iAtlantic Deliverable 2.6

Environmental drivers of ecosystem spatial patterns in the Atlantic

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List of Acronyms

BPI	Bathymetric Positioning Index
CWCs	Cold-Water Corals
EUNIS	European University Information Systems
GAMs	Generalised Additive Models
GBM	Generalised Boosted Models
GMM	Gaussian Mixture Models
HSM	Habitat Suitability Models
MAR	Mid Atlantic Ridge
MaxEnt	Maximum Entropy
POC	Particulate Organic Carbon
RF	Random Forest
SBA	Seabed Areas
SDM	Species Distribution Modelling
VME	Vulnerable Marine Ecosystem

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Executive summary

Spatial maps and an understanding of environmental drivers of ecosystem spatial patterns are key to implementing ecosystem-based management approaches to marine spatial planning. iAtlantic applies an integrated approach of multiple work packages to assess the health of the deep-sea and open-ocean ecosystems across the Atlantic. iAtlantic work package 2 'Mapping deep Atlantic Ecosystems' undertook species and habitat mapping at various scales enabling the identification of environmental drivers of ecosystem spatial patterns across the Atlantic.

Habitat suitability models (HSM) were built for various vulnerable marine ecosystem (VME) indicator taxa and commercial species at both the basin (iAtlantic deliverable D2.2) and regional scale (iAtlantic deliverable D2.5). Environmental predictors identified as important were tabulated and trends across scales compared. In addition, to better understand how environmental variables drive species' habitats across spatial scales, species response curves were compared between models of shared species and environmental variables. Lastly, distributions of taxa that are indicative of VMEs, were overlaid onto basin scale environmental classifications of seabed areas (SBA; iAtlantic deliverable D2.1) to assess how VMEs relate to spatial structuring of environmental data at the basin scale and evaluate the use of seabed areas as surrogates of VME distribution.

iAtlantic mapping provides a holistic viewpoint of the environmental drivers of ecosystem spatial patterns across the Atlantic at varying spatial scales. iAtlantic analyses of the environmental drivers of ecosystem spatial patterns in the Atlantic showed that continental shelves and slopes are the most important habitats for the modelled species. At ocean-basin spatial scale, our modelling work successfully identified large scale geomorphological features, such as oceanic island slopes and the mid-Atlantic ridge, as the preferential habitats for cold-water corals (CWCs). The regional scale modelling identified the importance of finer terrain complexity, such as vertical walls and ridges, occurring across the large-scale geomorphological features. This finer scale terrain complexity could not be discerned in the ocean basin scale data sets, as such basin models are useful in identifying those large geomorphological structures that could benefit from regional scale modelling work and inform management at the appropriated spatial scales.

iAtlantic regional models took into consideration hydrodynamics, which are postulated to interact with complex terrain to generate local environmental gradients in productivity to which species respond. Our analyses showed that species distributions also responded to large scale gradients in sea-surface and deep ocean productivity, which resulted in, for example, latitudinal gradients in the distributions of scleractinian CWCs in Region 3 (Azores) and distributional patterns in regional feeding habitats for fish and shark species associated with the Brazil–Malvinas Confluence and the Argentinean shelf break in Region 10.

Temperature was consistently identified as an important environmental predictor in most HSMs and is proposed to, in association with other environmental factors, limit species distribution through physiological constraints. This was corroborated by the unimodal species response curves at broad spatial scales. However, strong collinearity at the regional scale between temperature, depth and other water mass properties (i.e., pH, salinity, oxygen concentration) makes untangling the influence of each covariable difficult at that scale. Consequently, for some regions collective variables were developed that represented principal components of 'water chemistry', which were found to be of high exploratory power. Many Atlantic species' suitable habitats are correlated with water mass properties.

Additionally, species response curves and tabulated results of modelled predictor importance across scales highlighted the influence of environmental data resolution in determining predictor importance and relate this to the ability to discern ecologically relevant environmental heterogeneity to which species respond. Therefore, future efforts should be focused on acquiring high resolution data layers for these variables, along with a better understanding of species physiological response to changes.

Lastly, iAtlantic modelling work found that the distribution of VME indicator taxa was correlated with ocean basin-scale distribution of seabed areas (SBAs). In particular, the predicted distribution of CWC indicator taxa overlapped predominantly with SBA II and IV and slightly with SBA I. Each of these SBAs represent classes of seabed type with characteristic environmental qualities. SBA II represents seabed characterised by complex topography, SBA IV in deep waters is characterised by strong currents and high local and seasonal variability and SBA I is characterised by water mass formation and boundary currents flows, with the characteristic high oxygen concentrations indicative of mixing along the North Atlantic. Furthermore, the characteristics of the SBAs correlated with the environmental predictors identified via HSM for the mapped CWCs. These results highlighted the potential use of seabed areas to identify areas supporting potential VMEs where biological data is not available.

Comparing HSMs derived from different resolution data and extents, and with SBAs and European University Information Systems (EUNIS) classification maps, we have demonstrated the comparative accuracy of HSMs and identified which key environmental drivers can be detected when incorporating data at varying spatial resolutions. We have shown that broad scale modelling utilising low resolution data, either as landscape classes, EUNIS classification maps or basin scale HSM can be informative for identifying potential large-scale features or seabed types likely to support VMEs and hence guide further surveying and regional mapping at appropriate spatial scale to support regional management. Assessing the interplay of mapping confidence at various data resolutions and extents is key to marine spatial planning, ecosystem-based management and area-based conservation strategies of the Atlantic. Especially for deep-sea settings where high resolution or biological data may not be available.

By collating multiple habitat and species distribution maps, iAtlantic has increased our baseline knowledge of the Atlantic open ocean and deep sea, especially in the lesser-known central and southern Atlantic. The increased understanding of environmental drivers of species habitats, which in turn make up ecosystem spatial patterns, enables ecosystem-based management and helps assess future management options, including scenarios under climate change.

Overall, the results presented here contribute directly to achieving iAtlantic's five key objectives, and to creating the long-lasting impacts expected from the project. This report evaluates and summarises the new ecological insights obtained by the project's mapping activities at basin and regional scales, enabling a better assessment of the status and interactions of deep and open ocean ecosystems in the Atlantic. Direct links between species spatial patterns and physical and biogeochemical drivers are identified and described at the respective scales of their main effects. The results clearly point to the vulnerability of key species to changes in temperature and food supply, supporting the conclusions of iAtlantic's temporal and experimental research work packages, and pointing to the key factors that require management and monitoring by regulators, governments and industries worldwide. The outcomes described in this deliverable could only be reached thanks to the extensive mapping and habitat suitability modelling efforts across the entire project consortium. This demonstrates how the cooperative framework created by iAtlantic has led to a more complete assessment of ecosystem status, covering the entire Atlantic Ocean, from South to North.

1. Abstract

As the marine environment faces increasing anthropogenic and climate change pressures there is an equally increasing need to map and understand the environmental drivers of marine ecosystem spatial patterns to assist marine spatial planning. Ecosystems are complexes of living and non-living components that interact as a function unit in a certain area and are often considered higher-level organisations of habitats and species assemblages.

To increase our knowledge of ecosystem distributions and drivers, outputs from iAtlantic work package 2 '*Mapping deep Atlantic Ecosystems*' were collectively analysed to determine drivers of ecosystem spatial patterns across scales. Important environmental predictors identified from basin (iAtlantic deliverable D2.2) and regional (iAtlantic deliverable D2.5) habitat suitability models (HSM) were tabulated, and response curves of shared species and predictors compared to determine what are the important environmental predictors and how these change over spatial scales, plus potential mechanisms by which they influence spatial distributions.

Across the iAtlantic regions, cold-water corals (CWCs) were the predominant modelled species, followed by commercially important fish, shark and crustaceans. This was due to a mixture of species biogeography, regional conservation and management relevance, and data availability. The bias toward CWCs results in our interpretation largely being limited to drivers of CWC vulnerable marine ecosystems (VMEs). HSM identified temperature, measures of productivity, terrain derivatives, and hydrodynamics as important environmental drivers of ecosystem spatial patterns. The relative importance of these environmental predictors was in part influenced by the native resolution from which they were interpolated to be input into models, with those variables able to discern ecologically relevant environmental heterogeneity often identified as the most important. The combined review of the iAtlantic mapping studies as a collective indicates that CWC habitats principally driven at broad spatial scales by large geomorphic features (i.e., oceanic islands and mid-Atlantic ridges), water mass properties and latitudinal or regional gradients in productivity associated with circulation regimes and mixing zones.

At finer regional scales CWC habitats are driven by finer-scale terrain complexity occurring on the large-scale geomorphic features, which in turn influence substrate and local hydrodynamics to generate local gradients in productivity. The influence of these key environmental drivers is reflected in the overlap of CWC habitats with the basin scale classification of seabed areas based on the same characteristics identified as important environmental predictors in HSM for the mapped CWCs. This highlights the potential use of seabed areas to identify potential VMEs where biological data are not available. Results comparing VME spatial patterns with EUNIS classification maps indicate that the applicability of EUNIS maps as indicators of VMEs is influenced by the resolution and extent of data used. The results of this study collate important baseline maps and knowledge of environmental drivers of ecosystem spatial patterns across scales, including from the lesser-known central and southern Atlantic, which is needed to facilitate ecosystem-based management and help assess future management and climate change scenarios.

2. Introduction

The marine environment faces increasing pressure from anthropogenic activities (Glover and Smith, 2003; Pusceddu et al., 2014; Levin et al., 2020) against the backdrop of climate change (Doney et al., 2012; Levin and Le Bris, 2015; Henson et al., 2017; Sweetman et al., 2017). Marine spatial planning is increasingly being applied to manage these impacts, to support sustainable resource use (Ehler and Douvere, 2009) and implement area-based conservation strategies in line with the United Nations 2030 Sustainable Development Goal 14 'Life Below Water' (UNGA, 2015). Key to marine spatial planning is knowledge of ecosystem spatial patterns that comprise habitat and species distributions (Hortal et al., 2015; Howell et al., 2016; Georgian et al., 2019). Consequently, international legislation and management of the Atlantic requires habitat and species distribution maps (UNGA, 2006, 2009; FAO, 2009; McQuaid et al., 2023), especially in the deep sea and open ocean as exemplified in the N Atlantic by the H2020 ATLAS project[1]. Recent initiatives to generate Southern Atlantic or Atlantic wide maps have been undertaken (Schumacher et al., 2022; McQuaid et al., 2023). However, there is still a lack in our understanding of what drives the habitat and species distributions that comprise Atlantic ecosystems. This information is necessary to assess and predict anthropogenic and climate change impacts and to inform effective marine spatial management and assist in ecosystem-based management (Howell et al., 2016). The iAtlantic project is an Atlantic-wide initiative comprised of multiple work packages that fulfil a multidisciplinary research program seeking to assess the health of the deep-sea and open-ocean ecosystems across the Atlantic (Roberts et al., 2023). The integrated approach of iAtlantic work package 2 'Mapping deep Atlantic Ecosystems' encompasses mapping and modelling across deep-sea and open-ocean regions at multiple scales for various habitats and species providing a unique opportunity to identify environmental drivers of ecosystem spatial patterns across the Atlantic.

Here we define an ecosystem based on the UN and Convention on Biological Diversity definitions as 'a complex of all living (plants, animals, microorganisms) and non-living (soil, climate) components interacting as a functional unit in a certain area.' Habitats are defined here as the spatial extent over which a particular species or assemblage and its associated environment occurs (MESH, 2008; Brown et al., 2011). Ecosystems are thus generally considered a higher-level organisation of component habitats and species. These definitions are linked to the theory that species distributions are intrinsically driven by the species' environmental requirements (i.e., temperature and substrata) and how these environmental variables are structured in space and time (Hutchinson and MacArthuur, 1959). In reality, in addition to environmental constraints, many factors, including biological interactions, human disturbance, historical and stochastic events, interact across multiple scales to determine species distributions (Hutchinson and MacArthuur, 1959). However, species interactions typically happen at fairly close ranges, while historical and stochastic events are often difficult to constrain and/ or predict. Consequently, researchers routinely model suitable species' habitat as a surrogate of actual species distributions.

Habitat suitability modelling (HSM), also known as Species Distribution Modelling (SDM), is increasingly applied in the deep sea to generate continuous distribution maps of suitable habitat of species (Anderson et al., 2016; Georgian et al., 2019; Pearman et al., 2020). HSM models species-environment relationships, to enable predictions of species occurrence beyond their sampled extent but where

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[1] https://www.eu-atlas.org/

environmental data exist (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). HSM is also informative for identifying environmental drivers of suitable habitat distribution (Pearman et al., 2020). Integral to accurate predictions is the incorporation of environmental data at resolutions that capture ecologically meaningful variation in the environmental requirements of modelled species (Lecours et al., 2015; Porskamp et al., 2018).

Here in iAtlantic deliverable D2.6 we draw together results from iAtlantic work package 2 to identify how environmental variables act across multiple spatial scales to drive suitable habitat distributions of selected species which in turn drive spatial patterns of ecosystems across the Atlantic, including the little studied central and southern Atlantic.

iAtlantic work package 2 undertook HSM for a variety of species at various spatial scales across the Atlantic basin and eight iAtlantic regions (Figure 1 and Table 1) enabling environmental drivers of suitable habitat distribution across spatial scales to be identified. iAtlantic work package 2 also undertook unsupervised classification of the Atlantic basin to identify seabed areas representing different marine environments. This exercise highlighted key environmental factors that drive broad-scale environmental variation in the Atlantic and showed environmental spatial structuring at the basin scale that may influence ecosystem spatial patterns. Additionally, regional classification of iAtlantic regions based on the established EUNIS classification scheme can provide insight into how the environmental components of ecosystems are spatially structured at a regional scale. Understanding the spatial structuring of environmental drivers identified from HSM enables a greater understanding of how these factors interact spatially to determine species, habitat, and resultant ecosystem distributions (Taranto et al., 2023). Increasing our knowledge of the environmental drivers of ecosystem spatial patterns and the environmental mechanisms that support them will support mitigation efforts for the effects of climate change and anthropogenic impacts to provide robust guidance for future management scenarios.

3. Methodology

iAtlantic study areas

The study areas for iAtlantic deliverable 2.6 cover the Atlantic deep-sea basin from 74°N to 60°S and 25.8°E to 98°W together with the iAtlantic Regions (Figure 1).
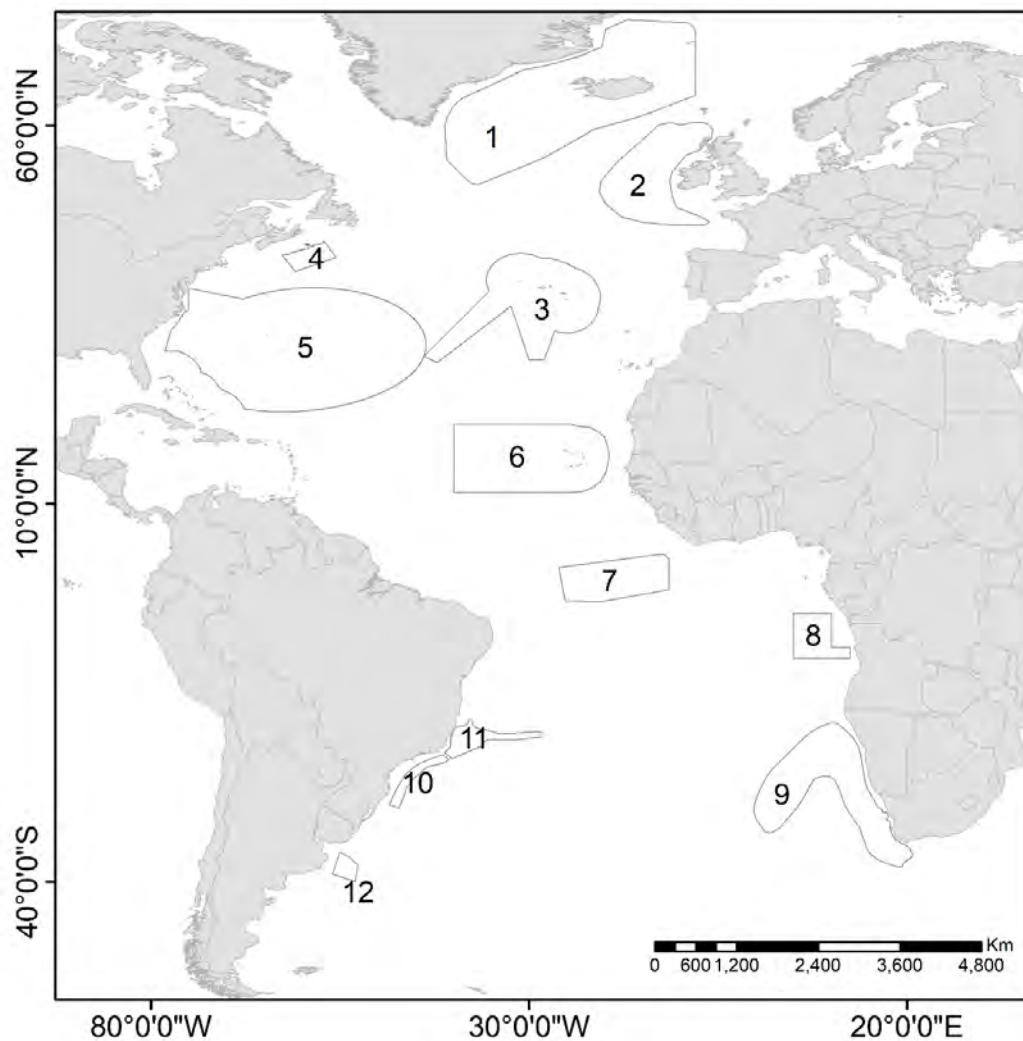
Figure 1. Location of the 12 iAtlantic study regions, EUNIS habitat maps were created for 11 of these regions (Regions 2–12). 1. Subpolar Mid-Atlantic Ridge, off Iceland*, 2. Rockall Trough to PAP*, 3. Central mid-Atlantic Ridge*, 4. NW Atlantic, Gully Canyon*, 5. Sargasso Sea, 6. Eastern Tropical North Atlantic, Cape Verde*, 7. Equatorial Atlantic, Romanche Fracture Zone, 8. Slope & margin off Angola & Congo Lobe, 9. Benguela Current, Walvis Ridge to South Africa*, 10. Brazil margin & Santos and Campos Basin*, 11. Vitória-Trindade Seamount Chain*, 12. Malvinas Current. * Denotes regions for which habitat suitability modelling was also undertaken.

Summary of iAtlantic studies analysed in deliverable D2.6

For iAtlantic deliverable D2.2, Vulnerable Marine Ecosystem (VME) indicator taxa and commercially important deep-sea species were modelled at the Atlantic basin scale not only to improve our current understanding of habitat suitability but also predict changes in distribution because of climate change (Table 1). The HSM of VME indicator taxa and commercially important deep-sea species were developed at a resolution of 3 x 3 km. Presence-only data were compiled from public data bases equating to 385,163 presence records of key species. Species distributions were modelled under varying climatic scenarios using Maximum Entropy (MaxEnt), Generalised Additive Models (GAMs) and Random Forest (RF). Pseudo-absence data were generated using the methodology described by Iturbide et al. (2015) adapted to the study area and data limitations, with background data generated from within four Atlantic quarters to account for geographical sampling bias. Although modelling included future climatic scenarios, for the purposes of this deliverable we focus on the model outputs for the present-day models (1951–2000). Full details of the methodology are detailed in iAtlantic deliverable D2.2.

For iAtlantic deliverable D2.5 the choice of species to be modelled was informed by the species conservation and/or management status, regional needs, and availability of data in the different iAtlantic study regions (Table 1). All mapping approaches combined environmental data with species presence / (pseudo)absence data to run models with either, or all of, the RF, MaxEnt, GAMs and Generalised Boosted Models (GBM/BRT) algorithms (Table 1). Where multiple algorithms were used, ensemble models of outputs were produced to improve the robustness of HSM predictions. The input resolution of model inputs and final output resolution of mapped distributions and extent varied between regions and is detailed together with the full methodology in iAtlantic deliverable D2.5 and summarised in Table 1. In most cases the resolution of the oceanographic data was lower than that of the other variables and interpolated prior to being included in the models.

