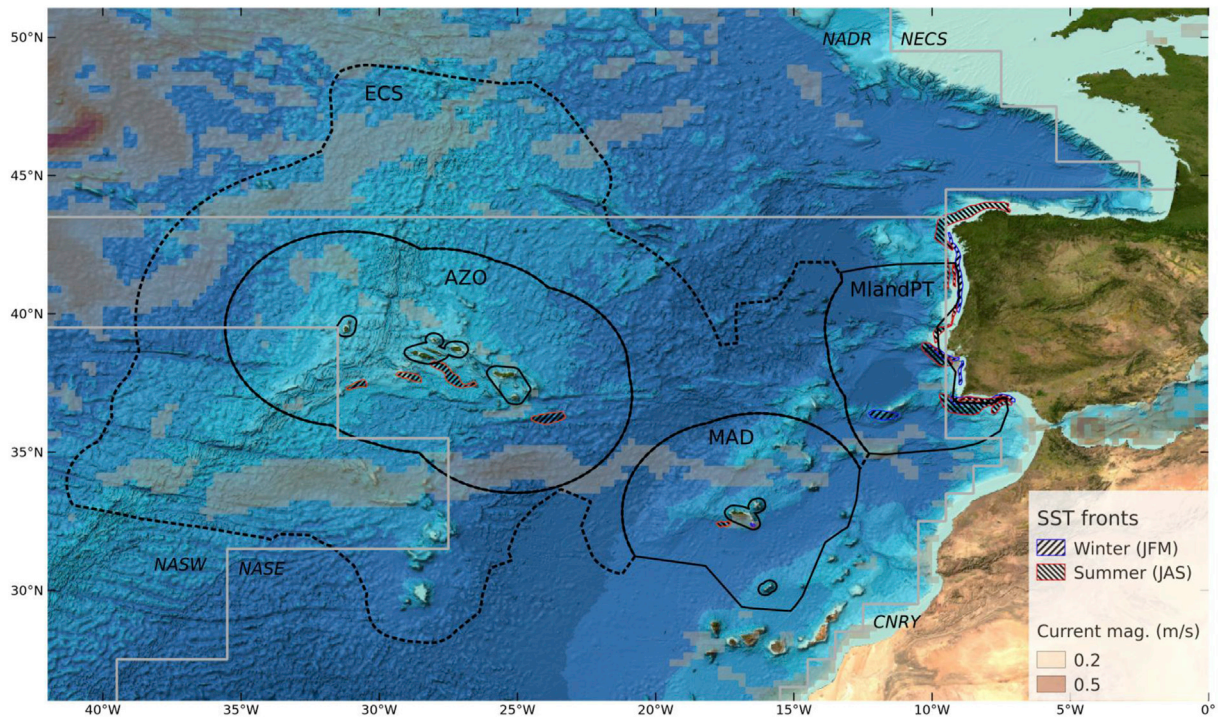


Fig. 1. Administrative regions of Portuguese marine space (MlandPT – Mainland Portugal, AZO - Azores, MAD - Madeira, solid black lines; and ECS – submitted Extended Continental Shelf, dashed lines) superposed on North-East Atlantic bathymetry (shading), Longhurst ecological provinces (gray lines), areas occupied by intense currents (pixelized shaded areas) and areas of increased probability of thermal front occurrence for the winter and summer seasons (diagonally striped areas).

Iberian Poleward Current, IPC – Teles-Machado et al., 2016; the MOW – Sánchez-Leal et al., 2017 and the formation of coherent vortices (meddies) – Pinheiro et al., 2010; and the wind-driven seasonal upwelling - Relvas et al., 2007), contributing to an eastern boundary region marked by strong seasonal and interannual surface current variability. The continental shelf and upper margin of mainland Portugal belong to the northern limit of the Canary coastal province, where seasonal upwelling dictates the main productivity patterns (Longhurst, 1995): higher productivity resulting from upwelling by northerly winds during the thermally stratified summer period, lower productivity during the winter relaxation period when the IPC transports warm and salty waters off the continental slope (Relvas et al., 2007; Teles-Machado et al., 2016). The latter is also the season of highest precipitation (Lima et al., 2013) that strengthens riverine turbid water plumes (Fernández-Nóvoa et al., 2017) and enhances land-based nutrient provision, but also the period of increased southerly winds frequency that constrain the plume extension to coastal mixed waters.

2.2. Methodology

The framework presented in this study was developed by a multidisciplinary task-force commissioned by the Portuguese Ministry for the Sea in March 2017. The mandate was to provide advice on how to extend the existing ad-hoc set of MPAs in the mainland and Portuguese Macaronesian regions to include new MPAs in order to form a coherent network across 14% of the marine space of Portugal by 2020. The remit of the group was the marine space beyond transition waters, including the four marine components depicted in Fig. 1 and using the information and data currently available from the Portuguese academia, administration and NGOs. The group met approximately every month from June 2017 to April 2018 and although its composition was predominantly academic and technical, it included elements from various administration levels (national and regional, fisheries and conservation) and a coordination team directly reporting to the minister. The meetings regularly involved over 30 members, including up to 25 marine scientists that have been working on the different marine habitats and/or groups of species across the Portuguese EEZ and submitted ECS (mainly biologists, but also geologists and oceanographers from universities, state laboratories and environmental NGOs). The long-term goals and medium-term strategic objectives for the network were determined prior to this exercise, as part of a hierarchical process, where definitions at a higher level served as guidelines for deliberation at lower levels of organization. The task force also contributed with proposals for the management, monitoring and research related to the build-up of the network but these are reported elsewhere.

