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# Benthic habitat modelling and mapping as a conservation tool for marine protected areas: A seamount in the western Mediterranean

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## Abstract

1. An ecologically representative, well-connected, and effectively managed system of marine protected areas (MPAs) has positive ecological and environmental effects as well as social and economic benefits. Although progress in expanding the coverage of MPAs has been made, the application of management tools has not yet been implemented in most of these areas.
2. In this work, distribution models were applied to nine benthic habitats on a Mediterranean seamount within an MPA for conservation purposes. Benthic habitat occurrences were identified from 55 remotely operated vehicle (ROV) transects, at depths from 76 to 700 m, and data derived from multibeam bathymetry. Generalized additive models (GAMs) were applied to link the presence of each benthic habitat to local environmental proxies (depth, slope, backscatter, aspect, and bathymetric position index, BPI).
3. The main environmental drivers of habitat distribution were depth, slope, and BPI. Based on this result, five different geomorphological areas were distinguished. A full coverage map indicating the potential benthic habitat distribution on the seamount was obtained to inform spatial management.
4. The distribution of those habitats identified as vulnerable marine ecosystems (VMEs) was used to make recommendations on zonation for developing the management plan of the MPA. This process reveals itself as an appropriate methodological approach that can be developed in other areas of the Natura 2000 marine network.

KEYWORDS
benthic habitat, generalized additive models, mapping, marine protected area, seamount, spatial management

## 1 | INTRODUCTION

Well-managed marine protected areas (MPAs) have positive ecological and environmental effects (Fenberg et al., 2012). Additionally, MPAs provide social and economic benefits by supporting various ecosystem services (Leenhardt, Low, Pascal, Micheli, & Claudet, 2015; Potts et al., 2014). As 60% of the world's major marine ecosystems have been degraded or are being used unsustainably (United

Nations Environment Programme (UNEP), 2011), countries have adopted policies to conserve at least 10% of marine and coastal areas by 2020 (Convention on Biological Diversity (CBD), 2010), through effectively and equitably managed, ecologically representative, and well-connected systems of protected areas. Embedding MPA design issues into European policies, such as the Marine Strategy Framework Directive (2008/56/CE), the Habitats Directive (92/43/CEE), and the Directive on Establishing a Framework for Maritime Spatial Planning (2014/89/EU), and into regional conventions, such as the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) and the Barcelona Convention, enhance the creation of ecologically coherent and representative networks of effectively managed MPAs as an instrument for marine biodiversity conservation and sustainable use in European waters.

To meet international protected area targets, nation states have increased the number and size of designated MPAs. Currently, this global network of MPAs covers approximately 4.12% of the world's seas and oceans or marine environments (just over 10% of the coastal and marine areas under national jurisdictions, and 0.25% of the marine areas beyond national jurisdictions; UNEP World Conservation Monitoring Centre (WCMC) & International Union for Conservation of Nature (IUCN), 2016). Although progress in expanding the coverage of MPAs has been made, the application of management tools has not yet been duly implemented in most of them. Of the total global coverage of MPAs, only 3% are protected in multiple-use managed areas, and only approximately 1.5% are no-take MPAs that are covered by strictly and permanently protected measures (UNEP WCMC & IUCN, 2016), i.e. areas that prohibit all forms of extractive practices, such as fishing and mining.

To design appropriate management plans and to properly zone activities in these MPAs, with a focus on biodiversity conservation, it is necessary to know the spatial distribution and extent of the main benthic habitats in the area (Gonzalez-Mirelis & Buhl-Mortensen, 2015); however, because these submerged areas are characterized by difficult accessibility, the research requires much more costly and complicated technologies than the methods used for terrestrial areas. Hence, approaches that involve a combination of broader-scale geological maps that are based on acoustic data and detailed ground-truthing biological data covering smaller spatial extent (Elvenes, Dolan, Buhl-Mortensen, & Bellec, 2014; Kostylev et al., 2001; Robert, Jones, Roberts, & Huvenne, 2016) are increasingly being used to describe patterns of benthic habitat distribution.

Techniques for predicting the suitability of a location for a given benthic habitat are known as habitat suitability models (HSMs; Rowden et al., 2017), predictive habitat distribution models (PHDMs; Guisan & Zimmermann, 2000), or simply distribution models (DMs; Reiss et al., 2015), and have been successfully and widely used across the marine realm for numerous conservation and management applications (Reiss et al., 2015; Ross & Howell, 2013; Vierod, Guinotte, & Davies, 2014). Displayed as cartographies, DMs are used to gain ecological and evolutionary insights and to make predictions about the potential distributions within the modelled area (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000; Reiss et al., 2015), including sites where no direct observations of the biota have been made. These predictive maps along with the identification of habitats that are considered to be sensitive to anthropogenic disturbances provide relevant information for the decision-making process. The distribution of vulnerable marine ecosystems (VMEs), which are at significant risk from the effects of fishing activity or other types of disturbance (Food and Agriculture Organization of the UN (FAO), 2009), can be used to devise appropriate measures to spatially manage biodiversity through the establishment of open and closed areas. In this way, high-resolution models of VMEs have recently been used to evaluate the feasibility of designing within-seamount spatial closures to protect these ecosystems in the South Pacific Ocean (Rowden et al., 2017).