Atlantic milestone 12 comprised the mapping of 11 of the 12 iAtlantic regions to level 3 of the EUNIS habitat classification. Level 3 of the EUNIS habitat classification combines classified biozones and substrate types to describe the physical environment. Full details of the methodology are presented in iAtlantic milestone 12. iAtlantic deliverable D2.1 used unsupervised classification based on an automated cluster analysis using Gaussian mixture models (GMM) to differentiate nine seabed areas or types that represent classes of similar environmental conditions across the Atlantic basin. These can be described as follows:

- SBA I: Oxic, mostly flat terrain with regionally thick sediment cover. Current influenced regions with low seasonal change.
- SBA II: Mid-Atlantic Ridge spreading centre including abyssal ridges, trenches and continental slopes.
- SBA III: Deep, cold, fresh and oxygen depleted abyssal plain with increased bottom current velocity.
- SBA IV: Shallow, warm, nutrient-rich and saline deeper shelf zones with thick sediment cover, strong local and seasonal changes.
- SBA V: Small and regional, cold and fresh deep water influenced areas in the North and South Atlantic at medium depth, with locally increased currents and current seasonal changes.
- SBA VI: Central deep Atlantic cool, nutrient-depleted area with very weak currents, covering some abyssal elevations and sinks.
- SBA VII: Wider region around the Mid-Atlantic Ridge covering new seafloor, faults and fracture zones, with extremely low sediment cover, no currents, very low oxygen and temperature.
- SBA IX: Nutrient-rich, fresh, warm water continental shelf regions with thick sediment cover and strong seasonal fluctuations.

Full details of the analysis and SBA characteristics can be found in iAtlantic deliverable D2.1.

Table 1. Details for the iAtlantic basin and eight iAtlantic Regions and species for which habitat suitability modelling was undertaken. The algorithm, predictor variables, resolution and regional objective for each region is given. Model outputs from Regions 1, 2, 3, 4, 6, 9 – 11 were sourced from iAtlantic deliverable D2.5 and basin modelling outputs from iAtlantic deliverable D2.2.

iAtlantic Region	Modelled taxa	Algorithm	Predictor variables and () native resolution	Model output resolution	Objective
1. Subpolar Mid-Atlantic Ridge, off Iceland	*Desmophyllum pertusum (*synonymised with *Lophelia pertusa)*	Ensemble - GAM/RF/MaxEnt	MBES & terrain (5 x 5 m)	5 x 5 m	Estimate extent of *D. pertusum* / VME
2. Rockall to PAP (incl. Darwin Mounds, Whittard Canyon, Porcupine Bank Canyon, Lampaul Canyon)	*Acanella arbuscula, Cidaris cidaris, Desmophyllum dianthus, Desmophyllum pertusum, Funiculina quadrangularis, Helicolenus dactylopterus, Hoplostethus atlanticus, Hoplostethus mediterraneus, Lophius budegassa, Madrepora oculata, Solenosmilia variabilis, Squalus acanthias*	RF - initial exploratory analysis conducted with GAM/RF/MaxEnt	Terrain (115 x 115 m), physical oceanography (5.3 x 5.3 km) & chemistry (3 x 3 km)	222 x 222 m	Predict distribution of 12 key taxa
3. Central MAR (Azores)	*Leiopathes expansa, Callogorgia verticillata, Narella bellissima, Narella versluysi, Paracalyptrophora josephinae, Viminella flagellum, Acanthogorgia* spp., *Dentomuricea aff. meteor, Desmophyllum pertusum, Madrepora oculata, Solenosmilia variabilis,* Coralliidae, *Paragorgia johnsoni, Errina dabneyi*	Ensemble - GAM/MaxEnt	Terrain (115 x 115 m), physical oceanography (5.5 x 5.5 km) & chemistry (111 x 111 km) (POC Flux 9 x 9 km)	1.11 x 1.13 km	Estimate CWC habitat extent/ VME
4. NW Atlantic (Scotian Shelf & Gully Canyon)	*Paragorgia arborea*	GAM/RF	Terrain (450 x 450 m), physical oceanography, (~ 6 x 6 km) biological oceanography (~ 9 x 9 km) & fishing effort (1 x 1 km)	1 x 1 km	Predict current and future distribution of *P. arborea* and adequacy of existing Conservation Areas for their protection/ VME
6. Eastern Tropical N Atlantic, Cabo Verde	*Acanella arbuscula, Enallopsammia rostrata, Metallogorgia* spp., *Pleuxauridae* spp.	Ensemble - GAM/RF/MaxEnt	MBES, terrain (100 x 100 m) & physical oceanography (5.3 x 5.3 km)	100 x 100 m	Predict distribution of CWC taxa/VME
9. Walvis Ridge to South Africa, Benguela Current	*Enallopsammia rostrata*	Ensemble - RF/MaxEnt	Terrain, physical oceanography & hydrodynamics (250 x 250 m)	250 x 250 m	Predict distribution of *E. rostrata* and assess model performance with inclusion of hydrodynamics

iAtlantic Region	Modelled taxa	Algorithm	Predictor variables and () native resolution	Model output resolution	Objective
10. Brazil margin and Santos & Campos Basin	*Aristaeopsis edwardsiana, Aristeus antillensis, Aristaeomorpha foliacea, Chaceon ramosae, Lophius gastrophysus, Polyprion americanus, Thunnus alalunga, Thunnus albacares, Lamna nasus, Prionace glauca*	Ensemble - GAM/RF/MaxEnt/GBM	Terrain (~490 x 490 m), physical oceanography, hydrodynamics (25 x 25 km), geomorphology (~490 x 490 m) & substrate (25 x 25 km)	~490 x 490 m	Predict distribution of demersal and pelagic commercial species
11. Vitoria-Trinidade Seamount Chain	*Desmophyllum pertusum, Solenosmilia variabilis, Enallopsammia rostrata, Madrepora spp., Acanella arbuscula*	Ensemble - GAM/RF/MaxEnt/GBM	Terrain (~93 x 93 m), physical oceanography, hydrodynamics (25 x 25 Km), geomorphology (~93 x 93 m) & substrate (25 x 25 km)	~93 x 93 m	Predict distribution of CWC taxa
Basin	*Helicolenus dactylopterus, Hoplostethus atlanticus, Hoplostethus mediterraneus,* and *Lophius* spp., including *L. americanus, L. budegassa, L. gastrophysus,* and *L. piscatorius; Aristaeopsis edwarsiana, Squalus acanthias, Madrepora oculata, Solenosmilia variabilis, Desmophyllum pertusum, Acanella arbuscula, Acanthogorgia armata, Funiculina quadrangularis, Kophobelemnon stelliferum, Cidaris cidaris*	Ensemble - GAM/RF/MaxEnt	Terrain (3 x 3 Km), physical oceanography (55 x 55 km)	3 x 3 km	Predict present and future distribution of CWC taxa under climate change scenarios

Analysis of iAtlantic case studies

iAtlantic outputs from HSM of deliverable D2.5 and D2.2 were compared to identify environmental drivers of ecosystem spatial patterns across spatial scales, which were then tabulated to identify trends. To determine species responses to environmental drivers across spatial scales, the response curves of shared species and environmental predictors modelled across spatial scales were compared. To ascertain the influence of using different resolution data in HSM, spatial predictions of suitable habitat for shared species modelled at both the basin and regional scale were converted to binary predictions and spatial overlap compared. Continuous predictions from HSM were converted to binary maps in ArcGIS using Reclassify in the Spatial Analyst Toolbox. Continuous predictions were converted to binary maps based on maximum sensitivity-specificity thresholds for Region 6. For Region 3 the ensemble model results had been combined with uncertainty metrics to provide an overall score of occurrence likelihood scaled between 1–3, which was converted to a binary map by reclassifying values of <3 as absent and 3 as present. Region 11 was reclassified based on the standard threshold of 0.5 (Liu et al., 2005).

To assess the relationship between the distribution of broad-scale environmental drivers and ecosystems the spatial overlaps of HSM were also compared to Atlantic seabed areas identified in iAtlantic deliverable D2.1. This analysis also allowed the potential role of seabed areas as surrogates of ecosystem distribution to be assessed.

4. Results

Spatial patterns of Atlantic ecosystems

Basin scale modelling identified continental Atlantic Shelf and Slope, especially at high latitudes, as preferential habitat for modelled species including predictions beyond current known distribution ranges. For example, basin scale modelling identified high latitude continental Shelf and Slope, as suitable for deep-water fish and sharks. On the other hand, suitable habitat for sea pens was predicted across the Atlantic, suitable habitat for the shrimp *Aristaeopsis edwardsiana* was predicted across the Atlantic Slope, and suitable habitat for the urchin, *Cidaris cidaris* was predicted to be highest in the northern Atlantic. Basin scale modelling predicted suitable habitat for cold-water corals (CWCs) (comprising representatives of Pennatualcea, Scleractinia, Stylasteridae and Alyconacea (including former Gorgonacea)) across the Atlantic Shelf and Slope with preference for ocean ridges, isolated seamounts and surrounding oceanic islands (Table 2). Regional modelling of CWCs corroborated results from basin modelling by predicting suitable habitat on the Atlantic Shelf and Slope (Table 2). Suitable CWC habitat coincided with areas of increased terrain complexity, hydrodynamic energy, and productivity (Table 2). Regional modelling of commercial demersal shrimp and fish in the South Atlantic showed that suitable habitat varied depending on the depth of the mixed layer and water mass properties (Table 2). Consistent with basin modelling the shrimp *Aristaeopsis edwardsiana* was predicted to have a wide distribution across the region. Comparative distribution maps of basin and regional models where the same taxa were modelled reveal that basin models identify suitable habitat at broad spatial scales often highlighting large geomorphological features (i.e., spreading ridges, seamounts) whereas regional models provide finer discrimination of suitable habitat within those features (i.e., steep cliff or ridge on seamount) (Figures 2 – 9). Additionally, regional models of Regions 3 and 6 were constrained to 2,000 m water depth and resulted in smaller predicted extents than overlapping basin models that extended to greater water depths.

Table 2. Summary table of environmental variables identified via habitat suitability modelling as important drivers of modelled species distribution across the Atlantic basin and eight iAtlantic regions that were modelled.

iAtlantic Region	Modelled taxa	Modelled suitable habitat	Model output resolution	Important environmental variables
1. Subpolar Mid-Atlantic Ridge, off Iceland	*Desmophyllum pertusum* (synonymised with *Lophelia pertusa*)	Shelf break/ upper slope ridges	5 x 5 m	GAM & RF - depth, BPI & rugosity. Maxent - depth, rugosity & eastness.
2. Rockall to PAP (incl. Darwin Mounds, Whittard Canyon, Porcupine Bank Canyon, Lampaul Canyon)	*Acanella arbuscula, Cidaris cidaris, Desmophyllum dianthus, Desmophyllum pertusum, Funiculina quadrangularis, Helicolenus dactylopterus, Hoplostethus atlanticus, Hoplostethus mediterraneus, Lophius budegassa, Madrepora oculata, Solenosmilia variabilis, Squalus acanthias*	Either cosmopolitan or with a southerly distribution across the shelf and shelf break or restricted to shelf.	222 x 222 m	RF- primary production reaching the seabed & disparity index of primary production reaching the seabed. Additionally potential temperature at the seabed for *H. mediterraneus*; dissolved O_2 disparity index for *A. arbuscula* and *H. atlanticus;* current speed and potential temperature for *L. budegassa*; potential temperature for *S. variabilis*.
3. Central MAR (Azores)	*Leiopathes expansa, Callogorgia verticillata, Narella bellissima, Narella versluysi, Paracalyptrophora josephinae, Viminella flagellum, Acanthogorgia spp., Dentomuricea aff. meteor, Desmophyllum pertusum, Madrepora oculata, Solenosmilia variabilis,* Coralliidae, *Paragorgia johnsoni, Errina dabneyi*	Complex geomorphic features on shelf and slope <1,500 m (seamounts, oceanic islands, and ridges). *D. pertusum, M. oculat*a and *L.* cf. *expansa* exhibiting latitudinal pattern with more northly distributions. Differentiated CWCs associated with upper and intermediate water masses.	1.11 x 1.13 km	GAM & MaxEnt - seawater chemistry, BPI_20 km & slope BPI_20 km. Maxent - POC flux in GAM important for only *D. pertusum*, *M. oculata* and *L.* cf. *expansa*. Near-seafloor water temperature was relevant for 9 of the modelled species: Coralliidae (GAM and MaxEnt), *D. pertusum* (GAM and MaxEnt), *Dentomuricea* aff. meteor (GAM and MaxEnt), *Errina dabneyi* (GAM and MaxEnt), *L.* cf. *expansa* (MaxEnt), *Narella bellissima* (GAM), *P. josephinae* (GAM), *Paragorgia johnsoni* (MaxEnt), *V. flagellum* (GAM and MaxEnt).
4. NW Atlantic (Scotian Shelf & Gully Canyon)	*Paragorgia arborea*	Complex geomorphic features on upper slope (i.e., steep slopes at km scale and vertical reef at 100 ms scale).	1 x 1 km	Rugosity & terrain variables.
6. Eastern Tropical N Atlantic, Cabo Verde	*Acanella arbuscula, Enallopsammia rostrata, Metallogorgia* spp., *Pleuxauridae* spp.	Complex topography of seamount flanks. For *A. arbuscula* -Flat to gentle sloping terrain on seamounts.	100 x 100 m	Broad-scale slope (33 x 33) and bottom salinity for *A. arbuscula*. Planar curvature (n=33 x 33) & terrain ruggedness (VRM, n= 33 x 33) *for E. rostrata* and *Metallogorgia* spp. Terrain ruggedness (VRM, n= 33 x 33), mean curvature (n= 33 x33) & current speed (U) for Pleuxauridae.