Data availability on habitat mapping and community characterization was very diverse across the study area, ranging from very high resolution maps of EUNIS biotopes in coastal MPAs (e.g. Henriques et al., 2015) and broad habitat classifications

from EMODnet (European Marine Observation and Data Network, <http://www.emodnet.eu/seabed-habitats>, e.g. Abecasis et al., 2017) to isolated descriptions of regionally-specific biotopes without associated synoptic mapping (e.g. Tempera et al., 2013) and large areas where very coarse bathymetry was the only data available (Vasquez et al., 2015). Analysis of remote-sensing and oceanographic modelling data at the scale of the North Atlantic (Fig. 1 - average current magnitude between 50 and 300 m from monthly Global ARMOR3D analyses available at Copernicus Marine Service for 1993–2016) were also used to characterize regional variations in climatology, surface and bottom circulation and productivity, and to estimate the spatial distribution of the two pelagic habitats considered in the study: the seasonally persistent frontal areas across the NEA (Relvas et al., 2007; Belkin et al., 2009) and the turbid plumes off the mainland coast related to river outflow (Fernández-Nóvoa et al., 2017). Sea surface temperature fronts were computed from daily, 1 km resolution, Multi-scale Ultra-high Resolution Sea Surface Temperature (MUR-SST, JPL, https://mur.jpl.nasa.gov/multi_resolution_analysis.php). The 200 m isobath was used as a proxy to separate coastal from deep-sea communities (Spalding et al., 2007), while the bathymetric approximation of Roff and Taylor (2000) was used to distinguish between light-induced productivity water layers: euphotic (0–50 m); dysphotic (50–200 m); aphotic (>200 m).

The relationship between environmental attributes relevant for marine conservation and the habitats that support them constitute the basis of this framework: the former are generic properties and functions that can link environmental theory with hierarchical conservation objectives for MPA networks (e.g., spawning aggregations are relevant for life-cycle closures, functional diversity is relevant for biodiversity, etc.); the latter are specific physicochemical and biological characteristics that can be mapped in space, hence characterizing the composition of the MPA network itself, and are also linked to the environmental attributes (e.g., seagrass meadows are important for the spawning of cryptic fish and invertebrates; mud volcanoes and cold seeps are important for chemosynthetic communities, etc.). The framework uses expert judgment to identify a list of desirable environmental attributes for conservation (according to the strategic objectives of the network) and score them for a list of habitats selected according to the parsimonious characterization of the marine space in Portugal. This approach results in a habitat aggregate conservation value to prioritize advice for habitat inclusion in new or redesigned MPAs.

The overarching national goals were translated into five long-term environmental objectives for the MPA network in Portugal: 1) to protect or recover representative areas of marine habitats; 2) to protect areas relevant for the completion of species' life cycles; or 3) areas of high biological diversity; 4) to maintain areas of high geological diversity; and 5) to maintain or restore the good environmental state of the marine ecosystems integrated in the network. Based on the above strategic objectives, 13 environmental attributes were selected to be included in the framework: 11 with biological and 2 with geological relevance (Table 1). These attributes were related with biodiversity ($n = 2$); ecological community structure ($n = 1$); species and habitat distributional aspects ($n = 4$); critical areas for life-cycle closures ($n = 4$); and geomorphology ($n = 2$), each group being in close correspondence with one of the strategic objectives for the network.

A list of 27 habitats of variable size, conservation value and information available was selected to classify the marine space of Portugal according to a comprehensive but parsimonious and regionally relevant system (full list and characterization in Table 2). These have a EUNIS correspondence (e.g., Monteiro et al., 2015), although often include several EUNIS levels and categories (e.g., all sandy and muddy EUNIS habitat combinations are merged into mobile sediments that include gravel and cobbles – Wallenstein and Neto, 2006). Unlike EUNIS (that currently has a much more detailed classification for the inner shelf than for the deep ocean), the selected list includes 12 habitats from the continental shelf (both in mainland Portugal and islands), two of which intertidal, 12 occurring in the deep-sea and two in the pelagic realm. The two pelagic habitats (turbid plumes and frontal areas) were chosen on the basis of temporal persistence that could justify spatial mapping (Belkin, 2009; Fernández-Nóvoa et al., 2017), despite the seasonal and interannual variation associated to mesoscale surface circulation (Relvas et al., 2007). One additional habitat (estuaries and coastal lagoons) was included in the list despite being beyond the spatial scope of the marine network, given its importance in the connectivity with hydrographic basins (Ribeiro et al., 2008; Newton et al., 2014; Stratoudakis et al., 2016; Gaspar et al., 2017).

To obtain a concrete but territorially unbounded representation of conservation value for each habitat, environmental attributes were scored by expert-judgment using a five-level ordination system: 1 - completely irrelevant; 2 - marginally relevant; 3 - moderately relevant; 4 - highly relevant; 5 - exceptionally relevant (with 0 for non-applicable or unknown). The scoring process was designed to maximize replicability and independence of scores within habitats: scores were obtained per attribute (not per habitat), by first identifying the most and least relevant habitats for each attribute and then ranking the remaining habitats by comparison to the extremes. For example, persistent fronts and seamounts with their top in the photic zone were scored as the most relevant habitats for trophic complexity, while mud volcanoes and fracture zones were scored as the least relevant, all other habitats being ranked in between. All decisions were taken by joint deliberation among participants, after discussion of individual arguments until a consensus was reached. This exercise was repeated for all habitats and the resulting matrix was revisited and refined in several dedicated workshops, always in the presence of experts with distinct regional and environmental knowledge (for specific scores see Supplementary Table).

An aggregate conservation value was estimated for each habitat by the unweighted mean of scores across each of the five groups of the 13 environmental attributes (biodiversity, community structure, species and habitat properties, aggregation areas and geomorphology – see for details Table 1). The mean score for each group was estimated as the unweighted mean of the exponent of the score for each attribute minus 1 (to discount for completely irrelevant attributes) to the base 2. This means that for a group of exceptionally relevant attributes the group score would be 16 (i.e. $2^{(5-1)}$, 5 being the maximum score), while for a group of completely irrelevant attributes the score would be 1 (the same range applies to the aggregate conservation value). Non-applicable attributes ($n = 2$, geomorphology for pelagic habitats) and attributes with insufficient

Table 1

List of the attributes used to estimate aggregate conservation value, vulnerability and climatic sensitivity indices (see framework dimension column to assess the attributes of each index and respective justification for their inclusion).

Framework Dimension	Group of Attributes	Attribute	Rationale for selection	
Conservation Value	Biodiversity	Taxonomic Biodiversity	Higher taxonomic diversity will increase local resilience to environmental and anthropogenic changes. In the absence of species abundance data this can be measured based on the species richness supported by each habitat. However, as species richness only accounts for presence, further efforts should be made to analyse a set of taxonomic diversity indices (i.e. diversity, equitability, dominance, rarity) in order to assess the stability of such biodiversity.	
		Functional Biodiversity	Functionally diverse communities have higher resilience to anthropogenic and environmental changes as well as higher capacity to maintain a healthy and functional ecosystem. This can be measured by functional richness, but ideally a set of functional diversity indices should be used (i.e. richness, diversity, equitability, dispersion and functional redundancy).	
	Community Structure	High trophic level species	Species from high trophic levels (usually large predators) are more vulnerable to some human activities. Its metric should account for the number and abundance of species, independently of their conservation status.	
	Species/habitat properties	Sessile or low mobility species	Species that remain most part of their life cycle in the same area (e.g., sessile, sedentary and territorial) have higher probability to be affected by habitat changes (independently of species geographic distribution or seasonal/annual migrations).	
		Sensitive species	Species more sensitive to anthropogenic and environmental changes due to life cycle features (e.g., k-strategists, low fecundity, late maturity, slow growth) are more vulnerable to local extinctions. Its metric should account the number and abundance of species with these features, independently of their conservation status.	
		Rare species or species with small geographic distribution	Species or populations that occur in a limited geographic area, mostly due to climatic, biologic or physical barriers (independently of their ability to move), or species with low abundance (rare). These species have higher probability of local extinction when their habitats are disturbed. Its metric should account for the number and abundance of species with these features.	
	Aggregation Areas	Rare habitat/biotope	There is a higher probability to lose species and functions supported by habitats with low coverage, in case of disturbance. Its metric should consider rarity at the biogeographic scale, as rarity in the national marine space is measured independently within the framework.	
		Spawning areas	Spawning/nesting areas for many species or key species to conservation (core areas for species life cycles). Its metric should account for the relative importance of such areas to the species population dynamics and their conservation status.	
		Nursery areas	Nursery/recruitment areas for many species or key species to conservation (core areas for species life cycles). Its metric should account for both the relative importance of such areas to the species population dynamics and their conservation status.	
		Feeding areas	Feeding areas for many species or key species to conservation (core areas for species life cycles). Its metric should account for both the relative importance of such areas to the species population dynamics and their conservation status.	
	Vulnerability to existing anthropogenic pressures	Geomorphology	Critical areas for migratory routes	Areas with specific environmental features critical for successful migrations of some species (e.g., refuge, feeding, passing), without which the migratory routes will be compromised, independently of the number of species they support.
			Habitat with high structural complexity	Habitats with more complex 3D structure have lower capacity to recover from disturbance and usually support a higher level of taxonomic and functional diversity.
		Geodiversity	Areas with unusual or exceptional geological features. Its metric should account for rarity and representativeness in terms of geological composition, structure and function.	
Threatened species		Species whose populations are declining (e.g., commercially threatened; not achieving a good environmental status in the scope of the Marine Strategy Framework Directive; bycatch) or are in an early recovery. Its metric should account for the number and abundance of species with these features.		
Protected species		Species with some conservation status (listed in EU Directives, etc.) without possible legal use. Its metric should account for the number and conservation status of the listed species.		
Habitat/biotope vulnerable to anthropogenic impacts	Habitats where the presence of specific human activities or anthropogenic impacts could easily compromise their integrity (e.g., physical destruction, organic contamination). Its metric should account for the degree, intensity and persistence of the impacts currently known to exist within the marine space.			

Table 1 (continued)

Framework Dimension	Group of Attributes	Attribute	Rationale for selection
Climate sensitivity		Sensitivity to climate change	Likelihood of modification in the habitat distribution, structure and function as a result of change in the range of physiochemical parameters currently experienced (temperature rise, acidification, sea level rise, hypoxia, change in circulation patterns, change in the frequency and intensity of rainfall, etc.).

group knowledge ($n = 2$, sensitive species and feeding aggregations in inactive vents) were not accounted for in the aggregate value.

In addition, a similar five-level ordination system was followed to score vulnerability to current anthropogenic pressures in Portugal (Batista et al., 2014) and sensitivity to climate-change (Johnson et al., 2018) based on expert knowledge and a regional literature review. Vulnerability was considered separately for protected species, protected habitats and for exploited marine species (fish and invertebrates) and, in line with the precautionary principle, the highest of the three scores was chosen to represent the vulnerability of the respective habitat.

Existing habitat maps and other sources were complemented with ordinal estimates of habitat extension (in the geographic regions and the existing MPAs) to define habitat representativity levels for each region (EE sub-Zones of the mainland, Azores and Madeira and proposed ECS) and the entire marine space of Portugal. To account for uneven information levels, area coverage (in Portugal and in the MPAs) was estimated to the order of magnitude in a five level scale ranging from (1) <0.01% of the regional or national marine space to (5) >10%. For the two intertidal habitats and for sea caves the scale was applied to the linear coverage of the coastline instead of its area. Spearman correlation coefficients of habitat scores between environmental attributes were used to test for the adequacy of the chosen attributes (i.e. higher correlation values indicate interdependence of environmental attributes). Non-metric multidimensional scaling (MDS) of the environmental attribute scores for each habitat was used to explore the relationships among habitats and to evaluate the consistency of the methodology to estimate the aggregate conservation value. Statistical analysis was performed in R 3.4.4 (R Core Team, 2018).