iAtlantic Region	Modelled taxa	Modelled suitable habitat	Model output resolution	Important environmental variables
9. Walvis Ridge to South Africa, Benguela Current	*Enallopsammia rostrata*	Complex topography experiencing increased energy dissipation on Slope (500–1,500 m).	250 x 250 m	Depth, slope (in RF models), kinetic energy dissipation (bottommost layer), and minimum vertical current speed for *E. rostrata*.
10.Brazil margin and Santos & Campos Basin	*Aristaeopsis edwardsiana, Aristeus antillensis, Aristaeomorpha foliacea, Chaceon ramosae, Lophius gastrophysus, Polyprion americanus, Thunnus alalunga, Thunnus albacares, Lamna nasus, Prionace glauca*	Feeding habitat driven by water mass properties coinciding with areas of regional mixing and upwelling. Species exhibiting differentiation in relation to depth of mixed layer occurring across the shelf and upper slope.	~490 – 490 m	Water column variables – Sea floor temperature, salinity and depth of the mixed layer (annual means and variation) for demersal species. Current speed for some species. Sea surface temperature, salinity and depth of the mixed layer (annual means and variation) for pelagic species.
11. Vitoria-Trinidade Seamount Chain	*Desmophyllum pertusum, Solenosmilia variabilis, Enallopsammia rostrata, Madrepora spp., Acanella arbuscula*	Oceanographically dynamic areas on Slope (500–1,200 m)	~ 93 x 93 m	Current speed, mixed layer depth, bottom temperature (annual means and variation). Current directions & bottom salinity. Aspect for *Madrepora* spp.
Basin	*Helicolenus dactylopterus, Hoplostethus atlanticus, Hoplostethus mediterraneus,* and *Lophius* spp*., including L. americanus, L. budegassa, L. gastrophysus, and L. piscatorius; Aristaeopsis edwarsiana, Squalus acanthias, Madrepora oculata, Solenosmilia variabilis, Desmophyllum pertusum, Acanella arbuscula, Acanthogorgia armata, Funiculina quadrangularis, Kophobelemnon stelliferum, Cidaris cidaris*	Shelf and Slope	3 x 3 km	Bottom temperature and POC flux for sea pens, Depth, slope, bottom temperature for deep-water shrimps, Aragonite saturation, slope, bottom temperature and POC flux for Scleractinian corals, Slope, Ph and POC flux for Octocorals, Bottom temperature and POC flux for sea urchins and depth, bottom temperature and POC flux for deepwater fish and sharks.
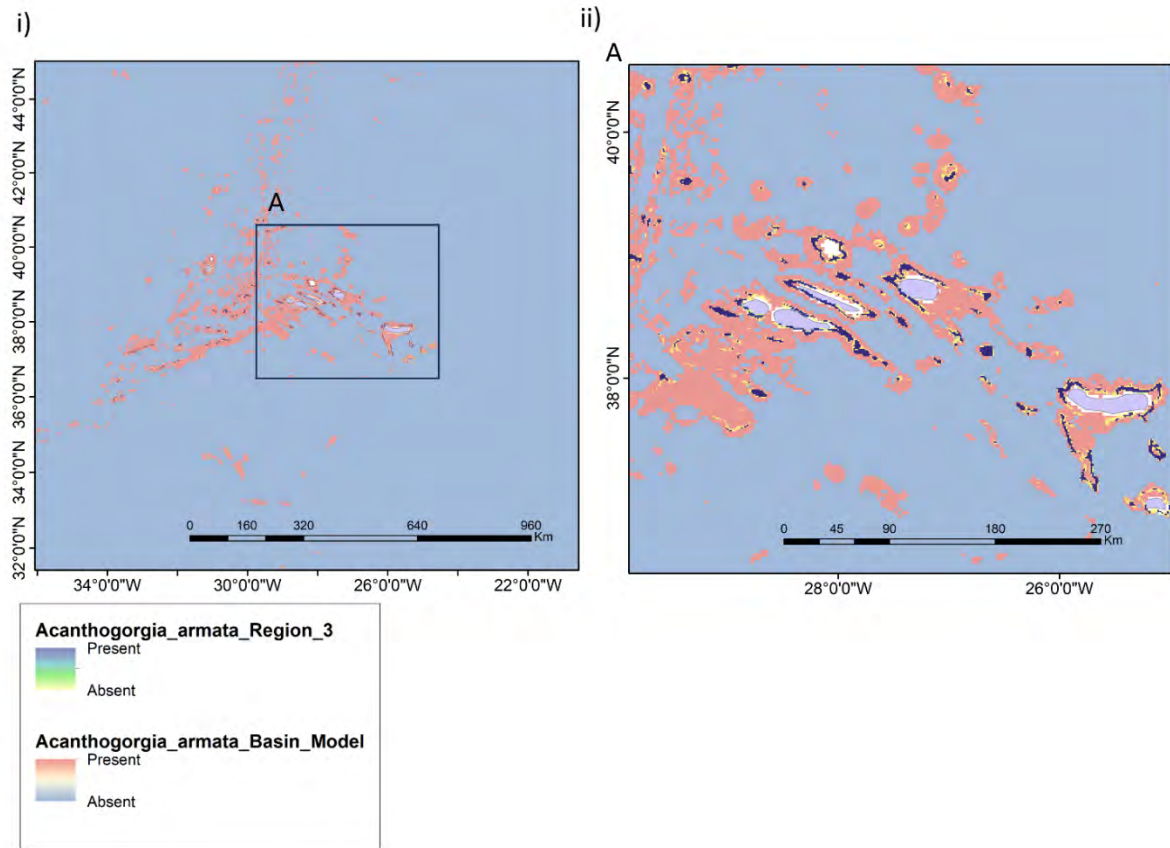
Figure 2. Regional scale modelling of Study area 3 (Central mid-Atlantic Ridge) overlain onto basin scale modelling for *Acanthogorgia armata.* i) Full extent of Region 3 mapping ii) Zoom inset from across Region 3.
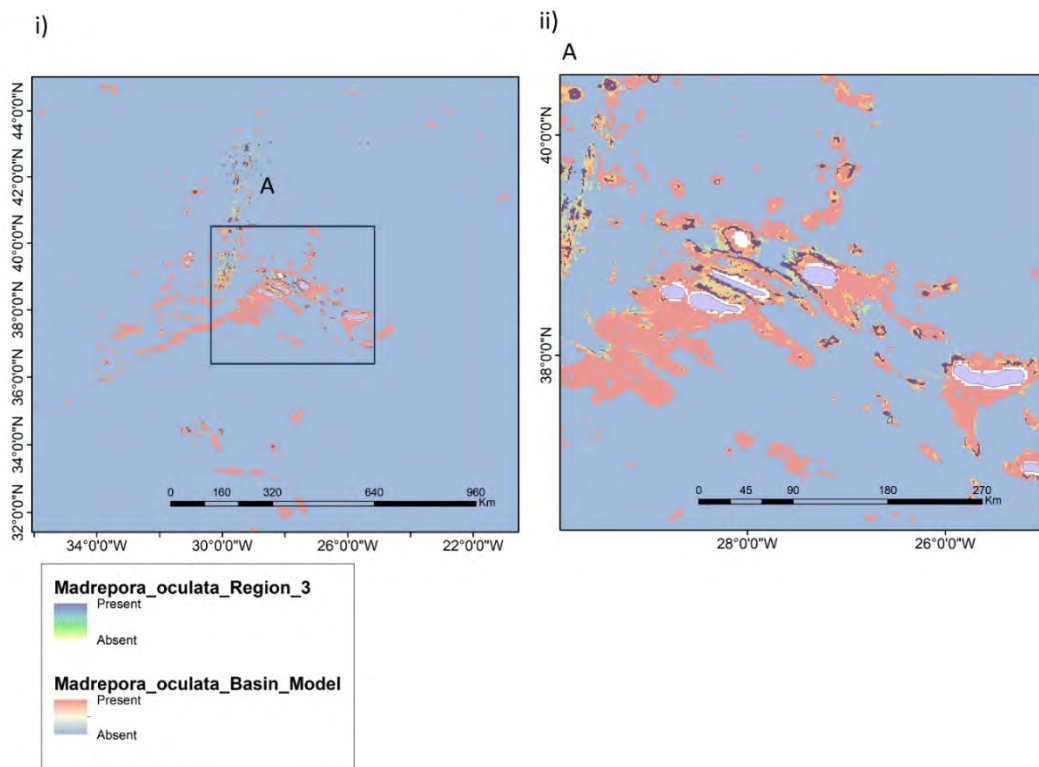
Figure 3. Regional scale modelling of Region 3 (Central mid-Atlantic Ridge) overlain onto basin scale modelling for *Madrepora oculata.* i) Full extent of Region 3 mapping ii) Zoom inset from across Region 3.
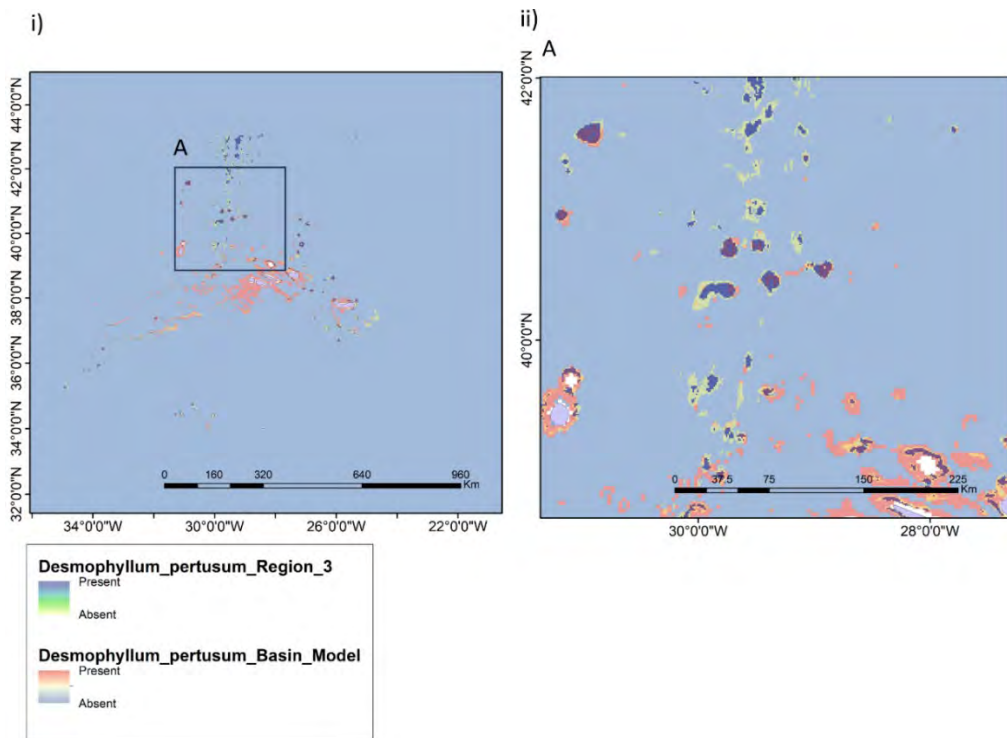
Figure 4. Regional scale modelling of Region 3 (Central mid-Atlantic Ridge) overlain onto basin scale modelling for *Desmophyllum pertusum.* i) Full extent of Region 3 mapping ii) Zoom inset from across Region 3.
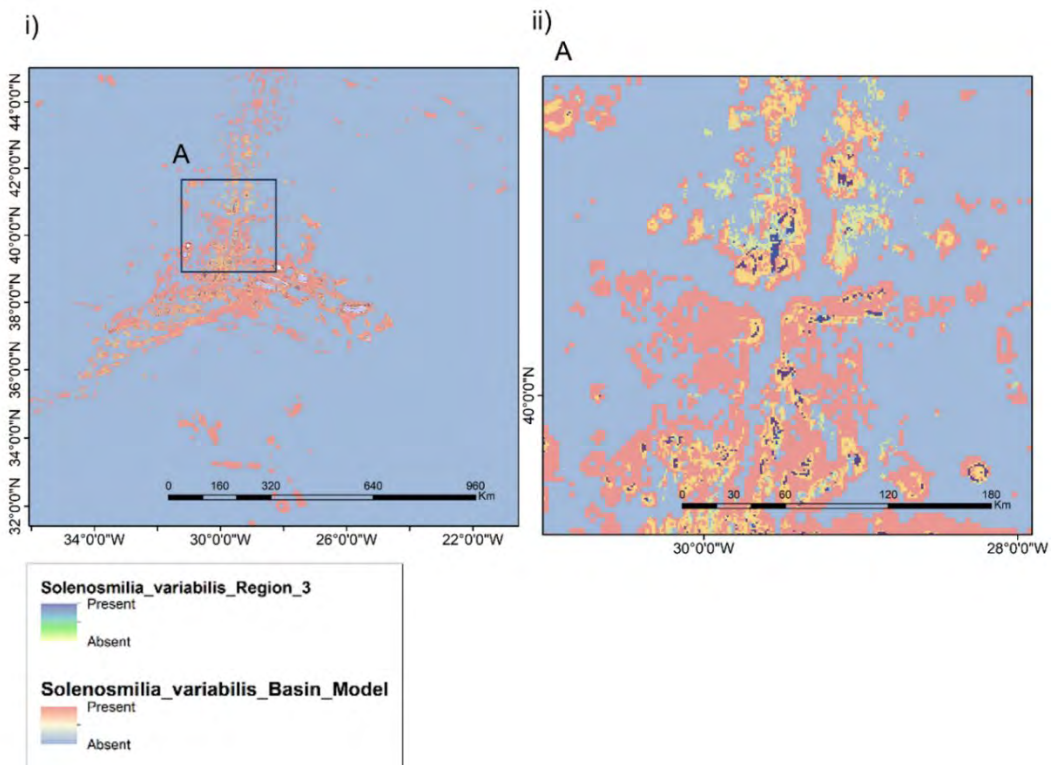
Figure 5. Regional scale modelling of Region 3 (Central mid-Atlantic Ridge) overlain onto basin scale modelling for *Solenosmillia variabilis*. i) Full extent of Region 3 mapping ii) Zoom inset from across Region 3.
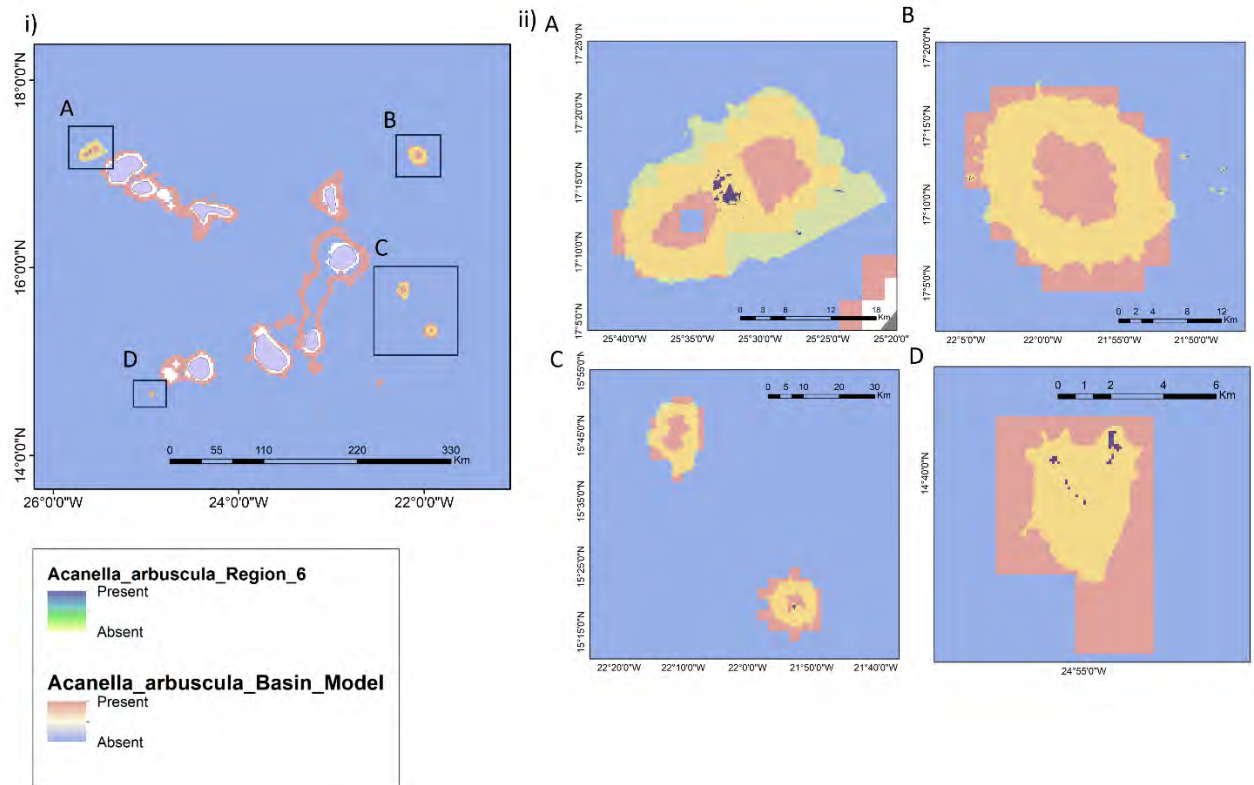
Figure 6. Regional scale modelling of Region 6 (Eastern Tropical North Atlantic, Cape Verde) overlain onto basin scale modelling for *Acanella arbuscula.* i) Full extent of Region 6 mapping ii) Zoom insets from across Region 6.
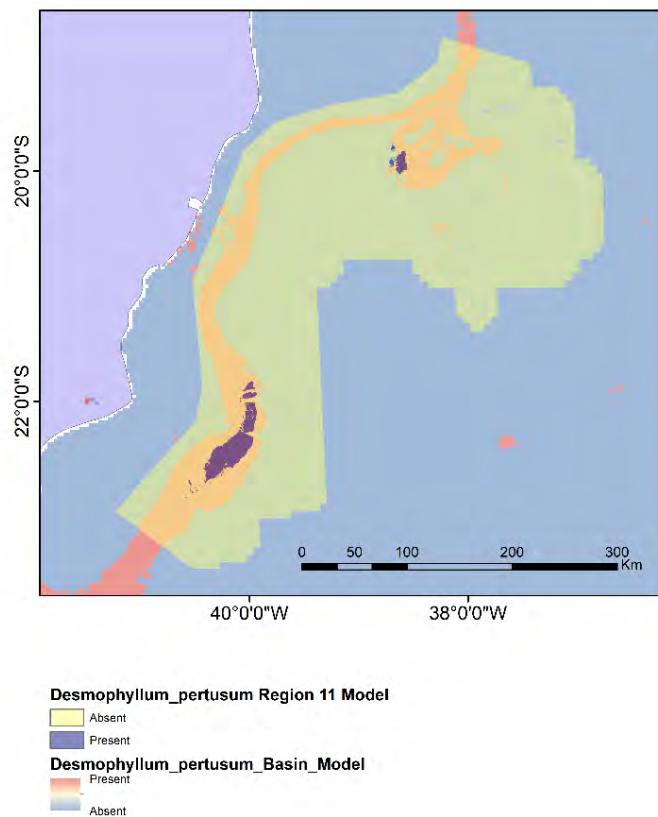
Figure 7. Regional scale modelling of Region 11 (Vitória-Trindade Seamount Chain) overlain onto basin scale modelling for *Desmophyllum pertusum.*
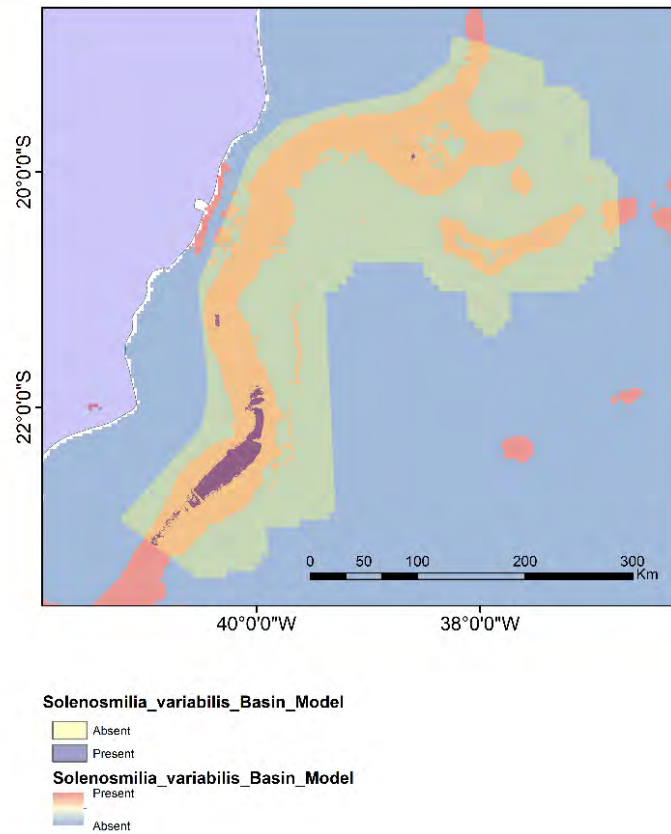
Figure 8. Regional scale modelling of Region 11 (Vitória-Trindade Seamount Chain) overlain onto basin scale modelling for *Solenosmilia variabilis.*
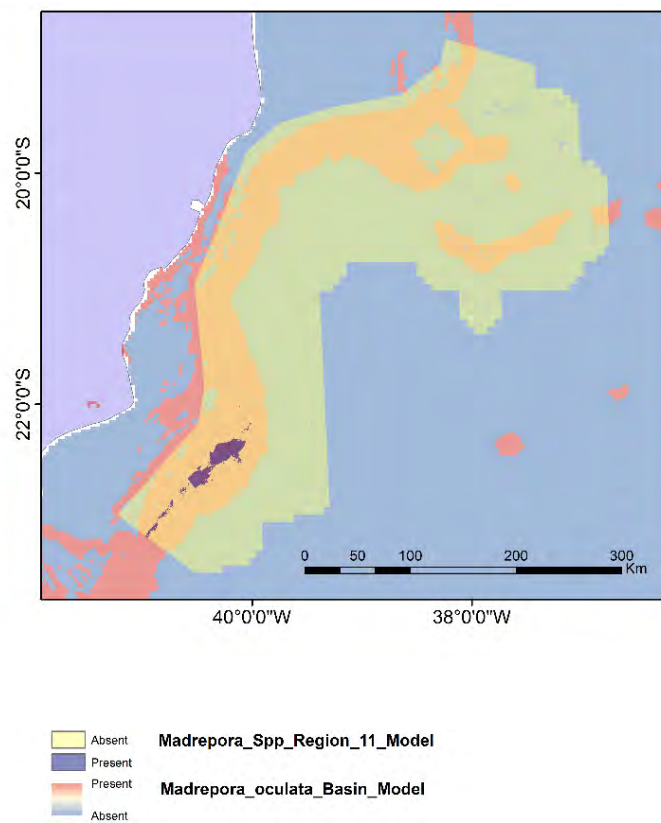
Figure 9. Regional scale modelling of Region 11 (Vitória-Trindade Seamount Chain) overlain onto basin scale modelling for *Madrepora* spp.

Superimposing regional habitat suitability models onto the basin wide habitat classification produced as part of the iAtlantic deliverable D2.1 shows habitats, including VMEs, coincide with distributions of seabed types (Figure 10–12 and Table 3). Cold-water coral VME indicator taxa are predominantly associated with the classes of Seabed Area (SBA) II, SBA IV while *Desmophyllum pertusum*, *Madrepora oculata* and *Paragorgia arborea* also show substantial overlap with SBA I, with *Paragorgia arborea* also overlapping with SBA VII and SBA IX (Table 3). On the other hand, modelled habitat for *Enallopsammia* in Region 9 overlapped with SBA II, SBA III, SBA IV, SBA V and SBA VIII (Table 3).

Seabed area II is characterised by complex terrain and is represented by the Mid Atlantic Ridge (MAR) spreading centre including abyssal ridges, trenches, seamounts and continental slopes as well as the Gulf of Mexico at 2,443–4,090 m water depth. SBA IV represents shallow, warm, nutrient-rich and saline deeper Shelf/upper Slope zones with thick sediment cover, strong currents and high local and seasonal variability in 300–1,395 m water depth and occurs along the Atlantic Shelf and Slope (Schumacher et al., 2022). SBA I represents oxygenated areas that are mostly flat with regionally thick sedimented coverage in regions influenced by currents with low seasonal change at 2,064–3,063 m water depth (Schumacher et al., 2022). SBA I occurs along the Slope of the North Atlantic and is associated with water mass formation and boundary currents flows, with the characteristic high oxygen concentrations of SBA I indicative of mixing (Schumacher et al., 2022).

Table 3. Spatial overlap between predicted habitat suitability for modelled cold-water coral species of iAtlantic deliverable D2.5 and seabed areas (SBA I- SBA IX) delineated in iAtlantic deliverable D2.1. Values in columns represent the number of overlapping pixels between the HSM and seabed area layers, and in brackets the spatial extent of overlapping pixels in km^2).