3. Results

Table 2 lists the 27 habitats selected to describe the marine space of Portugal (including estuaries and coastal lagoons), their correspondence to EUNIS, some key descriptive citation (from Portugal, where available) and their ordinal geographical extent (both nationally and regionally). The ranking by level of habitat coverage shows that the selected list ranges from habitats that are contained within some tens of hectares (such as seagrass beds, in the inner shelf and mainland estuaries) to few km² of a single region (such as mud volcanoes in the Gulf of Cadiz, off southern Portugal) up to seascapes that occupy >10% of the marine space of Portugal and are abundant in all regions (such as abyssal plains or slope and ramp soft sediments). More than half of these habitats (17) cover less than 0.1% of the total area under national jurisdiction, whether considering the EEZ or including the submitted ECS. To achieve the national objective of protecting 14% of the Portuguese marine space, large areas of the four most extensive habitats must be included, given that even the inclusion of the entire coverage area of most of the remaining habitats would be unable to meet such a target.

Correlations between environmental attributes based on their habitat scores were generally low to moderate, with 21 of the 78 pairwise comparisons (27%) above 0.5. Among the strongest correlations, eight were within the same group of environmental attributes and two were negative (between rare species and aggregation areas for feeding and migration). The three highest positive correlations were biologically meaningful: aggregation areas for feeding vs. trophic complexity (0.76), species richness vs. functional diversity (0.75), and low mobility species vs. structural complexity in the geomorphology (0.75). The aggregate conservation value for each habitat was found to have a strong negative correlation ($Rho = -0.79$; $p < 0.001$) with the first dimension in the MDS scores of environmental attributes for each habitat (Fig. 2), demonstrating that the former provides an adequate means to reduce dimensionality of habitat attributes.

Aggregate conservation values ranged almost five-fold among habitats (Table 3), from close to 10 (i.e. very relevant for all groups of attributes – inshore rocky reefs and seamounts with summits within the photic layer) to slightly above 2 (i.e. habitats of limited relevance for most groups of attributes – fracture zones and turbid plumes). Table 3 also shows the habitat scoring according to their vulnerability to existing anthropogenic pressures and anticipated levels of sensitivity to climatic change, together with key citations exemplifying anticipated consequences. The conservation value was negatively correlated with the habitat coverage area in the marine space of Portugal ($Rho = -0.45$; $p = 0.019$), positively correlated with anthropogenic vulnerability ($Rho = 0.46$; $p = 0.015$) and non-significantly correlated with sensitivity to climate change ($Rho = 0.32$; $p = 0.108$).

These four partially correlated dimensions (area coverage, aggregate conservation value, level of vulnerability to anthropogenic pressures and sensitivity to climate change) are relevant to inform representativity of habitats within the MPA network. Taken together with the level of representation of each habitat in the existing set of MPAs (i.e. the current extent of intended protection), they form a multi-dimensional aid-tool to assist the prioritization of habitat representation in the designation of new MPAs. Fig. 3 illustrates an example of this multi-level information, visually combining the four dimensions mentioned above with the ordinal level of habitat occurrence in the MPAs of the mainland sub-zone (approximately

Table 2

List of 27 habitats used for the classification of the marine space in Portugal ordered by rarity, according to ordinal scores of area coverage^a (linear for intertidal habitats and caves, separate at the bottom of the list) for each region and the national total. Empty cells indicate unconfirmed presence and unknown dimension of habitat. EUNIS correspondence and literature description are provided to facilitate characterization. Habitat abbreviations (in italics) are used in Figs. 2 and 3.

Habitat	EUNIS correspondence ^b	Key citation	Mainland	Azores	Madeira	Shelf extension	Total
Mud volcanoes and cold seeps, <i>MudVolc</i>	A5.714; A6.911; A6.912	Pinheiro et al. (2003)	1	0	0	0	1
Hydrothermal vents (active), <i>ActVent</i>	A5.716; A6.941	Desbruyères et al. (2001); Cardigos et al. (2005); Levin et al. (2016)	0	1	0	0	1
Seagrasses, <i>Seagrass</i>	A5.45; A5.53; A5.5312	Cunha et al. (2013); Monteiro et al. (2013b)	1	0	1	0	1
Hydrothermal vents (inactive), <i>InactVent</i>	A6.942	Levin et al. (2016)	0	2	0	1	1–2
Maërl, <i>Maerl</i>	A5.51; A5.511	Peña et al. (2014); Monteiro et al. (2013b)	1	1–2	2	0	1–2
Macroalgae forests, <i>Kelp</i>	A3.11; A3.12; A3.15; A5.52	Ramos et al. (2016); Amorim et al. (2015)	2	1–2	1	0	1–2
Seamounts (summit <200 m), <i>Seamount1</i>	A6.721; A6.724	Morato et al. (2008b); Cascao et al. (2017); Ramos et al. (2016)	2	1	1	1	2
Canyons, <i>Canyons</i>	A6.81	Arzola et al. (2008); Cunha et al. (2011); Quartau et al. (2018)	2–3	0	1	0	2
Estuaries and coastal lagoons, <i>Estuaries</i>	X01; X02; X03; A5.22	Ribeiro et al. (2008); Newton et al. (2014); Gaspar et al. (2017)	3	1	0	0	2
Turbid plumes, <i>Plume</i>	A7.7	Fernández-Nóvoa et al. (2017)	3	1	0	0	2
Aggregations that change physiography in soft sediment, <i>Aggregations</i>	A6.62	Henriques et al. (2015); Ramos et al. (2016); Tempera et al. (2013)	2	2	2	0	2
Biogenic reefs (<200 m), <i>Biogenic1</i>	A2.7; A3.1; A3.2; A3.3; A4.22; A4.24; A5.6	Boavida et al. (2016); Ramos et al. (2016)	3	1–2	2	1	2
Inner shelf rocky reefs (<50 m), <i>Hard1</i>	A3.1; A3.15_PT12; A3.15_PT13; A3.1_PT14; A3.1_PT15; A3.2; A3.3; A3.24_PT2; A3.24_PT3; A3.31_PT16; A3.712; X32	Monteiro et al. (2013b); Friedlander et al. (2017); Amorim et al. (2015); Gaspar et al. (2017)	3	2	2	0	2
Inner shelf soft sediment (<50 m), <i>Soft1</i>	A5.13; A5.13_PT17; A5.13_PT25; A5.14; A5.14_PT26; A5.15; A5.23; A5.23_PT4; A5.23_PT18; A5.23_PT19; A5.23_PT27; A5.24; A5.25; A5.25_PT5; A5.25_PT20; A5.25_PT28; A5.26; A5.26_PT21; A5.27; A5.27_PT22; A5.27_PT23; A5.33; A5.34; A5.34_PT6; A5.35; A5.36; A5.37; A5.37_PT24; A5.43; A5.44; A5.45; X32	Martins et al. (2013); Monteiro et al. (2013b); Henriques et al. (2015)	3	2	2	0	2
Rocky reefs (50–200 m), <i>Hard2</i>	A4.1; A4.2; A4.27_PT1; A4.3; X33	Monteiro et al. (2013b); Boavida et al. (2016); Gomes et al. (2018)	3	2	2	0	2–3
Biogenic reefs (>200 m), <i>Biogenic2</i>	A6.61	Tempera et al. (2013)	3	3	1	0	2–3
Seamounts (summit 200–1000 m), <i>Seamount2</i>	A6.722; A6.724	Morato et al. (2008a); Alonso et al. (2018)	3	3	2	1	2–3
Soft sediment (50–200 m), <i>Soft2</i>	A5.14; A5.15; A5.25; A5.26; A5.27; A5.35; A5.36; A5.37; A5.44; X33	Martins et al. (2013); Monteiro et al. (2013b); Gomes et al. (2018)	4	2	2	0	3
Persistent fronts, <i>Fronts</i>	A7.A2	Relvas et al. (2007); Belkin et al. (2009)	4	3–4	2–3	0	3
Slope and ramp rocky reefs, <i>Hard3</i>	A6.11	Braga-Henriques et al. (2013)	3	4	3	0	3
Fracture zone and hadal trenches, <i>Fracture</i>	A6.82	Ramirez-Llorda et al. (2010)	4	5	0	3	3–4
Seamounts (summit >1000 m), <i>Seamount3</i>	A6.723; A6.724	Morato et al. (2008a)	5	4	3	4	4
Slope and ramp soft sediment, <i>Soft3</i>	A6.2; A6.3; A6.4; A6.51	Tempera et al. (2013)	5	5	5	5	5
	A6.52	Ramirez-Llorda et al. (2010)	5	5	5	5	5

Table 2 (continued)

Habitat	EUNIS correspondence ^b	Key citation	Mainland	Azores	Madeira	Shelf extension	Total
Abyssal plains, <i>AbyssalP</i>							
Sea caves, <i>Caves</i>	A3.71; A3.74; A3.74_PT7; A4.71;	Karamanlidis et al. (2004); Calado et al. (2004); Monteiro et al. (2013a)	2–3	2–3	2	0	2–3
Intertidal rocky reefs, <i>InterHard</i>	A1; A1.11_PT8; A1.2_PT9; A1.2_PT10	Boaventura et al. (2002); Wallenstein and Neto (2006); Monteiro et al. (2013b)	4	5	5	0	5
Intertidal soft sediment (including gravel and cobbles), <i>InterSoft</i>	A2	Hawkins et al. (2000)	5	5	5	0	5

^a 0 – absent; 1 < 0.01% of area; 2 < 0.1%; 3 < 1%; 4 < 10%; 5 > 10% of area.

^b Based upon: <http://eunis.eea.europa.eu/habitats-code-browser.jsp>.

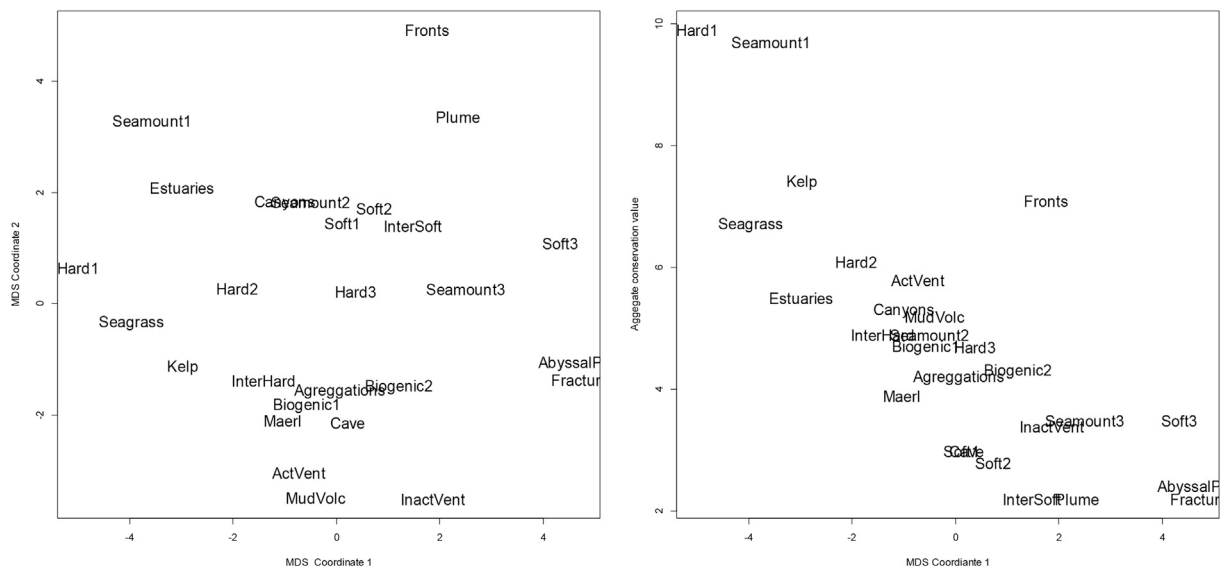


Fig. 2. Multidimensional scaling plot of habitats according to the non-metric distances among scores for the 13 environmental properties (a) and evidence for strong negative correlation between MDS coordinate 1 and aggregate conservation value for each habitat (b). For habitat abbreviations see Table 2.