Region	Habitat suitability model	SBA I	SBA II	SBA III	SBA IV	SBA V	SBA VI	SBA VII	SBA VIII	SBA IX	Pixel size (m²)
9	*Enallopsammia rostrata*		137,953 (33,646.7)	10,278 (2,506.8)	737 (179.8)	3,114 (759.5)			52,552 (12,817.4)		244
6	*Acanella arbuscula*		814 (80.6)	1 (0.1)	1 (0.1)						99
6	*Enallopsammia rostrata*		2,210 (218.8)								99
3	*Acanthogorgia* spp.		1,271 (1,527.7)		2,003 (2,407.6)				2 (2.4)		1,202
3	*Callogorgia verticillata*		923 (1,084.5)		2,516 (2,956.3)						1,175
3	Coralliidae spp.		1,380 (1,621.5)		1,236 (1,452.3)						1,175
3	*Dentomuricea aff meteor*		259 (304.3)		789 (927.1)						1,175
3	*Desmophyllum pertusum*	218 (256.1)	3,345 (3,930.4)		1,630 (1,915.3)	32 (37.6)	8 (9.4)		24 (28.2)		1,175
3	*Errina dabneyi*		65 (76.4)		904 (1,062.2)						1,175
3	*Leiopathes cf expansa*	71 (83.4)	2,688 (3,158.4)		1,236 (1,452.3)	17 (20.0)			15 (17.6)		1,175
3	*Madrepora oculata*	122 (143.4)	3,221 (3,784.7)		2,160 (2,538.0)	28 (32.9)			20 (23.5)		1,175
3	*Narella bellissima*		1,298 (1,525.2)		1,500 (1,762.5)						1,175
3	*Narella versluysi*	9 (10.6)	1,557 (1,829.4)		1,165 (1,368.9)	2 (2.3)					1,175
3	*Paracalyptrophora josephinae*		424 (498.2)		962 (1,130.4)				7 (8.2)		1,175
3	*Paragorgia johnsoni*	10 (11.8)	1,720 (2,021.0)		1,496 (1,757.8)	1 (1.2)					1,175
3	*Solenosmilia variabilis*		2,048 (2,406.4)		1,879 (2,207.8)				1 (1.175)		1,175
3	*Viminella flagellum*		618 (726.2)		1,494 (1,755.5)						1,175
11	*Solenosmilia variabilis*		11,029 (1,113.9)		189,967 (19,186.7)						101
11	*Madrepora* spp.		23 (2.3)		88,639 (8,952.5)						101
11	*Enallopsammia rostrata*		7,303 (737.6)		141,120 (14,253.1)						101
11	*Desmophyllum pertusum*		2,047 (206.7)		164,178 (16,581.9)						101
11	*Acanella arbuscula*		85,213 (8,606.5)		538,563 (54,394.9)						101
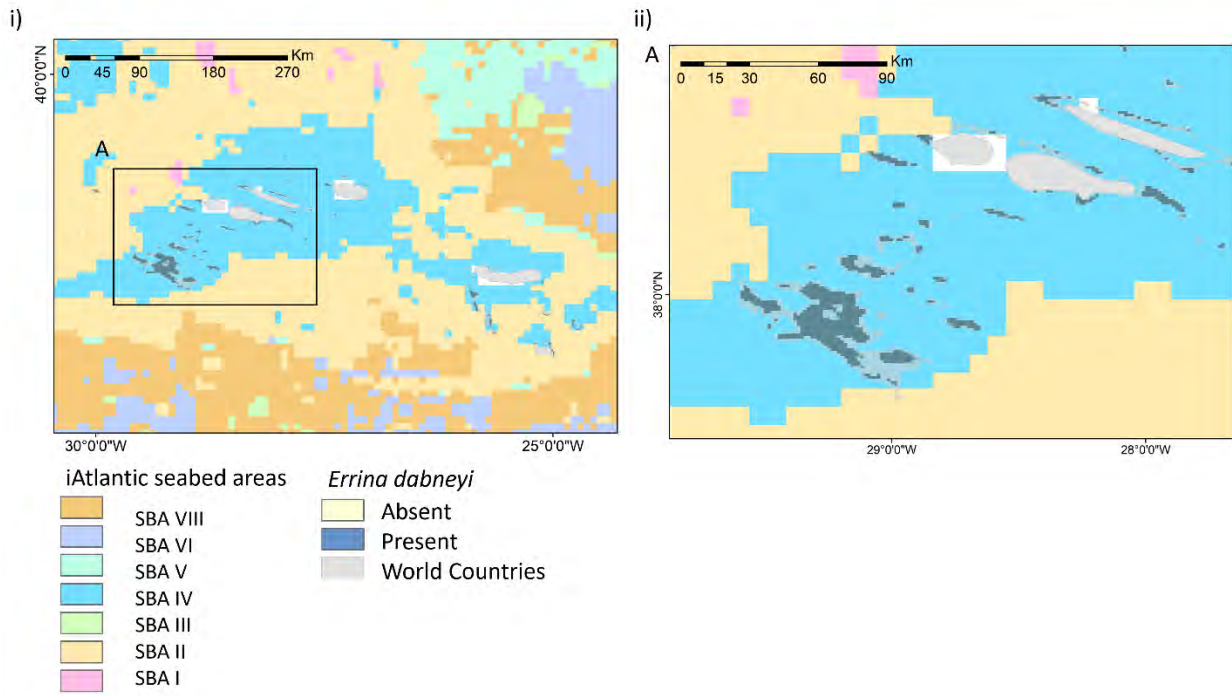
Figure 10. Spatial overlap of binary suitability map for *Errina dabneyi* from Region 3 (Central mid-Atlantic Ridge) overlain on to iAtlantic seabed areas from iAtlantic deliverable D2.1. i) Full extent of Region 3 mapping ii) Zoom inset of box A from across Region 3.
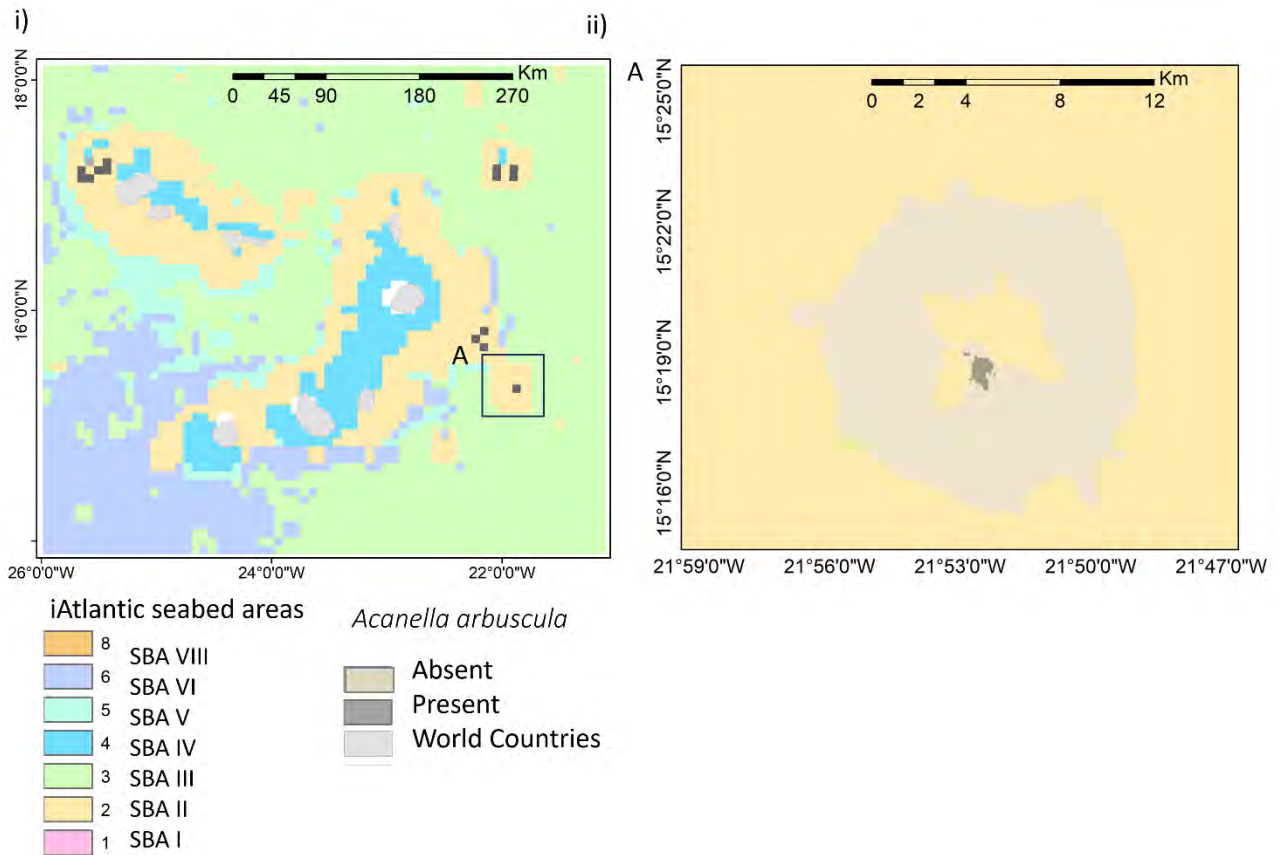
Figure 11. Spatial overlap of binary suitability map for *Acanella arbuscula* from Region 6 (Eastern Tropical North Atlantic, Cape Verde) overlain on to iAtlantic seabed areas from iAtlantic deliverable D2.1. i) Full extent of Region 6 mapping ii) Zoom inset of box A from across Region 6.
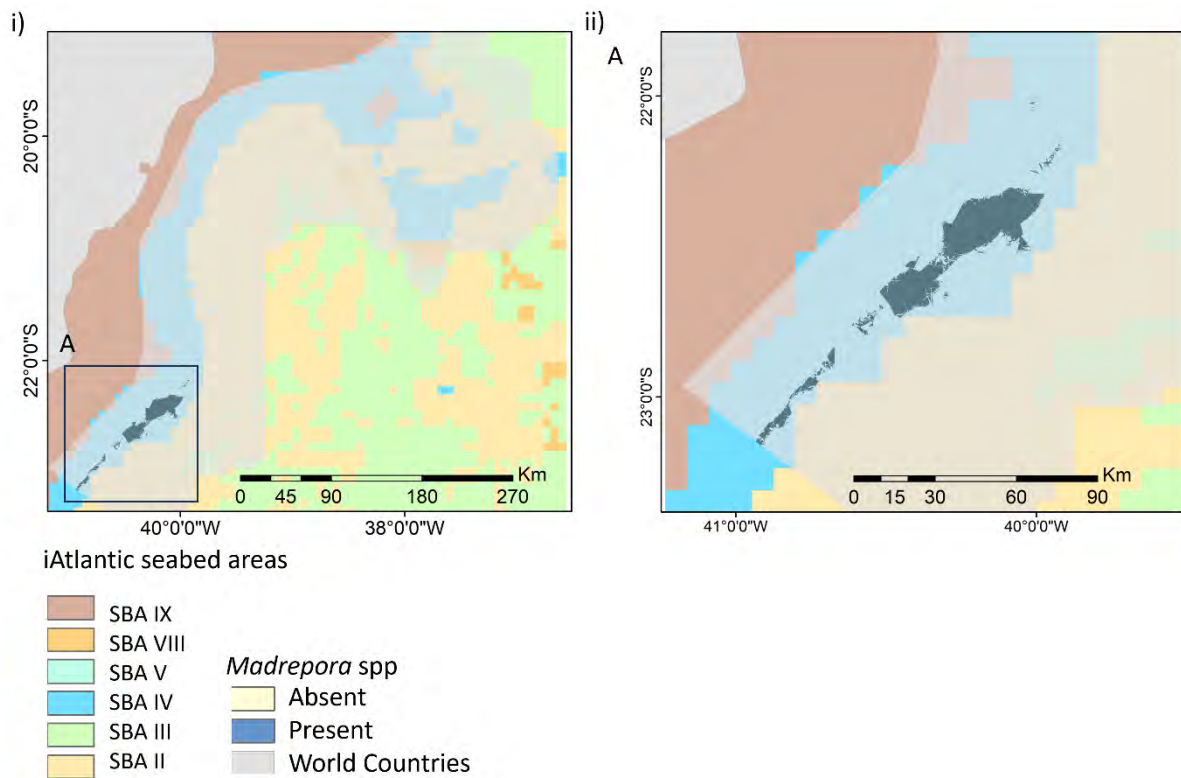
Figure 12. Spatial overlap of binary suitability map for *Madrepora oculata* from Region 11 (Vitória-Trindade Seamount Chain) overlain on to iAtlantic seabed areas from iAtlantic deliverable D2.1. i) Full extent of Region 11 mapping ii) Zoom inset of box A from across Region 11.

Superimposing regional habitat suitability models onto the regional EUNIS habitat classification produced as part of the iAtlantic milestone 12 shows that spatial extents mapped differ between regions and that CWC VME indicator taxa coincide with bathymetric 'biozones' but less so with EUNIS classifications (Figures 13–27) due to suitable habitat predicted across EUNIS substrata classes that would be deemed ecologically unsuitable.

Comparisons of shared CWC VME taxa superimposed on regional EUNIS habitat classifications indicates suitable habitat for these CWCs is predominately in the upper and lower bathyal biozones (which equates to Slope environments) (Figures 13–27). The lack of differentiation of HSM across substrata could reflect the omission of substrate data from all HSM (apart from Regions 10 and 11) (Table 1) coupled with the low resolution of substrate layers used for the EUNIS classification that fail to capture substrata heterogeneity driving the spatial patterns of VMEs.

Comparisons of spatial predictions from HSM and EUNIS classification show that HSM distributions show spatial patterns that are largely consistent with bathymetry, reflecting the influence of depth and water mass properties on species habitat distribution (Figures 13–15 and 18–22). In general, HSM reflect general trends in broad-scale terrain that capture large geomorphic features with suitable habitat distributed at specific depths around these features, irrespective of substrata type as indicated by the EUNIS classification (Figure 13–16 and 18–22). On the other hand, where HSM incorporated higher resolution data (or ground-truth imagery) than that used in the EUNIS classification, important high-resolution features and environmental heterogeneity identified in HSM are not discerned in the EUNIS classification again resulting in a disparity between the two mapping approaches (Figures 16–

17). Consequently, when assessing how useful EUNIS is as an indicator of VMEs, both the input resolutions and extents being mapped should be considered.

Madrepora oculata modelled in Region 3 predominantly overlapped with the EUNIS classified Atlantic upper and lower bathyal mud and upper bathyal mixed sediment (Figure 13). In region 11, *M. oculata* also overlapped with mud but showed a preference for upper bathyal depths, and in addition overlapped with Atlantic upper bathyal sand and biogenic habitat (Figure 18). *Desmophyllum pertusum* and *Solensmilia variabilis* modelled in Regions 3 and 11 showed similar patterns in spatial overlap with EUNIS classifications (Figures 14, 15, 19 and 20). Across both regions suitable habitat for *D. pertusum* and *S. variabilis* overlaps with Atlantic upper and lower bathyal mixed sediment, mud and sand with lesser extents across upper and lower bathyal rock (Figures 24 and 25). Additionally, in Region 11 *D. pertusum* and *S. variabilis* overlap with Atlantic upper and lower bathyal biogenic habitat (Figures 24 and 25). *Madrepora oculata*, *D. pertusum* and *S. variabilis* are reef forming species that can form biogenic habitat, consequently the co-occurrence of suitable *M. oculata*, *D. pertusum* and *S. variabilis* habitat with areas classified as biogenic habitat corroborates the EUNIS classification and illustrates its use for identifying VMEs. *Desmophyllum pertusum* is a species associated with contourites and like *M. oculata* and *S. variabilis* is often observed among mixed substrata. Suitable habitat of *M. oculata*, *D. pertusum* and *S. variabilis* coinciding with mud could represent areas where the EUNIS classification fails to delineate ecologically important substrata heterogeneity or an over-prediction of suitable habitat.

In iAtlantic deliverable D2.5, *Enallopsammia rostrata* was modelled in Regions 6, 9 and 11. However, the HSM of Region 9 did not overlap with EUNIS classified areas and is therefore omitted. Suitable habitat for *E. rostrata* in Region 11 predominantly overlapped with EUNIS classified Atlantic upper and lower bathyal mud, mixed sediment and sand, with a small extent overlapping with lower bathyal rock (Figure 27). Suitable habitat for *E. rostrata* in Region 6 overlapped with EUNIS classified lower bathyal mud and mixed sediment (Figure 27). The HSM from Region 6 covered a smaller extent than that of Region 11, which likely explains why fewer EUNIS habitat classification classes overlap with the predicted habitat of *E. rostrata* in Region 6 compared to Region 11. *Enallopsammia rostrata* requires hard substratum as a colonisation base. However, the predicted distribution of suitable habitat for *E. rostrata* extends across Atlantic upper and lower bathyal mud and sand. The inconsistency between HSM and EUNIS classifications could represent areas where the EUNIS classification fails to delineate ecologically important substrata heterogeneity, is derived from models with few data points and exhibits high uncertainty of substrate type. Alternatively, it could represent an over-prediction of suitable habitat.

Acanella arbuscula modelled in Region 11 predominately overlapped with the EUNIS classified Atlantic upper and lower bathyal mud and to a lesser extent across other classes of upper and lower bathyal soft substrata (mixed, coarse and sand) (Figure 26). In contrast *A. arbuscula* modelled in Region 6 predominantly overlapped with the EUNIS classified Atlantic upper and lower bathyal rock and to a lesser extent with Atlantic upper and lower mixed sediment (Figure 26). *A. arbuscula* is a soft substratum species, that has been observed from in situ imagery on soft, mixed and hard substrata in Regions 6 and 11. However, in Region 6 the substrate layer of the EUNIS classification classified the majority of seamounts where HSM were run as rock, resulting in the observed disparity between the HSM and EUNIS classification.

Figure 13. (i) Spatial overlap of binary suitability map for *Madrepora oculata* encompassing Region 3 (Central mid-Atlantic Ridge) overlain on to iAtlantic EUNIS classification of Region 3 from iAtlantic milestone 12. (ii) zoom inset of binary suitability map for *Madrepora oculata* encompassing Region 3 overlain on to iAtlantic EUNIS classification of Region 3.