corresponding to $28 \times 10^3 \text{ km}^2$, c.a. 80% of this area in a single large oceanic MPA over the Gorrige seamount). As can be seen from this example, the current set of MPAs in the mainland sub-zone of Portugal does not include some of the identified habitats (e.g., mud volcanoes, maërl or fracture zones), includes minor fringes of others (e.g., canyons, persistent fronts), but also has a reasonable coverage of some highly valuable ones (inner rocky shelf reefs and seamounts with their top in the photic zone).

4. Discussion

The framework presented here, demonstrated through its application to the Portuguese marine space, is relevant for marine conservation efforts worldwide in two ways:

- 1) to assist planning of MPA networks over large scales, under pressing timelines and with limited, spatially uneven and poor information. Although a few countries already have detailed habitat maps for their entire marine space, the deeper part of large EEZs is typically underexplored and poorly characterized (e.g., Ramirez-Llorda et al., 2010), and the same goes for the ECS (e.g., Thurber et al., 2014). In such cases, collaborative participation of national scientific expertise to provide region-specific habitat lists and context-specific environmental attributes is a feasible and cost-effective approach to inform the decision-making process;
- 2) to provide a tool for scrutiny of proposals and decisions on MPA networks, based on a rational articulation between stated conservation objectives and resulting habitat coverage of the marine space to be protected. The latter is independent of

Table 3

Ordered list of habitats with decreasing aggregate conservation value and respective level of vulnerability to current anthropogenic pressures and climate change sensitivity (i.e. responsiveness to deviation in environmental conditions beyond previously exposed range) as determined by expert judgment scoring.

Habitat	Conservation value	Anthropogenic vulnerability	Main element of anthropogenic vulnerability	Climatic sensitivity	Main element of climatic sensitivity
Inner shelf rocky reefs (<50 m)	9.9	Very High	Bycatch mortality and habitat destruction (e.g., bycatch of invertebrates by trammel nets – Gonçalves et al., 2008)	High	Temperature (Belkin, 2009)
Seamounts (summit <200 m)	9.7	Very High	Top predator mortality (e.g., <i>Katsuwonus pelamis</i> , <i>Delphinus delphis</i> , <i>Calonectris borealis</i> – Morato et al., 2008b)	Low	–
Macroalgae forests	7.4	High	Habitat destruction (e.g., eutrophication from agricultural effluents - Gaspar et al., 2017)	Very High	Temperature (especially for <i>Saccorhiza polyschides</i> - Assis et al., 2017 , but also Ramos et al., 2016); pH (Kroeker et al., 2013)
Persistent fronts	7.1	Very High	Target and bycatch top predator mortality (including turtles and protected pelagic sharks - Scales et al., 2014)	Moderate	Precipitation intensity and seasonality (Lima et al., 2013); Upwelling-favourable winds (Relvas et al., 2007)
Seagrasses	6.7	Very High	Habitat destruction by dredging and anchoring, sedimentation and eutrophication (e.g., <i>Zostera noltii</i> - Cunha et al., 2013)	High	Temperature (especially for <i>Zostera marina</i> - Cunha et al., 2013); pH (Kroeker et al., 2013)
Rocky reefs (50 –200 m)	6.1	High	Protected species mortality (e.g., black coral <i>Leiopathes</i> spp. bycatch in longline fisheries – Sampaio et al., 2012)	Low	–
Hydrothermal vents (active)	5.8	Low	–	Very Low	–
Estuaries and coastal lagoons	5.5	High	Protected species habitat destruction and mortality (e.g., impact of seining on <i>Hippocampus guttulatus</i> - Curtis et al., 2007)	High	Precipitation intensity and seasonality (Lima et al., 2013); pH (Range et al., 2012)
Canyons	5.3	High	Habitat destruction (e.g., sinks for marine litter – Mordecai et al., 2011)	Moderate	Oxygen and pH (Levin and Le Bris, 2015)
Mud volcanoes and cold seeps	5.2	Low	–	Very Low	–
Intertidal rocky reefs	4.9	High	Habitat destruction (e.g., trampling on <i>Sabellaria alveolata</i> reefs – Plicanti et al., 2016)	High	pH (Kroeker et al., 2013)
Seamounts (summit 200 –1000 m)	4.9	High	Top predator mortality by fishing to 400 m depth (Morato et al., 2008b)	Low	–
Slope and ramp rocky reefs	4.7	Moderate	Protected species mortality (e.g., cold water corals in longlines – Braga-Henriques et al., 2013)	Low	–
Biogenic reefs (<200 m)	4.7	Very High	Habitat destruction (e.g., <i>Corallium rubrum</i> – Boavida et al., 2016)	High	pH (Kroeker et al., 2013)
Biogenic reefs (>200 m)	4.3	High	Habitat destruction (e.g., secondary bycatch of deep water corals attached to corals or rocks caught by longlines - Sampaio et al., 2012)	Moderate	pH (Hennige et al., 2014)
Aggregations that change physiography in soft sediment	4.2	High	Habitat destruction (e.g., <i>Atrina fragilis</i> field in MPA without dredging – Henriques et al., 2015)	Moderate	pH (Range et al., 2013)
Maërl	3.9	High	Destruction of coralline algae beds (e.g., Peña et al., 2014)	High	Temperature and pH (Peña et al., 2014)
Slope and ramp soft sediment	3.5	High	Erect mega-epibenthos destruction (e.g., <i>Pennatula</i> sp. - Ramalho et al., 2017)	Low	–
Seamounts (summit >1000 m)	3.5	Moderate	Bycatch species mortality (e.g., deepwater sharks – Moura et al., 2014)	Low	–
Hydrothermal vents (inactive)	3.4	Low	–	Very Low	–
Inner shelf soft sediment (<50 m)	3.0	High	Protected species mortality (e.g., <i>Rostroraja alba</i> - Sousa et al., 2018)	Moderate	pH (Range et al., 2013)
Sea caves	3.0	Moderate	Habitat destruction (e.g., <i>Monachus monachus</i> pupping and resting habitat – Karamanlidis et al., 2004)	Low	–
Soft sediment (50 –200 m)	2.8	Very High	Protected species mortality (e.g., <i>Caretta caretta</i> bycatch - Nicolau et al., 2016) and habitat degradation (Kaiser et al., 2006)	Low	–
Abyssal plains	2.4	Low	–	Very Low	–
Intertidal soft sediment	2.2	High	Habitat destruction (e.g., resting habitat of <i>Monachus monachus</i> – Karamanlidis et al.,	Moderate	pH (Range et al., 2014); Temperature (Neiva et al., 2014)

Table 3 (continued)

Habitat	Conservation value	Anthropogenic vulnerability	Main element of anthropogenic vulnerability	Climatic sensitivity	Main element of climatic sensitivity
(including gravel and cobbles)			2004; ecotourism pressure – Monteiro et al., 2013a)		
Turbid plumes	2.2	Moderate	Anadromous species mortality (e.g., <i>Alosa alosa</i> caught by nets in the inner shelf close to estuaries – Stratoudakis et al., 2016)	High	Precipitation intensity and seasonality (Lima et al., 2013)
Fracture zones	2.2	Low	–	Very Low	–

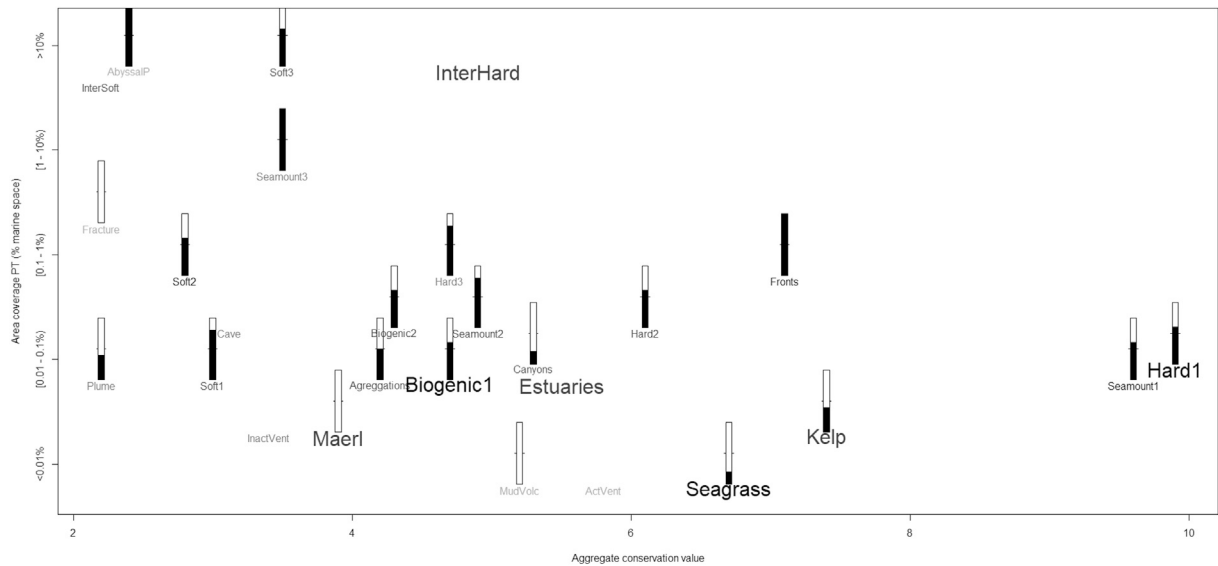


Fig. 3. Example of multilevel visualization of advice for MPA network representativity: bivariate plot of the 27 habitats considered (see Table 2 for abbreviations) as a function of aggregate conservation value (x-axis) and percent area coverage in the mainland sub-zone (y-axis, ordinal level in logarithmic scale). Larger font indicates habitats more sensitive to climate change and darker font indicates more vulnerable habitats. Thermometer fills indicate ordinal scale of habitat representation in the set of mainland sub-zone MPAs (complete fill indicates >10% of the approximately 28×10^3 km² of delimited MPA area containing the respective habitat). Habitats with linear measure coverage and those absent from the mainland sub-zone are presented without thermometer fills.

data deficiencies and can strengthen conservation decisions through transparent and informed public debate, at times where political commitments for dedicating larger fractions of the ocean to MPA networks are becoming more frequent and popular.

The application of the proposed framework to the marine space of Portugal showed a negative correlation between aggregate conservation value and habitat area, as well as a positive correlation between aggregate conservation value and vulnerability to anthropogenic pressures. This relates to the physiography of the Portuguese marine space, with point and diffuse stressors currently most abundant in the inner continental shelf of the mainland (Batista et al., 2014), where some coastal habitats can be considered severely degraded (e.g., seagrasses - Cunha et al., 2013) or threatened by local extinction due to synergistic actions with climate change (e.g., forests of brown macroalgae in SW and southern Portugal - Assis et al., 2017). Dedicating larger fractions of marine space to conservation expectedly leads to the inclusion of larger, deeper and less explored seascapes (usually less impacted areas and further away from the coast). This transition also places the focus on less studied ecosystems that can be more sensitive to change, due to the narrower natural range of variation in physicochemical conditions and corresponding long time scales, and may also be more vulnerable to the expansion of human activity in the ocean (Thurber et al., 2014; Cunha et al., 2017; Dunn et al., 2018). However, this approach has two associated risks that must be addressed. The first, highlighted by the current application, is that small, rare and vulnerable habitats, some of which requiring urgent conservation action, may fall back when percentage area targets alone determine decisions – finding a balance between such divergent requirements is of critical importance and part of the aim of the multi-level aid tool developed within this framework. The second, network effectiveness, is a step further, after delimitation, as it pertains to the common risk of having “paper” MPAs and networks. Although beyond the scope of this framework, the task-force also made

specific recommendations based on the recent development of heuristics to evaluate effectiveness indirectly from the management rules that should come together with delimitation (Horta e Costa et al., 2016).