Figure 14. (i) Spatial overlap of binary suitability map for *Desmophyllum pertusum* encompassing Region 3 (Central mid-Atlantic Ridge) overlain on to iAtlantic EUNIS classification of Region 3 from iAtlantic milestone 12. (ii) zoom inset of binary suitability map for *Desmophyllum pertusum* encompassing Region 3 overlain on to iAtlantic EUNIS classification of Region 3.
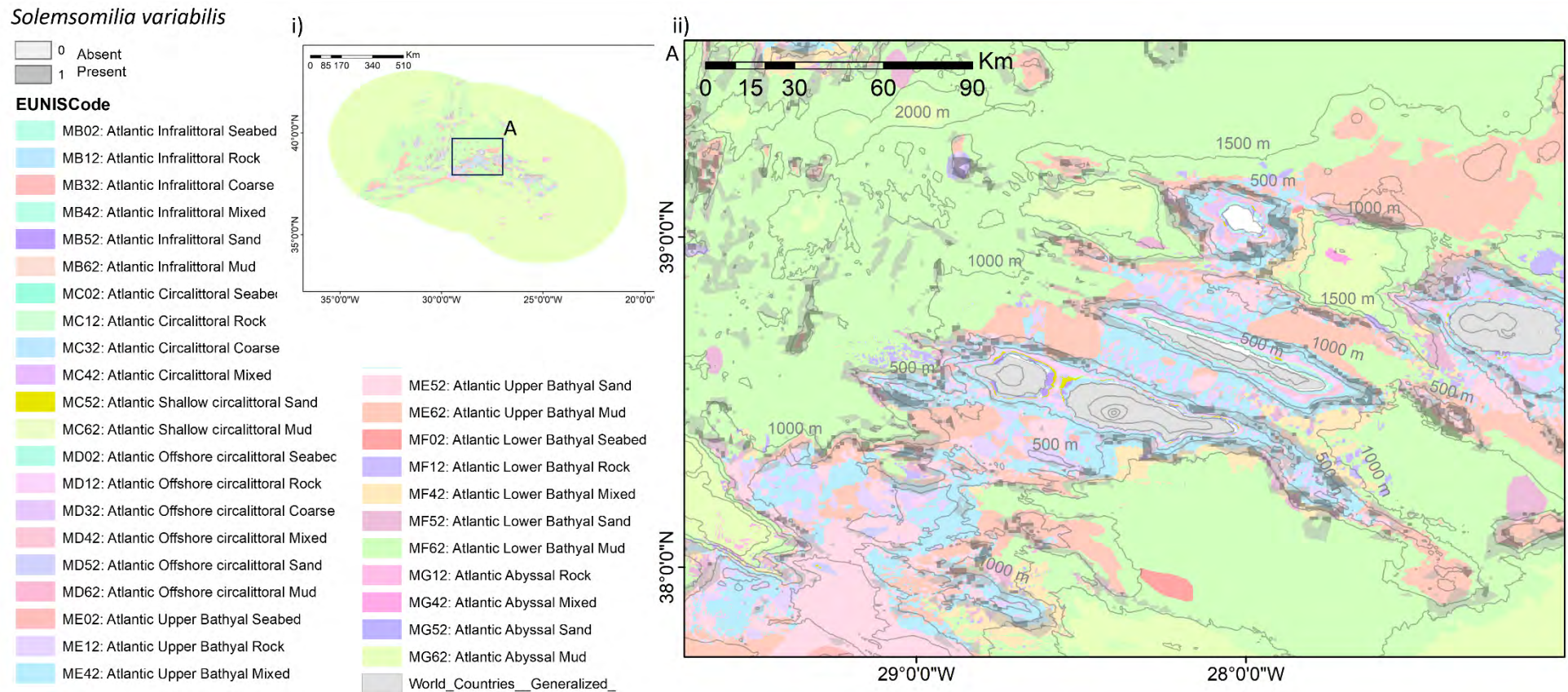
Figure 15. (i) Spatial overlap of binary suitability map for *Solensomilia variabilis* encompassing Region 3 (Central mid-Atlantic Ridge) overlain on to iAtlantic EUNIS classification of Region 3 from iAtlantic milestone 12. (ii) zoom inset of binary suitability map for *Solensomilia variabilis* encompassing Region 3 overlain on to iAtlantic EUNIS classification of Region 3.
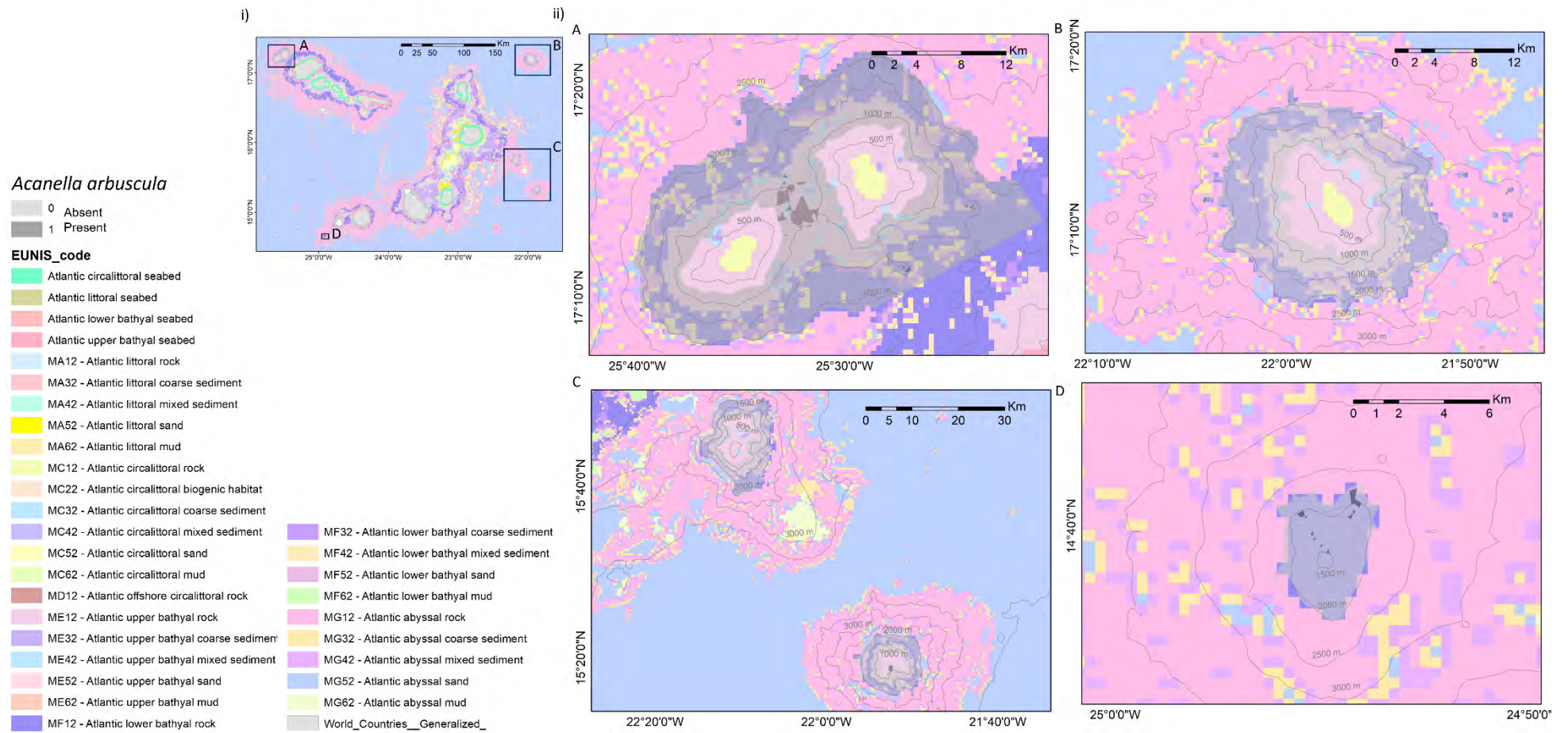
Figure 16. (i) Spatial overlap of binary suitability map for *Acanella arbuscula* encompassing Region 6 (Eastern Tropical North Atlantic, Cape Verde) overlain on to iAtlantic EUNIS classification of Region 6 from iAtlantic milestone 12. (ii) A-D zoom insets of binary suitability map for *Acanella arbuscula* encompassing Region 6 overlain on to iAtlantic EUNIS classification of Region 6.
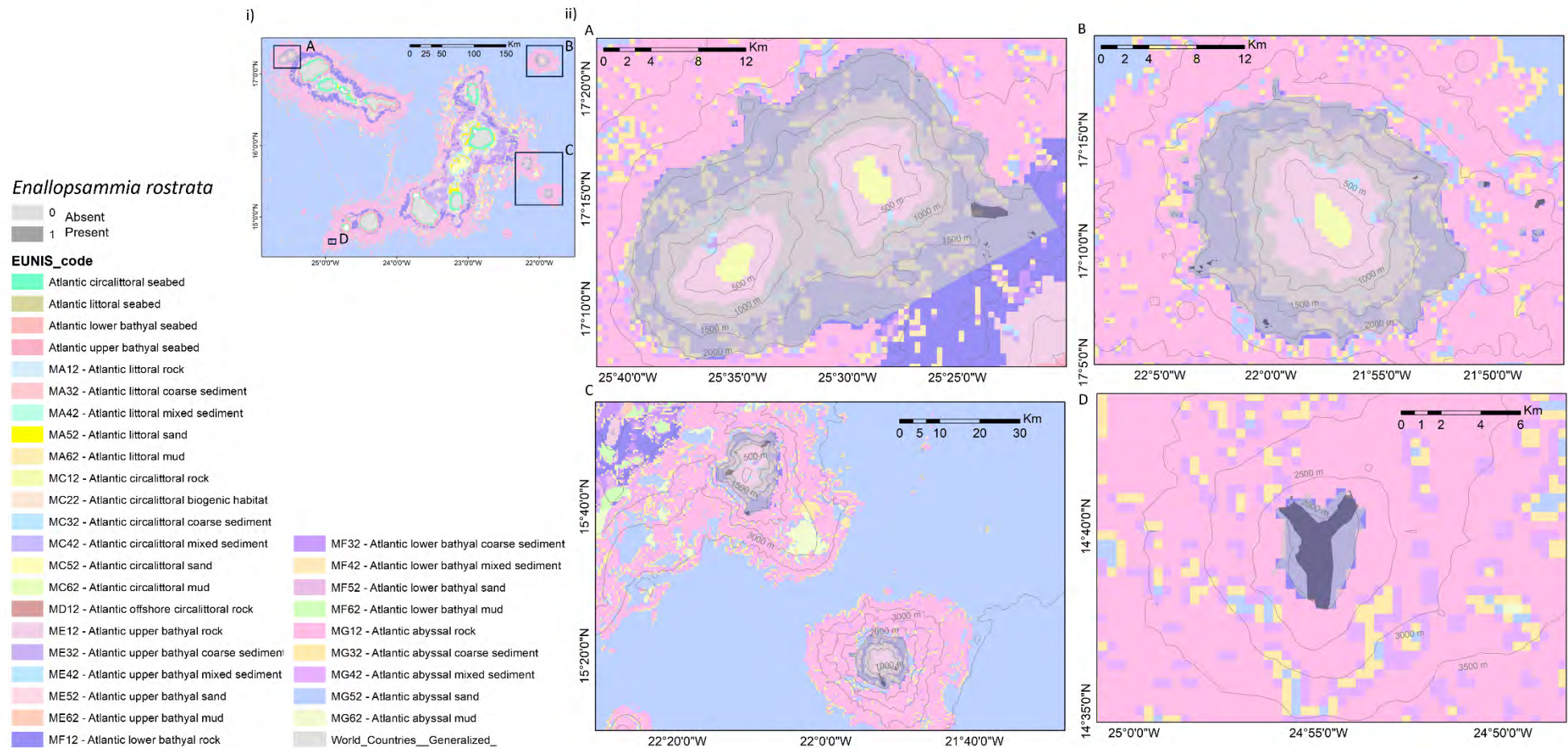
Figure 17. (i) Spatial overlap of binary suitability map for *Enallopsammia rostrata* encompassing Region 6 (Eastern Tropical North Atlantic, Cape Verde) overlain on to iAtlantic EUNIS classification of Region 6 from iAtlantic milestone 12. (ii) A-D zoom insets of binary suitability map for *Enallopsammia rostrata* encompassing Region 6 overlain on to iAtlantic EUNIS classification of Region 6.

Figure 18. Spatial overlap of binary suitability map for *Madrepora oculata* encompassing Region 11 (Vitória-Trindade Seamount Chain) overlain on to iAtlantic EUNIS classification of Region 11 from iAtlantic milestone 12.

Figure 19. Spatial overlap of binary suitability map for *Desmophyllum pertusum* encompassing Region 11 (Vitória-Trindade Seamount Chain) overlain on to iAtlantic EUNIS classification of Region 11 from iAtlantic milestone 12.

Figure 20. Spatial overlap of binary suitability map for *Solensomilia variabilis* encompassing Region 11 (Vitória-Trindade Seamount Chain) overlain on to iAtlantic EUNIS classification of Region 11 from iAtlantic milestone 12.

Figure 21. Spatial overlap of binary suitability map for *Acanella arbuscula* encompassing Region 11 (Vitória-Trindade Seamount Chain) overlain on to iAtlantic EUNIS classification of Region 11 from iAtlantic milestone 12.

Figure 22. Spatial overlap of binary suitability map for *Enallopsammia rostrata* encompassing Region 11 (Vitória-Trindade Seamount Chain) overlain on to iAtlantic EUNIS classification of Region 11 from iAtlantic milestone 12.

Figure 23. Spatial overlap of binary suitability map for *Madrepora oculata* within Regions 3 (Red) and 11 (Blue) overlain on to iAtlantic EUNIS classification of the corresponding Region from iAtlantic milestone 12. To maximise axis eligibility, several EUNIS habitats for which there was no spatial overlap have been removed. Note that the spatial resolutions of the HSMs, input variables and EUNIS classifications differed between the regions, the impact of which is discussed in section 5.4.
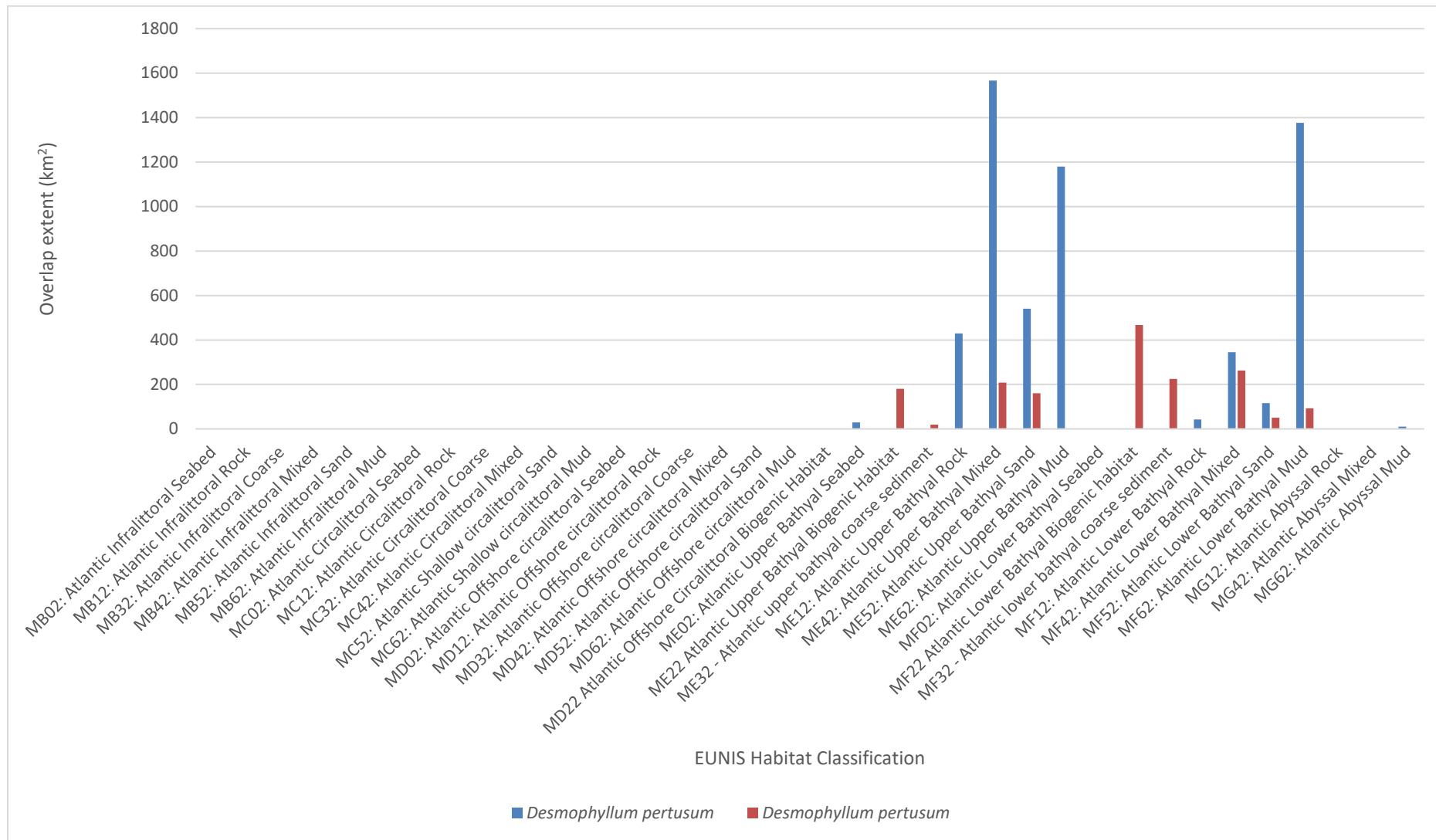
Figure 24. Spatial overlap of binary suitability map for *Desmophyllum pertusum within* Regions 3 (Red) and 11 (Blue) overlain on to iAtlantic EUNIS classification of the corresponding Region from iAtlantic milestone 12. To maximise axis eligibility, several EUNIS habitats for which there was no spatial overlap have been removed. Note that the spatial resolutions of the HSMs, input variables and EUNIS classifications differed between the regions, the impact of which is discussed in section 5.4.
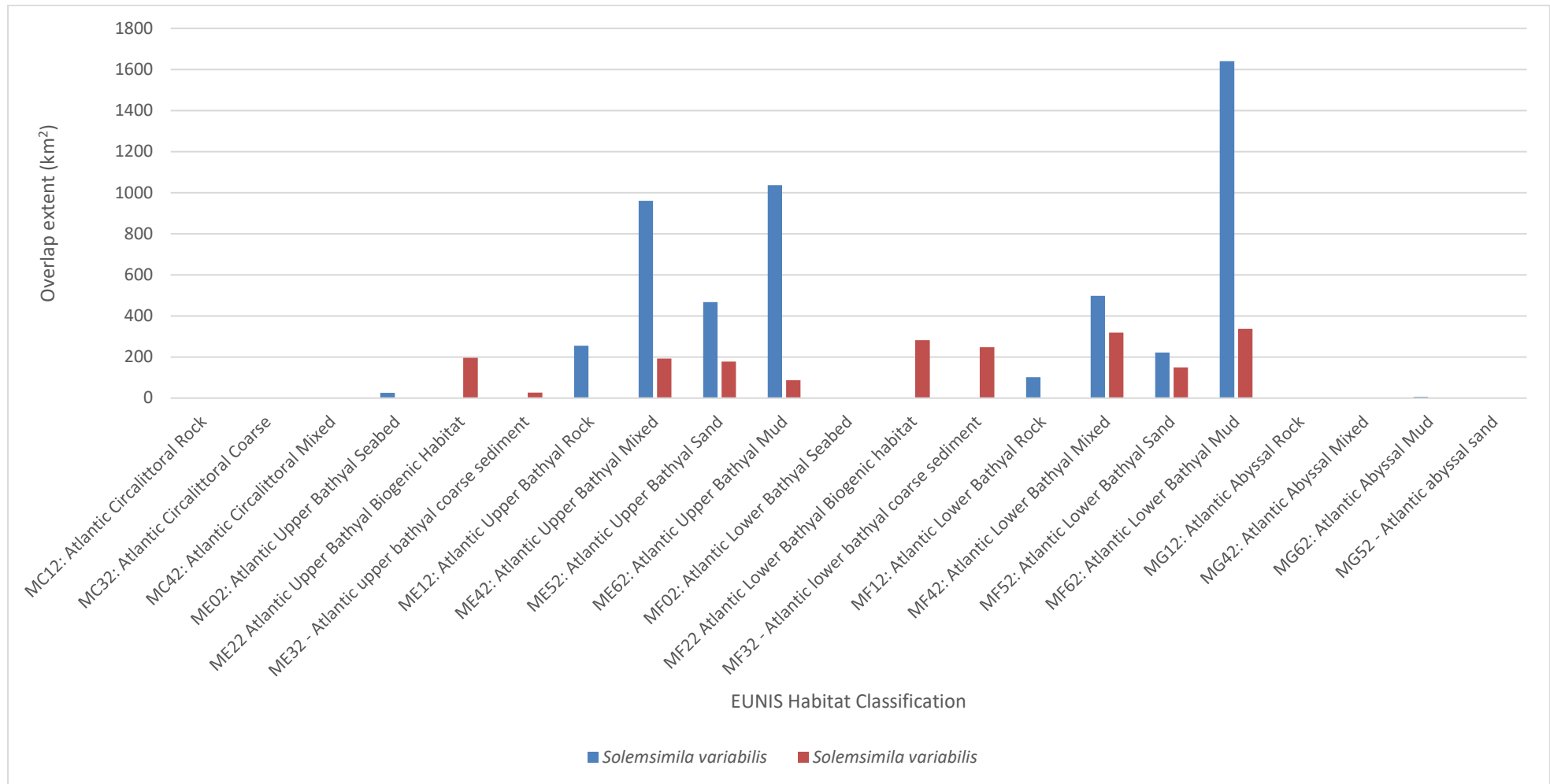
Figure 25. Spatial overlap of binary suitability map for *Solenosmilia variabilis* within Regions 3 (Red) and 11 (Blue) overlain on to iAtlantic EUNIS classification of the corresponding Region from iAtlantic milestone 12. To maximise axis eligibility, several EUNIS habitats for which there was no spatial overlap have been removed. Note that the spatial resolutions of the HSMs, input variables and EUNIS classifications differed between the regions, the impact of which is discussed in section 5.4.
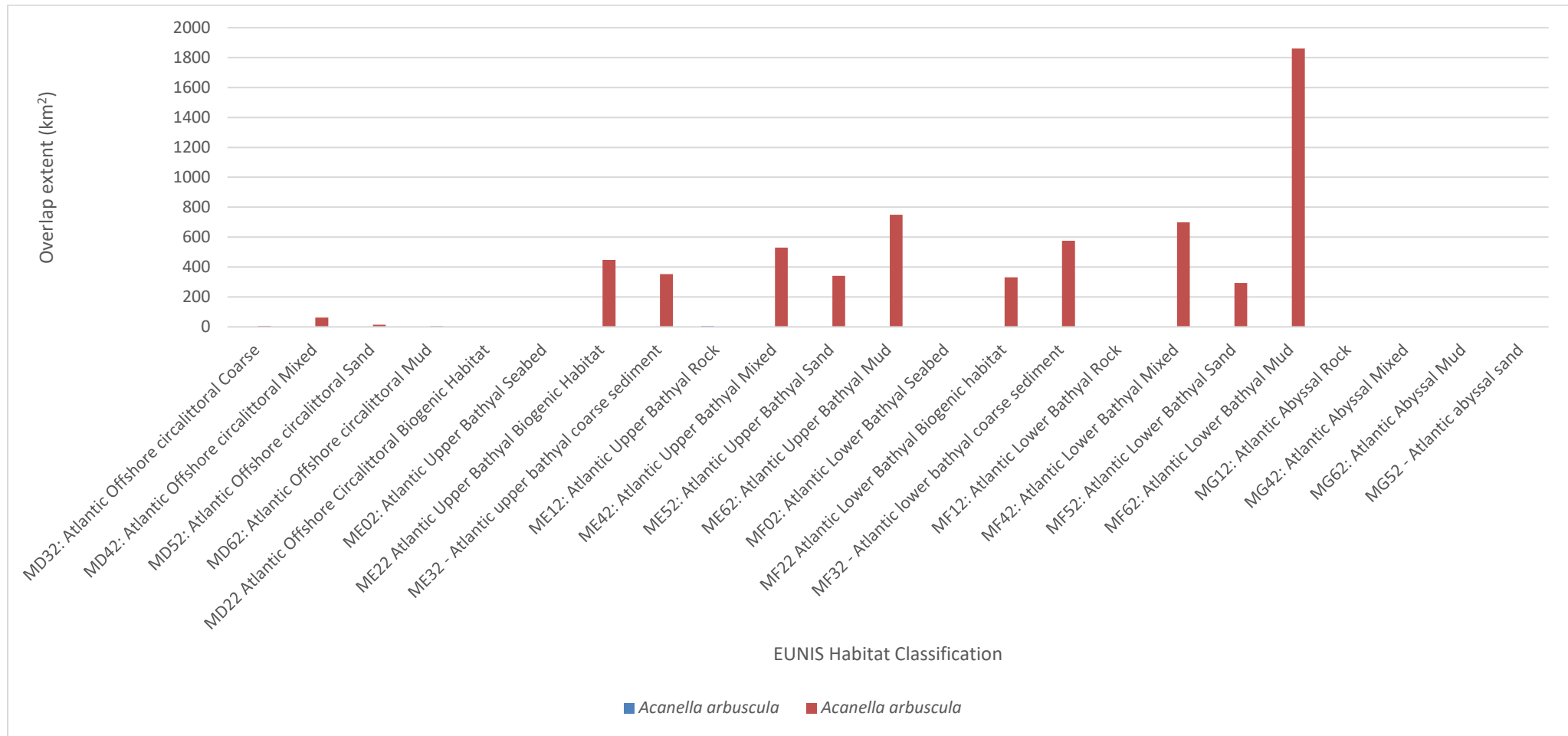
Figure 26. Spatial overlap of binary suitability map for *Acanella arbuscula* within Regions 6 (Blue) and 11 (Red) overlain on to iAtlantic EUNIS classification of the corresponding Region from iAtlantic milestone 12. To maximise axis eligibility, several EUNIS habitats for which there was no spatial overlap have been removed. Note that the spatial resolutions of the HSMs, input variables and EUNIS classifications differed between the regions, the impact of which is discussed in section 5.4.
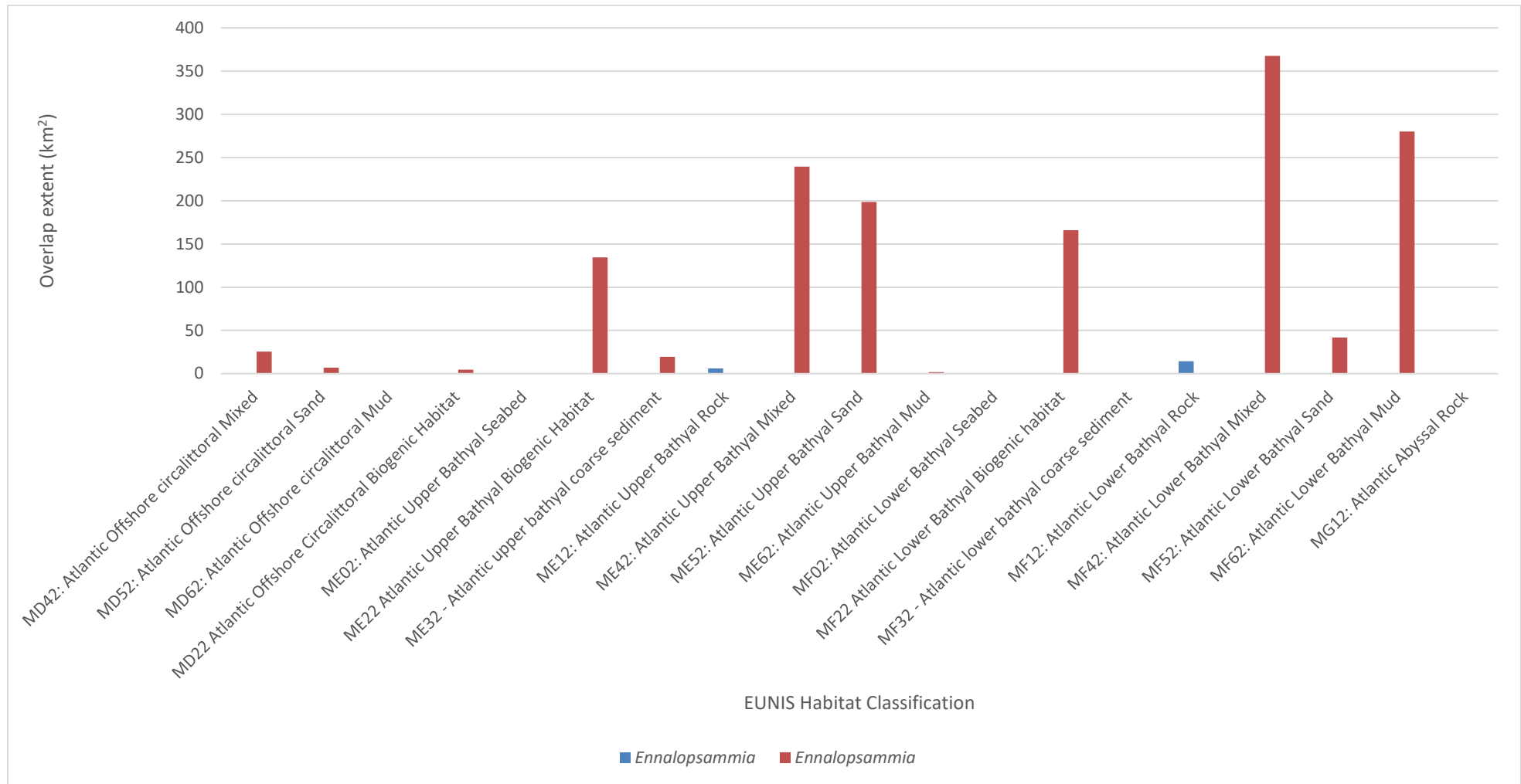
Figure 27. Spatial overlap of binary suitability map for *Enallopsammia rostrata* within Regions 6 (Blue) and 11 (Red) overlain on to iAtlantic EUNIS classification of the corresponding Region from iAtlantic milestone 12. To maximise axis eligibility, several EUNIS habitats for which there was no spatial overlap have been removed. Note that the spatial resolutions of the HSMs, input variables and EUNIS classifications differed between the regions, the impact of which is discussed in section 5.4.

Environmental predictors used in habitat suitability models

The iAtlantic basin and regional HSM considered 74 environmental predictors in total (Table 4). These predictors fell into several broad categories representing measures of terrain complexity, water mass properties, hydrodynamics, productivity, and anthropogenic impact (Table 4). Terrain derivatives were included in all models. Of the terrain derivatives used, slope was included in all models, followed by eastness, northness, rugosity and bathymetric positioning index (BPI) which were all included in at least five regional models (Table 4). Depth was also considered in the initial model selection but was omitted in several regions due to collinearity (Table 4). Bottom temperature was the most commonly included measure under the water mass property category and was included in all models apart from Regions 1 and 9 (Table 4). The second most frequently included measure of water mass properties was bottom salinity (Table 4). Hydrodynamic variables were only used at regional scales, and it was mean current speed that was most included (Table 4). Measures of productivity were not included in all models and varied across regions with particulate organic carbon (POC) flux and the depth of the mixed layer most used (Table 4).

High collinearity between depth and variables such as slope and temperature often led to one of these variables being omitted from final regional models (Table 4). Under these circumstances the colinear variables are equally likely to be contributing to influencing species' habitat distributions even when not identified in the final model outputs. For example, in Region 1 slope was omitted from models due to collinearity with depth. Consequently, when identifying environmental drivers of ecosystem spatial patterns both the identified variable and its covariates must be considered.

Environmental predictors identified as important

At the basin scale different combinations of environmental variables were identified by models as important predictors for deep-sea fishes and sharks, shrimps, scleractinian corals, sea pens and urchins (Table 2 and 4). Common among several of these groups was the importance of temperature, POC flux, depth, and measures of terrain complexity (slope or BPI) (Table 2 and 4). Temperature, measures of terrain complexity and productivity (POC flux, depth of mixed layer, primary productivity reaching the seabed) were also identified as important environmental predictors at regional scales (Table 2 and 4). Several regional models also included hydrodynamic variables (current speed, direction and kinetic energy), which were identified as important environmental predictors, the exception being some species from Region 10 (Table 2 and 4).

Environmental predictor importance and resolution of model input

The resolution at which environmental variables are input to models can influence their importance as predictors of suitable habitat because resolution determines the scale at which environmental variability can be quantified. If an environmental variable is added to the model at a resolution at which it cannot discern environmental heterogeneity at an ecologically relevant scale to the species being modelled, it will not have the ability to explain variance in the species' distribution patterns at that scale. This concept could explain why terrain variables are identified as the most important predictors in finer resolution models. This is because in order to match the resolution of the bathymetry data, oceanographic and hydrodynamic data have often been resampled and interpolated from much broader native resolutions (i.e. 5.3 km) and as such are unable to discern environmental heterogeneity at finer spatial scales, which the terrain variables can, resulting in terrain variables explaining greater variance in species' habitat distributions. As the extent of mapping increases and the resolution of the

input data for terrain and oceanographic/hydrodynamic variables becomes more comparable (i.e., Region 9) the influence of terrain is reduced because it conveys comparatively less relevant information in explaining species distributions at these scales than oceanographic/hydrodynamic variables (Tables 1, 2 and 4). Furthermore, at certain scales (e.g. basin scales) the inclusion of certain terrain variables does not make sense (e.g. eastness as a proxy to current regimes when both sides of the Atlantic east and west are included in the analysis).

Table 4. Environmental predictors used in habitat suitability models for the Atlantic basin and eight iAtlantic regions. Environmental predictors identified as important by modelling are denotated by a red cell with a cross; environmental predictors that were not found to be of importance are denoted by a green cell with a zero; environmental predictors removed due to collinearity are denoted by a blue cell with a star; environmental predictors not considered in the model are denoted by a grey cell with a dash.

Legend: X = red cell (important); O = green cell (not important); * = blue cell (removed due to collinearity); - = grey cell (not considered).

iAtlantic Region	Depth	Slope	BPI	TPI	Rugosity – Vector Ruggedness Measure (VRM)	Eastness	Northness	Aspect	Channel Network Base Level	Channel Network Distance	Valley Depth	Relative Slope Position	LS-Factor	Positive and Negative Openness	Wind Exposition Index	Roughness	Terrain Ruggedness Index (TRI)	Profile curvature	Planar curvature	Mean Curvature	Geomorphic Classes	Substrate class	Bottom temperature	Bottom temperature (SD)	Min bottom temperature	Max bottom temperature	Dispersal index for bottom temperature	Surface temperature	Bottom salinity	Bottom salinity (SD)	Min bottom salinity	Max bottom salinity	Surface salinity	Nitrate	Phosphate	Ph	Silicate	Iron	Aragonite saturation	Calcite saturation	Dissolved O₂	Dispersal Index for O₂	Oxygen Saturation	Oxygen Utilization	Seawater Chemistry	Energy at the seabed from currents	Mean Kinetic Energy Dissipation – Water column (2009)	Mean Kinetic Energy Dissipation – Bottom-most layer	Bottom current speed	Bottom current speed (SD)	Bottom Zonal (U) velocity	Minimum Annual Vertical Velocity	Maximum Annual Vertical Velocity	Bottom Meridional (V) velocity	Minimum Horizontal (V) Current Speed	Max Horizontal (V) Current Speed	Surface current speed	Current Direction (mean)	Current Direction (SD)	Mean Internal Wave Slope Criticality	POC Flux (epc)	Primary productivity reaching the seabed	Dispersal Index for Primary productivity reaching the seabed	Spring Primary Production	Summer Primary Production	Annual Primary Production	Chlorophyll	Annual Chlorophyll a	Spring Chlorophyll a	Fall Chlorophyll a	Phytoplankton	Mixed layer depth	Mixed layer depth (SD)	Bottom Fishing Effort
1	*	O	X	-	X	O	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-
2	*	O	-	*	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	O	-	*	-	-	-	*	*	-	*	*	-	O	O	-	-	-	O	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	*	-	-	-	*	-	-	-
3	*	X	X	-	*	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	-	-	-	*	-	-	-	*	-	*	*	-	*	-	*	-	*	-	O	O	*	X	-	-	O	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-
4 (47 variables)	-	X	O	-	X	O	O	-	X	O	X	O	X	X	O	-	-	-	-	-	-	-	O	-	-	-	-	X	X	-	-	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	-	-	-	-	O	-	-	-	-	-	O	O	O	-	O	O	O	-	-	O
6	O	X	-	O	X	O	O	-	-	-	-	O	O	-	X	-	-	-	-	-	O	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	*	X	-	X	-	-	-	-	*	*	*	*	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	X	X	-	O	-	O	O	-	-	-	-	*	O	-	*	-	-	-	-	-	*	-	*	*	-	*	-	O	*	*	*	*	*	*	*	-	*	-	-	-	-	-	-	-	-	-	-	-	*	-	*	-	-	-	X	X	-	-	-	-	X	X	X	-	-	-
10	-	X	O…	O	O	O	-	-	-	-	-	-	O	O	X	X	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	X	X	X	-
11	O	O	O	O	O	O	O	-	-	-	-	-	O	X	X	-	-	-	-	-	-	O	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	O	O	-	-	-	-	-	-	X	X	X	-
Basin: Sea pens	O	O	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Basin: Deep-water shrimps	X	X	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	*	-	*	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	-	-	-	-	-
Basin: Scleractinian coral	*	X	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	*	-	X	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Basin: Octocorals	*	X	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	X	-	*	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Basin: Sea-urchins	O	O	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	O	-	*	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Basin: Deep-water fish and sharks	X	O	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	*	-	*	*	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-

Species responses to environmental predictors

Despite the same environmental variables being identified as important predictors among modelled groups at the basin and regional scales (Table 2 and 4), the responses to the environmental variables varied for many species.

At the basin scale most species exhibited unimodal responses to seabed temperature and when included in regional models unimodal or positive responses to current speed (Figures 28–31). The response to terrain derivatives varied with scale but generally benthic species exhibited positive responses to measures of terrain complexity at spatial scales where ecologically relevant features were identified (BPI, curvature, slope) (Figure 28). The responses of pelagic species to terrain were more variable. At regional scales species responses to measures of productivity (POC flux, primary production reaching the seabed, mixed layer thickness) varied, and often exhibited multiple peaks (as shown in D2.5, Figure 53–55, for example).

Variable response curves between species likely reflect the different niche requirements of the species and their occupancy along environmental gradients (Ashcroft et al., 2016). The shape of response curve may also vary across scales because at larger spatial scales a wider range of environmental conditions is likely to be encountered, including those either side of the species tolerance so that a unimodal response is observed. On the other hand, where only a small area is modelled it is less likely that the full environmental range of the species has been captured so that the response curve may resemble an upward slope or if the variable in question is irrelevant at that scale a flat line. Even though the curves may look different, inspection can reveal similar trends over the shared environmental range that is represented by both response curves enabling comparisons to be made.

Where the same species are modelled at both the basin and regional scales it provides an opportunity to assess how species respond to environmental variables across spatial scales. In iAtlantic, the stony coral*, Desmophyllum pertusum* (*Lophelia pertusa*) was modelled at the basin scale and in Regions 1, 2, 3 and 11, each at varying spatial scales (5 m, 222 m, ~1.1 km and ~93 m, respectively). Review of species response curves indicates that across multiple scales, *D. pertusum* exhibits an overall positive response to increasing BPI except when modelled at 1.1 km with a neighbourhood of ~ 5.5 km where only a weakly positive or no response was observed (Region 3) or at the basin scale where variable responses were observed across models with RF showing the strongest unimodal response (Figure 28). The overall positive response of *D. pertusum* across scales reflects that the species is associated with complex terrain. BPI at neighbourhoods of 22 and 75 km (Region 3 and basin modelling, respectively) likely captures broad scale terrain variability that highlights large geomorphological features such as seamounts and canyons, both of which are associated with CWCs. On the other hand, within Region 1, BPI at neighbourhoods of 15 m captures smaller features such as slopes, ridges, and depressions which were identified as high suitability habitat for *D. pertusum*. The lack of response between *D. pertusum* and BPI at 5.5 km in Region 3 could indicate that at this scale, terrain variability is not as important a driver as terrain complexity captured by BPI at the other neighbourhoods. In addition to BPI, current speed was modelled across scales for *D. pertusum,* which exhibited an overall positive response with increasing current speed across scales (Region 3) until 0.06 ms^{-1} (Region 11).

The stony coral, *Madrepora oculata* was modelled at the basin scale and in Regions 2, 3 and 11, each at varying scales (222 m, ~1.1 km and ~ 93 m, respectively) (Figure 30). *M. oculata* exhibited a similar unimodal response to temperature as *D. pertusum* when modelled with temperature data interpolated from native resolutions of > 25 km with an optimal peak between 8 – 12 °C (Figure 29). On the other

hand, *M. oculata* exhibited variable responses to temperature when modelled with temperature data interpolated from native resolutions of ~1.1 km in Region 3 (Figure 30). GAM produced an overall positive response curve, while MaxEnt modelled a steep positive incline between 4–6 °C that then plateaued to then rise steadily to 14 °C. The Maxent output is more consistent with the responses observed from model outputs at broader resolutions because it appears to also capture a lower temperature limit (Figure 29). The lack of a unimodal response of *M. oculata* to temperature in Region 3 may reflect inadequate sampling of areas of different temperatures as modelling was constrained to within 2,000 m water depth. Additionally, algorithms like GAM have the tendency to extend response curves where data are missing, resulting in continued trends in the direction of the last data point.