Basing the framework on generic environmental attributes, prior to considering its consequences in space, allowed for a deviation from potential conflicts related to institutional relations that could have contaminated the task-force performance (such as diverging views between different levels, regions or sectors of administration). Furthermore, the approach used to score environmental attributes (i.e. assessing each attribute at a time and ranking it among habitats) reduces potential bias from expert subjectivity and habitat coverage on the aggregate conservation value. For example, Gomes et al. (2018) used the marine biological valuation protocol to macrobenthos, seabirds, demersal fish and marine mammals' data from the continental shelf of mainland Portugal to show a significant decrease in total biological value from rock, to sand, to mixed sediment and mud that is in agreement with the theoretical findings of the framework presented here. This is relevant in a context of limited resources, where conservation value will help to prioritize habitats that should be first included within the network (see recommendations at Supplementary Figure). Subsequently, additional precautions about habitats' replication, representation and level of protection within the network should be taken according to their vulnerability and climate sensitivity. The assessment of these three components individually (ecology, vulnerability and climatic sensitivity) aims to improve habitat representativity by guiding the selection of habitats in space.

The task-force also created a common space for multidisciplinary and realm interactions that have rarely existed in the past and which are relevant beyond the original group's objectives, e.g., for the application of the EU Marine Strategy Framework Directive. Further, this framework and the process related with it allowed the identification of knowledge gaps that should be addressed in future review exercises of the MPA network. Among these, the gathering of information about the connectivity of the marine populations at different spatial and temporal scales (mainland, archipelagos) and according to the characteristics of the habitats used in the present approach is an urgent need that is recognized across European seas (Olsen et al., 2013). An additional area of focus is the pelagic realm that is particularly difficult to consider in the definition of MPAs due to its dynamics, dimension, lack of clear and noticeable limits and poor knowledge about its complexity, although many migratory species use it in recurrent ways (Block et al., 2011). The persistent fronts delimited in the present exercise is a first step in this direction (Scales et al., 2014), highlighting the need of further effort to understand and better represent attributes and habitats of the pelagic realm in the MPA network (e.g., the importance of upper slope and canyons for deep diving top predators – Thorne et al., 2017).

Another characteristic of this framework is its adaptive nature, as it can easily incorporate new knowledge and refine targets as new information and finer-scale data become available. For example, the current list of habitats includes some very broad definitions and the scale for estimating the extent of each habitat is very coarse. This limitation was partly due to the current unevenness of the EUNIS classification system (reflecting discrepancies in knowledge with ocean depth and between OSPAR sub-regions – Ardron, 2008; Johnson et al., 2014; Foster et al., 2017) but also due to the uneven availability of digital habitat maps across the marine space of Portugal (Vasquez et al., 2015). An additional difficulty was to create a common habitat list for the entire marine space, despite regional differences in physical and biogeochemical processes (e.g., the euphotic/mesophotic limit in the oligotrophic Macaronesia is deeper than in mainland Portugal (Monteiro et al., 2015), with Amorim et al. (2015) showing the presence of dense kelp down to 80 m depth in the Formigas MPA, Azores, where light penetration is still around 1%). As the habitat list improves with the better exploration of deep-sea ecosystems and the wider availability of habitat maps, the whole exercise can be repeated with a refined list of habitats and a more precise quantification of their coverage, to re-evaluate the adequacy of environmental representation in the network.

Regular review and adaptation of the network is further required by the recognition that environmental representativity is a necessary but not sufficient property for an effective MPA network (Olsen et al., 2013; Grorud-Colvert et al., 2014; Roff, 2014). Despite the existing knowledge on the geological, oceanographic and physiographic features that drive biological processes and shape communities at larger spatial scales (e.g., Longhurst, 1995; Spalding et al., 2007), understanding of the mechanisms that structure biodiversity remains incomplete (Zacharias and Roff, 2000), especially for the deep sea (Ramirez-Llorda et al., 2010; Cunha et al., 2017) and considering the modifications that can result from climate change (Johnson et al., 2018). Related, but antithetic to the above, is the study of the processes that create spatial, temporal and functional connectivity within the marine space, both actively and passively (Olsen et al., 2013). Measures of connectivity are essential to the design of MPA networks, including the size of individual reserves, the number of reserves and cumulative total reserve area. Each MPA should be adequately connected to the others to support the persistence and recovery of local populations from disturbance (Gaines et al., 2010). If MPAs are isolated from one another they are more vulnerable to local extinction as they cannot be replenished by immigrants. The trade-off between a few large or several small reserves, and the spacing and locations of reserves, can be varied to achieve different conservation goals, and largely depend on the connectivity between populations (Jones et al., 2007). Thus, a more detailed knowledge on the patterns of space use and migration for high mobility species (e.g., Alonso et al., 2018) and on the physical-biological interactions that drive the transport of planktonic phases (e.g., Jones et al., 2007; Hilário et al., 2015) is crucial to improve the effectiveness of the MPA network. Finally, this would help the progressive merging with the species-based conservation approaches, such as the species component of the NATURA 2000 network (Pereira et al., 2018), which is now accounted for only indirectly through the scoring of related environmental attributes and vulnerability.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00545>.

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