The stony coral, *Solenosmilia variabilis* modelled at the basin scale and in regions 2, 3 and 11, each at varying scales (222 m, ~1.1 km and ~93 m, respectively), exhibited a similar response to temperature across scales. A unimodal response was observed where temperature was interpolated from broader spatial scales with an optimal peak between 8–12 °C for Region 11 (native temperature resolution 25 km) and 5–10 °C at the basin scale (native temperature resolution 55 km). No response was observed at the finer spatial scale in Region 3 (native temperature resolution 5.5 Km) (Figure 30).
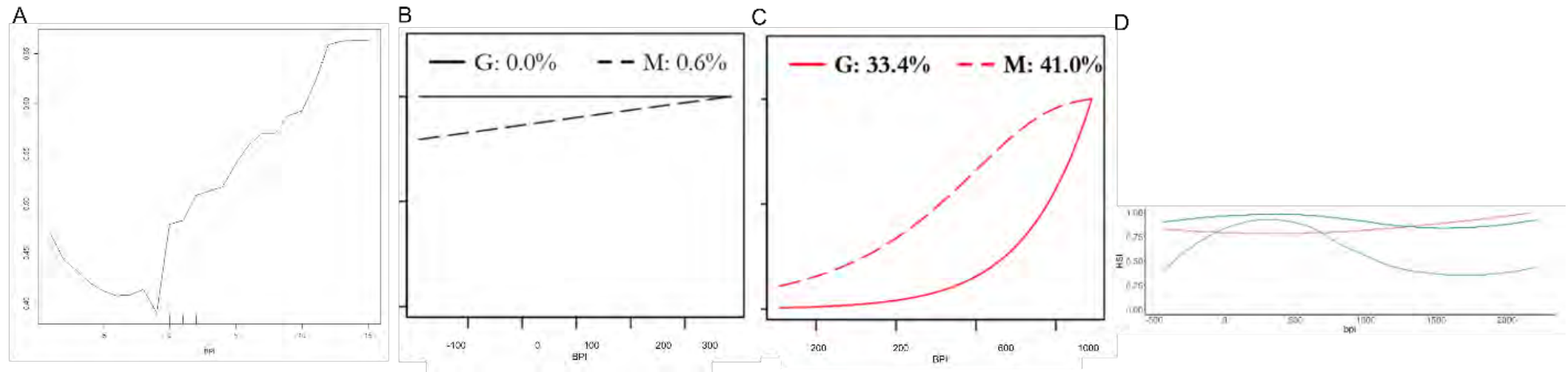
Figure 28. A) Region 1, partial dependence plots from the '2000–2011–2020' random forest model showing the likelihood of presence of *D. pertusum* in relation to bathymetric positioning index (BPI) ~ 15 m neighbourhood; B) Region 3, GAM (Solid line) and MaxEnt (Dashed line) response curves for BPI ~ 5.5 Km neighbourhood; C) Region 3, GAM (Solid line) and Maxnt (Dashed line) response curves for BPI ~ 22 Km neighbourhood; D) Basin model GAM (Red line), MaxEnt (Green line) and RF (Blue line) response curves for BPI ~ 75 Km.
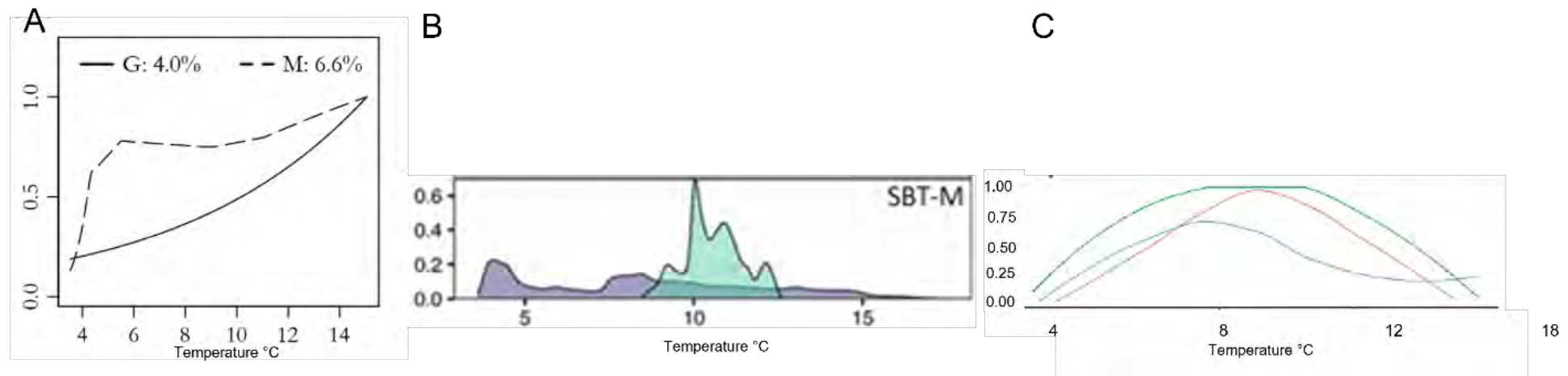
Figure 29. A) Region 3, GAM (Solid line) and MaxEnt (Dashed line) response curves for *M oculata* and temperature °C; B) Region 11, probability densities of temperature °C for the ensemble models fitted for *M oculata*. Grey area, background distribution; green area, presence locations; Basin model GAM (Red line), MaxEnt (Green line) and RF (Blue line) response curves for temperature °C.
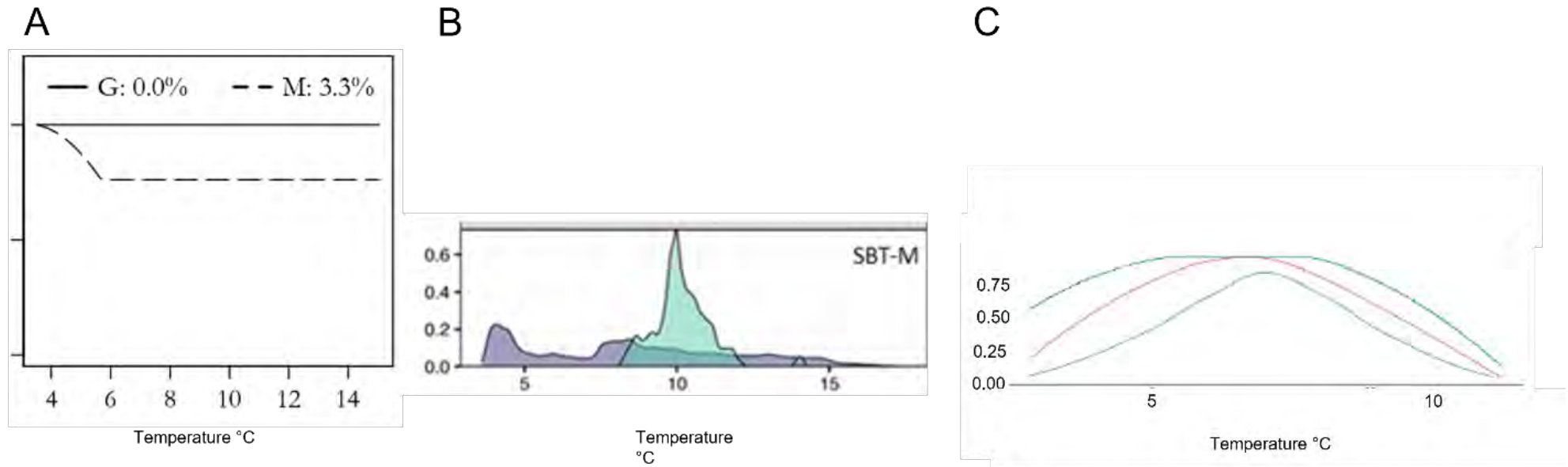
Figure 30. A) Region 3, GAM (Solid line) and MaxEnt (Dashed line) response curves for *Solenosmilia variabilis* and temperature °C; B) Region 11, probability densities of temperature °C for the ensemble models fitted for *S. variabilis*. Grey area, background distribution; green area, presence locations; C) Basin model GAM (Red line), MaxEnt (Green line) and RF (Blue line) response curves for temperature °C.

5. Discussion

Environmental drivers of ecosystem spatial patterns in the Atlantic at varying scales

The results of the analysis of the iAtlantic mapping outputs provides an opportunity to develop a more holistic viewpoint of environmental drivers of ecosystem spatial patterns across the Atlantic at varying spatial scales. By comparing habitat suitability maps derived from different resolution data sets, we have been able to assess comparative accuracy of habitat suitability maps and identify which key environmental drivers can be detected when incorporating data at varying spatial resolutions.

Spatial patterns in ecosystems are driven by a combination of patterns in environmental conditions and patterns in species' habitat distributions. The latter, in addition to being determined by the species' environmental niches, are also driven by ecological and evolutionary processes acting over geological time scales. Globally, temperature and productivity are considered important drivers of species distribution based on the theory of the species – energy hypothesis (Currie et al., 1991; Tittensor et al., 2011; Wooley et al., 2015). The species – energy hypothesis proposes that variation in species diversity is driven by geographical variation in available energy. In the deep sea, energy is available as either thermal (kinetic) or chemical (potential) energy, which relate to temperature and productivity (i.e., particulate organic carbon flux), respectively (Wolley et al., 2015). Both temperature and proxies of productivity were identified as important environmental drivers across spatial scales in iAtlantic studies (Table 2 and 4). Variation in temperature and productivity have been proposed as driving latitudinal gradients in marine diversity (Wolley et al., 2015). Temperature and productivity also decrease with depth and have been attributed with driving patterns of decreased marine diversity with depth (Lambshead et al., 2000; Rex et al., 2005; Stuart and Rex, 2009; O'Hara and Tittensor, 2010; Brault et al., 2013; Yasuhara and Danovaro, 2016; Hernández-Ávila et al., 2018).

Temperature poses a physiological constraint on species metabolism, fecundity and distribution (Brown and Thatje et al., 2014; Gori et al., 2016; Chapron et al., 2021). The influence of temperature on species' physiological constraints can be seen in the unimodal response curves observed for several iAtlantic species that exhibit a specific tolerance range over which that species occurs (Figures 29 and 30). This response is more evident at broad spatial scales, where HSMs cover larger spatial extents and the temperature range encountered is larger (Figures 29 and 30) allowing a better cover of the thermal niche of the species which reduces the risk of extrapolating outside the analysed range of the species. Temperature is a key characteristic of water masses that exhibit strong vertical gradients, and as a result, depth is co-varying with multiple variables that capture water mass properties (Temperature, salinity, pressure, aragonite, pH) (Puerta et al., 2020). The covariance of depth with water mass properties can make disentangling the exact environmental (physiological) drivers of species' habitat distributions difficult, especially working at regional or local scale when usually depth is the main driver of temperature changes. For several iAtlantic regions high collinearity was observed among variables that capture water mass properties and depth (Table 4). At basin scale, the same depths can have different temperatures (at different latitudes) and correlation between depth and temperature is low, but the inclusion of other correlated variables such as pH also causes multicollinearity problems. The difficulty of collinearity was overcome for Region 3 (Central mid-Atlantic Ridge) by using the variable 'water chemistry' that represented a principal component derived from multiple water mass properties on which principal component analysis was run. The 'water chemistry' variable was able to dissociate the influence of depth and was identified as a key environmental predictor of habitat suitability. In other studies, the combination of water mass properties that characterise a water mass 'envelope' has been

found to be an important exploratory variable of species' habitat distribution at broad and fine (hundreds of meters) spatial scales (Puerta et al., 2020; 2022). Water masses have been linked to present-day and past CWC habitat distribution across the Atlantic (De Mol et al., 2005; Dullo et al., 2008; Arantes et al., 2009; White and Dorschel, 2010; Henry et al., 2014; Pearman et al., 2022). For example, in the North-East Atlantic CWC occurrence has been linked to Mediterranean Outflow Water (De Mol et al., 2005; Dullo et al., 2008; White and Dorschel, 2010; Henry et al., 2014) and in the South-West Atlantic CWC occurrence is linked to Antarctic Intermediate Water (Arantes et al., 2009; Henry et al., 2014; Pearman et al., 2022). In Region 3 the strong bathymetric zonation of CWCs is attributed to vertical turnover of species in relation to the regional oxygen minimum and is associated with the stratification of water masses captured by the variable 'seawater chemistry' (Taranto et al., 2023). Examples of bathymetric zonation are reported across the deep sea literature (Rex, 1973; 1983; Howell et al., 2002; Carney, 2005; Olabarria, 2005; Pearman et al., 2023) and have been attributed to the different properties of water masses (Levin et al., 2001; Conlan et al., 2015; Roberts et al., 2021; Puerta et al., 2022; Pearman et al., 2023) that can represent physiological boundaries to species and affect dispersal and connectivity (Choo et al., 2020). Additionally, adjoining water masses can form density gradients that can facilitate the aggregation of food or hydrodynamic phenomena such as internal tides which are linked to species distributions (Pearman et al., 2020; 2023).

The environmental variables POC flux, depth of the mixed layer and primary productivity reaching the seabed were identified by iAtlantic as key predictors of species' habitat (Table 2 and 4) and are proxies of primary production reaching the benthic environment, and the strength of pelagic–benthic coupling. Proxies of productivity represent ecological gradients in productivity and highlight areas with high production regimes. At finer spatial scales these variables capture variability in available food quantity and quality that is often facilitated by terrain modified hydrodynamics (White et al., 2005; Allen and Durrieu de Madron, 2009; Wilson et al., 2015; Demopoulos et al., 2017 Campanyà-Llovet et al., 2018). The amount of primary productivity reaching the seabed was identified as an important environmental predictor of CWCs in Region 2 (Rockall Trough to PAP). In Region 3 (Central mid-Atlantic Ridge) different primary production regimes on either side of the Mid Atlantic Ridge and the resulting latitudinal gradient in productivity were attributed to driving species turnover and latitudinal distribution patterns in the region (Taranto et al., 2023). HSM in Region 3 identified POC flux as an important environmental variable for the CWCs, *Desmophyllum pertusum*, *Madrepora oculata* and *Leiopathes* cf. *expansa* which was postulated as driving the species northern distribution that coincides with the more productive waters north of the Mid Atlantic Ridge and that the enhanced carbon fluxes may enable these species to inhabit deeper hard substrates than in the South (Taranto et al., 2023). Regional mapping along the Brazilian continental Shelf and Slope (Region 10) highlighted the importance of temperature, salinity and depth of the mixed layer which were attributed to capturing proxies for oceanographic processes that take place at the slope and generate trophic-wide productivity (Briscoe et al., 2016). Modelling from Region 10 highlighted the importance of annual variability in temperature and salinity (Table 2 and 4) from which the importance of water mass mixing zones of the Brazil – Malvinas Confluence and regional upwelling at the Argentinean shelf break for pelagic species was inferred. These oceanographic processes promote increased productivity which supports a complex pelagic food chain (Brandini et al., 2000; Acha et al., 2004; Piola et al., 2018) and important feeding habitats for the migratory albacore (*T. alalunga*), the yellowfin tuna (*T. albacares*) and the blue shark (*P. glauca*) and the non-migratory porbeagle shark. In Region 11 (Vitória-Trindade Seamount Chain), the influence of water mass mixing zones and aggregation of particulate organic matter (POM) along water mass density gradients was

attributed to driving CWC habitat distributions in the Campos Basin. Modelling from Region 11 also highlighted the importance of annual variability, including in current direction, indicating that CWCs favour dynamic environments with increased hydrodynamics.

At finer spatial scale (<250 m), iAtlantic regional HSMs from Regions 1 (Subpolar Mid-Atlantic Ridge, off Iceland), 6 (Eastern Tropical North Atlantic, Cape Verde) and 9 (Benguela Current, Walvis Ridge to South Africa) did not incorporate measures of productivity (Table 2 and 4). However, the interpretation of their results supported the hypothesis of topographically enhanced hydrodynamics facilitating increased productivity or benthic -pelagic coupling to drive species' habitat distributions. For example, high resolution modelling of *D. pertusum* in the Lónsdjúp area (Region 1) highlighted suitable habitat in areas of complex morphology (i.e., mounds and ridges) on the Shelf break and upper Slope that coincide with intensified currents and terrain-modified hydrodynamics increasing the quality and quantity of POM delivered to the corals (Thiem et al., 2006; Davies et al., 2009; Duineveld et al., 2012; Soetaert et al., 2016). Similar examples of CWCs being sustained by hydrodynamically enhanced food supply mechanisms in association with complex terrain are reported across the literature (Davies et al., 2009; Mienis et al., 2009; Rengstorf et al., 2013; Mohn et al., 2014; Soetaert et al., 2016; Demopoulos et al., 2017). In addition to modifying hydrodynamics, terrain complexity is an important proxy of geomorphology, habitat heterogeneity and substrate type (Wilson et al., 2007) all of which are known to influence species' habitat distributions (Levin et al., 2001; Robert et al., 2015; Pearman et al., 2020).

iAtlantic basin modelling shows that suitable habitat for CWCs is predicted across the Atlantic with preference for ocean ridges, isolated seamounts and surrounding oceanic islands (Table 2). Several iAtlantic regions (Regions 1, 3, 6 and 9) modelled CWC habitat suitability over ocean ridge features and oceanic islands where CWCs were associated with local topographic features (Table 2 and Figures 2-6). Terrain derivatives were identified as important environmental predictors of species distribution, especially CWCs as they capture indirect environmental drivers of CWC distribution relating to seabed characteristics (geomorphology and substratum characteristics) and local hydrodynamics (Wilson et al., 2007; Hall et al., 2017; Puig et al., 2017). Bathymetry derived terrain variables such as slope, BPI and ruggedness act as proxies of terrain complexity. High terrain complexity generates seabed heterogeneity in substratum characteristics (Huvenne et al., 2011; Huvenne and Davies, 2014) and current exposure (Ismail et al., 2015). CWCs are preferential to high terrain complexity (Howell et al., 2011, Gori et al., 2013; Rengstorf et al., 2013; Fabri et al., 2017; van den Beld et al., 2017; Pearman et al., 2020) and topographic highs that enable CWCs to exploit local current regimes to increase food encounter rates (Mohn et al., 2014; Fabri et al., 2017; Lo Iacono et al., 2020). Topographic highs and steep slopes are also associated with hard substratum (Stewart et al., 2014; Carter et al., 2018), which is a prerequisite for settlement for many of the CWCs in the iAtlantic studies (Baker et al., 2012). On the other hand, CWCs species such as *Acanella arbuscula* colonise soft substratum (Hansteen et al., 2014) and results from Region 6 show that this species is associated with flat to gentle sloping terrain (0–10°) and was observed from mixed soft substrata.

Terrain derivatives were identified as important environmental predictors in regional models apart from Regions 10 and 11 that mapped wider extents and thereafter at the basin scale. At the broader basin scale, spatial variability in terrain captures large geomorphological features such as canyons, oceanic ridges and seamounts that are features associated with CWCs (FAO, 2009; Davies and Guinotte, 2011; Victorero et al., 2018; Pearman et al., 2020; Price et al., 2020). At finer scales, captured by regional models using higher resolution bathymetry data, terrain derivatives capture variation superimposed on these large geomorphological features, such as ridges and depressions that

determine the distribution of CWCs across the large geomorphological feature. For example, in Region 1 positive BPI values, indicated steep ridge features such as mounds or ridges (BPI value of ~ +5) and negative BPI, indicated depressions relative to the steep positive ridge features (BPI value ~ -10 − -5) both of which were associated with higher habitat suitability of *D. pertusum*. Furthermore, models in Region 4 (NW Atlantic, Gully Canyon) found that terrain derivatives identified steep and rugged areas along the upper continental shelf at scales of km and tens of km and at scales of hundreds of meters identified finer resolution vertical relief, such as ridges, gullies and moraines (Sowers et al., 2020). The iAtlantic results and response curves indicate that the incorporation of terrain derivatives derived from bathymetry at resolutions < 1.1 km into the regional models mostly enabled finer scale variability in terrain to be ascertained (ridges and mounds). However, when incorporated at the basin scale at ~ 3 km resolution the ability to discern finer scale variability is reduced, and so too the explanatory power of these variables with regards to CWC distributions at relevant spatial scales. These results also exemplify the influence of the data resolution on variable importance. The influence of data resolution can also be seen when comparing basin and regional HSM that consistently show regional predictions falling within areas predicted as high suitability by basin models (Figures 2–9). This means that the extent of predicted suitable habitat is less in regional models than in the basin-wide models (Figures 2–9). This likely reflects spatial variability in species distribution identified by regional models across the broad-scale features identified by the basin mapping and that certain region (i.e. Regions 3 and 6) constrained models to 2,000 m water depth. In fact, *basin scale model outputs should be interpreted mainly as broad suitable habitat areas which rarely will be completely occupied* (depending on local scale factor not included in the models such as terrain variables, sediment type, currents, etc) whereas regional scale outputs are a better proxy to a map with the probability of presence of the species.

Substrate type is a known driver of sessile benthic species distribution (e.g. Roberts et al., 2008; Howell et al., 2010) due to their requirement to attach themselves within or on to particular substrate types (Baker et al., 2012). *Substrate layers at ecologically meaningful resolutions are rarely available for HSM*. In Regions 10 and 11, substrate classes were included but interpolated from a native resolution of 25 km, which is unlikely to capture the spatial heterogeneity in substrate driving species distributions. In a study of megabenthic assemblages across banks and seamounts of the central North Atlantic, substrate was found to be an important driver of species distributions at fine scales and water masses were important across broad scale bathymetric gradients (Puerta et al., 2022). It is likely that a similar scale-dependent scenario drives spatial patterns of ecosystems in the Atlantic. However, until there are environmental substrate data to incorporate into regional mapping this cannot be tested, and our better option is to use proxies such as terrain variables.

The results from iAtlantic indicate that spatial patterns in Atlantic ecosystems are driven by multiple environmental factors that interact at various spatial scales to generate environmental gradients along which species differentiate according to their niche requirements. At the tempo-spatial scales studied in iAtlantic, results indicate that the *interplay between physiological constraints applied by temperature coupled with hydrodynamically influenced geographic variation of POC and available colonisation substrate represent the key environmental drivers of ecosystem spatial patterns*. For CWC VMEs specifically, modelling results indicate CWC VME distribution is driven at broad scales by temperature tolerances and is associated with both broad and fine scale complex geomorphology on the shelf- break and upper slope environments in areas with high food supply, enhanced by terrain modified hydrodynamics or water mass characteristics that facilitate the concentration of POM (Davies and Guinotte 2011; Morato et al., 2020; Tong et al., 2022).

The modelling results are corroborated by the basin wide habitat classification produced as part of the iAtlantic deliverable D2.1. Superimposing HSMs onto the basin wide habitat map shows that CWCs are preferentially associated with seabed areas characterised by key environmental predictors for the species of the region (Table 3 and Figures 10–12). For example, CWC habitats of Region 11 coincided with SBA IV (Table 3 and Figure 12) which is characterised by strong currents and high seasonal variability which were also highlighted in HSM as key drivers of CWC habitats in that region (Table 2 and 4). Likewise, CWC habitats for Regions 3, 6 and 9 occur in areas of complex terrain associated with oceanic islands and ridges (Table 2 and Figures 2–6) which also characterise SBA II (Table 3 and Figures 10–11). Consequently, these results show that *where biological data is absent, iAtlantic seabed area classes could be used as surrogates of likely occurrence of CWC VMEs at broad spatial scales and so support management and target areas for sampling where biological data is scarce or has not yet been collected*.

Similarly, overlying HSM outputs onto EUNIS habitat classifications shows that EUNIS classifications can provide an indication of VMEs, but accuracy depends on the type and resolution of underlying data used in models. The resolution of EUNIS input data offers little explanatory power at finer scales as it cannot resolve fine-scale terrain and substrate heterogeneity. Instead, it is more useful in capturing broad-scale patterns of VME distributions that are driven by depth and broad-scale geomorphology. The utilisation of the iAtlantic outputs in this hierarchal manner is extremely powerful for deep-sea environments where limited scientific knowledge is identified as a primary limitation for assessing anthropogenic impacts (Ramirez-Llodra et al., 2010; Mengerink et al., 2014) and applying effective marine spatial management.

iAtlantic has contributed to our understanding of deep-sea ecosystems by facilitating the collation of habitat and species distribution modelling to produce a series of maps at various spatial scales covering the 12 iAtlantic regions and Atlantic Basin (Figure 1). The provision of these habitat and species distribution and confidence maps of key species that represent ecosystems, including VMEs is key to marine spatial planning of the Atlantic (FAO, 2009). Marine spatial planning in turn supports the application of ecosystem-based management and area-based conservation strategies, in line with the UN sustainable agenda goal 14 'Life Below Water' (UNGA, 2015). With increasing anthropogenic pressure of the deep sea including planned deep-sea mining in the Atlantic (ISA, 2021) it is paramount to provide baselines of knowledge (i.e., habitat and species distribution maps) prior to impact from which to monitor change. Equally, fishing is a current pressure exerted on deep-sea environments and there is international and increasing national legislation to identify and map VMEs protected on the high seas under the United Nations General Assembly resolutions (UNGA, 2006, 2009; FAO, 2009). iAtlantic mapping of CWC VME indicator taxa has increased our baseline knowledge of where these VMEs are likely to occur in previously little sampled locations (i.e., Cape Verde and Walvis Ridge). Additionally, by demonstrating the link between CWC VME taxa distribution and broader-scale basin wide seabed areas, iAtlantic exemplifies the ability to use such classes as indicators of where VME or other ecosystems of interest may occur and thus facilitate further surveying and monitoring or, management where biological data is not available.

Strength of integrating iAtlantic studies across scales

The iAtlantic HSM that underpins this deliverable focused on commercially important and VME indicator species (Table 1) with a prevalence for CWCs that constitute key species of several VMEs. As a result of this bias, the results in our study provide most insight into the environmental drivers of VMEs

across the Atlantic. However, since these ecosystems are deemed most vulnerable, understanding the environmental drivers of their distribution could be argued a priority so that iAtlantic brings important knowledge of these ecosystems. The increased knowledge is further progressed by the integrated approach of iAtlantic which has enabled greater insight into the drivers of spatial patterns of ecosystems in the Atlantic across spatial scales than would have been possible from single studies. Review of cross regional and scale studies has enabled the scale at which environmental drivers operate to be elucidated and the consequence of building models over varying spatial extents from environmental variables interpolated from different native spatial resolutions to be assessed, which is fundamental to better understanding mechanisms and sources of uncertainty in HSM (Figure 31).
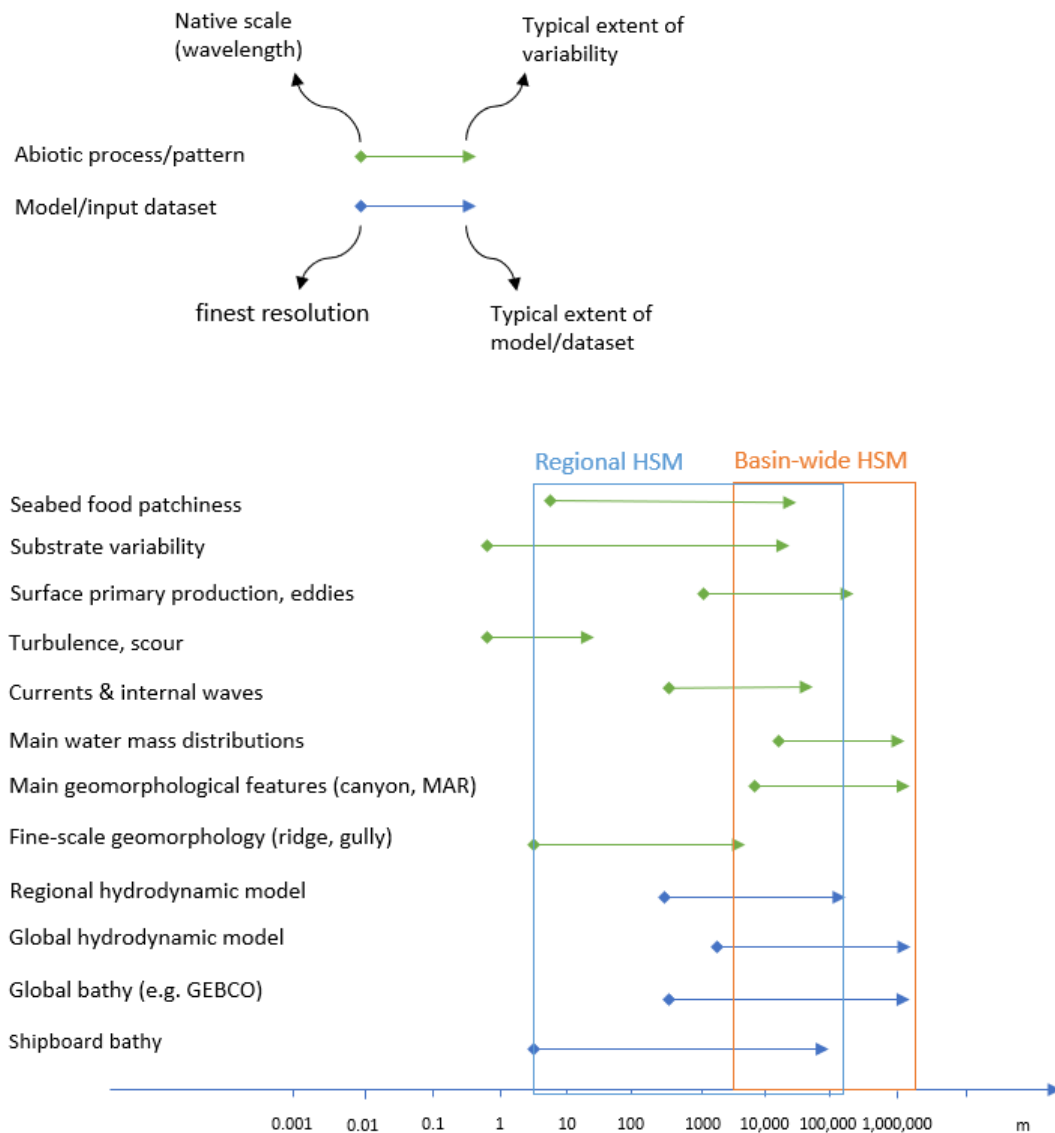
Figure 31. Conceptual schematic illustrating native scale and extent of example abiotic processes influencing ecosystem spatial patterns (denoted by green lines) against the finest resolution and typical extent of model input data representing these processes (dark blue lines) incorporated into habitat suitability models (HSMs). The light blue box encloses the scales of relevance of most regional HSMs, ranging from their minimal resolution (left boundary) to their maximal extent (right-hand boundary). The orange box similarly encloses the scales of relevance of most basin-wide habitat suitability models.

The comparison of multiple case studies has enabled knowledge gaps to be identified. For example, the utilisation of 74 environmental variables highlights the inconsistency of predictors incorporated into

HSM but also reflects variable data availability across the Atlantic. Environmental predictors such as water mass properties, hydrodynamics and productivity metrics are not consistently available at comparative resolutions to bathymetry data from which terrain derivatives are calculated. Instead, low resolution data are routinely interpolated to match the resolution of the bathymetry or excluded from models. Additionally, regional variability in surveying generates regional bias in the number of ground-truth locations for models influencing the resolution and confidence of data outputs. This can clearly be seen in EUNIS habitat classification confidence scores for Central and Southern Atlantic regions compared to the North East Atlantic (iAtlantic Milestone 12) and the low number of biological records available for HSM in Region 9 on the Walvis Ridge. However, these maps still provide valuable baselines and tools from which to plan future survey work, especially in the less studied central and south Atlantic.

Additionally, by comparing models built from data interpolated from various native resolution data we have shown that the relative importance of the environmental predictor depends on the native resolution from which variables are interpolated and the spatial extent of the model both of which influence whether the environmental variable can adequately capture ecologically relevant environmental heterogeneity. Comparison of HSM results shows that water mass properties and terrain are important at the basin scale. As the resolution of mapping increases and extent decreases, productivity, hydrodynamics and water mass properties become important until scales at which environmental variables are incorporated into models at native resolutions <5 km from which point terrain and hydrodynamics become important. However, it must be noted that metrics of productivity and water mass properties are not available at such fine native resolutions resulting in bias and the variable incorporated at the highest resolution becoming the most important.

The overarching importance of temperature corroborates findings from other iAtlantic work packages that found temperature to be key in driving changes in fish composition (work package 3; see e.g. Perez & Sant'Ana (2023)) and that increasing temperature increases basal respiration rates and reduces carbon processing of infauna in soft sediment assemblages (work package 4, de Jonge et al. (in review)[2]). This has important implications for future climate scenarios, as demonstrated in iAtlantic deliverable D2.2 (see below).

The updated maps from work package 2 provide updated spatial data which has supported regional prioritisation of spatial management areas in the Azores and South Africa under iAtlantic work package 5.

Looking forward HSM can support outputs from Atlantic work package 1 by providing distribution maps of species for which genomic connectivity studies were undertaken by relating species distribution across the Atlantic to genetic structure and/or areas of hybridisation for VME taxa such as *Desmophyllum pertusum* and *Madrepora oculata* which will better identify areas for prioritisation for protection and where best to place networks of marine protection areas.

Future directions

Due to the influence that data resolution has on HSM, future research should focus on increased sampling across the Atlantic deep- and open- ocean at ecologically relevant resolutions. Environmental data layers of high-resolution oceanography, hydrodynamic and productivity measures (and their

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- [2] de Jonge, D., Smith, A., & Sweetman, A.K. Changes to upper-ocean ecosystems may directly impact abyssal scavenger communities. In review to *Limnology and Oceanography*.

derivatives that quantify their short-term variability) comparable to those available for bathymetry and terrain derivatives would likely improve model performance and our understanding of the interaction of these environmental variables at comparative scales. In particular, iAtlantic results indicate the importance of POC input, especially measures of POC reaching the seabed. Research to produce maps of POC input and POC reaching the seabed across the different regions, would greatly benefit future HSM. Substrate is a key factor determining benthic species distributions that is rarely available for deep-sea modelling or is extrapolated from a limited number of ground-truth samples. Consequently, the acquisition of large substrate data sets and maps to feed into habitat models would also improve performance.

Climate change effects are expected to exceed annual variability in water mass properties (temperature, oxygen) experienced by species at which point range shifts will be experienced (Burrows et al., 2014). Future scenarios were modelled in iAtlantic deliverable D2.2 and Region 4 of iAtlantic deliverable D2.5, and the authors came to exactly such conclusions, particularly for the modelled deep-sea fish, sharks, shrimps and sea pen distributions which were predicted to shift to higher latitudes. Modelled cold-water corals, on the other hand, were predicted to shift to lower latitudes, but would mainly see their predicted suitable habitat decrease. Implementing this knowledge with improved modelling inputs will support robust management scenario generation for Atlantic ecosystems.

Future modelling should also be guided by outputs from iAtlantic work package 3 that investigated deep and open ocean ecological timeseries alongside oceanographic drivers for signs of tipping points and integrate the environmental variables identified as important into HSM. Corroboration of environmental drivers identified from HSM and stressors identified as effecting species in work packages 3 and 4 enable an opportunity for greater predictive capability of HSM under varying climatic scenarios where environmental spatial data that encapsulates stressors can be incorporated into HSM to better predict how species under stress may respond in terms of their distributional patterns.

Limitations of comparing models across scales and species

There are several limitations to modelling that must be considered when drawing a conclusion of environmental predictor importance. These include limitation of quantity, quality, resolution, and spatial coverage of environmental data which we have shown can influence the predictor importance because of the ecologically relevant environmental heterogeneity it is able to capture. Additionally, the iAtlantic case studies exhibit bias toward sessile benthic and specifically CWC species (Table 1). Collectively this can limit the universal applicability of results in space and across species. Still the study presents important information relating to Atlantic VMEs and which environmental drivers are likely to be identified via HSM at different resolutions for those VMEs, which can support ecosystem-based management.

Relevance within the iAtlantic project

Overall, the results presented here contribute directly to achieving iAtlantic's five key objectives, and to creating the long-lasting impacts expected from the project. Deliverable D2.6 evaluates and summarises the new ecological insights obtained by the project's mapping activities at basin and regional scales, enabling a better assessment of the status and interactions of deep and open ocean ecosystems in the Atlantic. Direct links between species spatial patterns and physical and biogeochemical drivers are identified and described at the respective scales of their main effects. The results clearly point to the vulnerability of key species to changes in temperature and food supply,

supporting the conclusions of iAtlantic's temporal and experimental research work packages, and pointing to the key factors that require management and monitoring by regulators, governments and industries worldwide.

Species distribution models developed by work package 2 are of paramount importance for the development of regional- and ocean basin-scale area-based management scenarios under work package 5. The use of habitat suitability modelling of selected habitat-structuring cold-water corals, fish and other invertebrates was considered appropriated to address several the management goals and objectives related with ensuring the protection of vulnerable, endangered, or critically endangered species, and with ensuring the protection of VMEs, but also with the goal of maintaining the biological diversity of deep-sea ecosystems. These models predicted the distribution under present-day conditions (1951–2000) and under future (2081-2100) climate projections (i.e., RCP2.6, RCP4.5, RCP8.5) and were used in the systematic conservation planning analyses (D5.3) to identify areas where different management regimes can be applied and to inform sustainable development strategies in the Atlantic.

The outcomes described in this deliverable could only be reached thanks to the extensive mapping and habitat suitability modelling efforts across the entire project consortium. This demonstrates how the cooperative framework created by iAtlantic has led to a more complete assessment of ecosystem status, covering the entire Atlantic Ocean, both North and South.

Conclusion

- iAtlantic deliverable D2.6 has shown that spatial patterns in Atlantic Ecosystems are driven by water mass properties (temperature and/or its covariates) and proxies of food supply (productivity). Also, terrain derivatives and hydrodynamics were identified as important categories of environmental variable driving spatial patterns.
- The relative importance of these variables appears to be influenced by the resolution at which they are input into the model.
- Basin wide and regional models of broad extent identify temperature as important compared to regional models of smaller extent, indicating that this variable is scale-dependent, and only influences distributions at a broad scale because it does not often show sharp gradients.
- Future HSM should endeavour to incorporate high resolution oceanographic and hydrodynamic variables, which should be incorporated into 'present day scenario' basin HSM.
- iAtlantic results indicate the importance of POC input, particularly the importance of POC reaching the seabed. Therefore, further research is needed to develop maps of POC input and POC reaching the seabed in the different regions, so that it can be included in future HSM.
- Substrate type is another variable for which information is lacking, both at regional and basin-wide scale. International efforts should focus on collating reliable substrate information to support future modelling and habitat classification studies.
- iAtlantic deliverable D2.6 has shown that continental shelves and slopes are the most important habitats for the modelled species.
- iAtlantic seabed areas can be used to identify broad-scale seabed types likely to support VMEs.
- EUNIS habitat classifications can provide an indication of VME spatial patterns, but their relevance depends on the input data and resolution used in both HSM and EUNIS mapping.
- Comparison of HSM derived from different resolution data and extents, and with SBAs and EUNIS classification maps provides greater insight into modelling accuracy across spatial scales and how SBAs, EUNIS classification maps and HSM can be applied in a hierarchical manner to

identify areas potentially supporting VMEs. This knowledge is impactful for marine spatial planning, ecosystem-based management and area-based conservation strategies of the Atlantic deep ocean where high resolution or biological data may not be available.

- The updated spatial data deposited into iAtlantic's GeoNode has supported regional prioritisation of spatial management areas in the Azores and South Africa under iAtlantic work package 5.

- HSM can support outputs from work package 1 by providing distribution maps of species for which connectivity studies were undertaken by relating species distribution across the Atlantic to genetic structure and areas of hybridisation for VME taxa such as *Desmophyllum pertusum* and *Madrepora oculata* which will better identify areas for prioritisation for protection and where best to place networks of marine protection areas.

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7. Document Information

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		CO Confidential restricted under conditions set out in Model Grant Agreement		
		CI Classified, information as referred to in Commission Decision 2001/844/EC		

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