In Spain, approximately 8.4% of the marine environment is covered by the Spanish network of MPAs (UNEP WCMC, 2017); however, most of these MPAs have no effective management plans based on an ecosystem approach. This is the case for the Special Area of Conservation (SAC) 'Sur de Almería-Seco de los Olivos', which was integrated into the Natura 2000 European network of protected areas (Orden AAA/2280/2014, 2014) for the presence of two marine species, i.e. the loggerhead turtle (*Caretta caretta*) and the bottlenose dolphin (*Tursiops truncatus*), and two important habitats, the conservation of which requires the designation of an MPA, i.e. the '*Posidonia oceanica* beds' and 'reefs'. Submarine ridges, elevations, and canyons characterize the deep-sea floor of this MPA (Muñoz et al., 2008). The Seco de los Olivos seamount stands out from the other topographic features, with benthic habitats distributed from its summit, which protrudes into the euphotic zone, to its base in the deep ocean, a characteristic reserved for only a small subset of all known seamounts (Morato et al., 2013; Ramos et al., 2016), with the variety of habitats recorded at different depths increasing the local diversity. According to the Dark Habitats Action Plan for the Mediterranean (UNEP Division of Environmental Policy Implementation (DEPI)/MED, 2013), measures to reduce pressures that could impact benthic assemblages on seamounts should be identified in order to develop legislative measures and plans for their conservation. In this scenario, the management of the Seco de los Olivos seamount is a priority for biodiversity conservation.

The epibenthic fauna of the Seco de los Olivos seamount has been studied in depth, and 13 assemblages were identified in a previous study (De la Torriente, Serrano, Fernández-Salas, García, & Aguilar, 2018). Characterized by sessile, long-lived, habitat-forming species with slow growth rates, these assemblages were considered as habitats: although some were dominated by single habitat-forming species, such as circalittoral detritic sands with sea pens (*Pennatula rubra*) and bathyal mud with bamboo gorgonians (*Isidella elongata*), others were mixed habitats with corals and sponge species. These latter habitats included threatened, endangered, and declining species, such as *Madrepora oculata*, *Leiopathes glaberrima*, and *Savalia savaglia*. All of these faunal assemblages meet the criteria for a VME indicator recommended by the FAO (2009), with a slow recovery from disturbance: they are characterized by habitat-forming species with life-history traits that make recovery difficult, create complex physical structures, and are necessary for the survival, function, spawning/reproduction, or recovery of fish stocks, or of rare, threatened, or endangered species.

In this study, the distributions of the benthic habitats previously described on the Seco de los Olivos seamount were modelled to: (i) gather insight into the environmental drivers that control their distribution; and (ii) obtain a full-coverage map that supports the spatial management of benthic habitats in an offshore MPA based on the distributions of VMEs. To accomplish these objectives, a biological dataset comprising 2435 video samples of benthic images recorded with a remotely operated vehicle (ROV) and a dataset of seafloor characteristics that are known to influence and determine the shape of benthic habitats as independent variables were analysed.

## 2 | METHODS

### 2.1 | Study area

The Seco de los Olivos is a completely submerged volcanic seamount located approximately 10 miles off the southern Spanish coast, at the north-eastern margin of the Alboran Sea in the Western Mediterranean (Figure 1). The summit of the flat-top main elevation or ‘guyot’ is at a depth of 75 m rising to a height of approximately 550 m from the sea bed; therefore, strictly speaking, it cannot be considered as a seamount, but rather as a knoll or a bank (Kennett, 1982; OHI, 2008). The customary name Seco de los Olivos seamount was retained, however, by adopting an ‘ecological’ definition that includes seamounts, knolls, and hills (Morato et al., 2013; Pitcher et al., 2007; Staudigel, Koppers, Lavelle, Pitcher, & Shanks, 2010). Surrounding the guyot are two main ridges that range from water depths of 150 m to 700 m. Overall, these features cover an area of 100 km$^2$.

Located in an area where both the Atlantic and the Mediterranean water masses, which have different speeds, directions, and temperatures, come together, the Seco de los Olivos seamount offers a wide range of substrates and geomorphological features. Circalittoral and bathyal communities occur, supporting a broad range of marine life (De la Torriente et al., 2014, 2018). Atlantic water (AW) flows eastwards in a surface layer of 150–200 m depth and Mediterranean water (Levantine intermediate water, LIW), which is denser and more saline, flows westwards at depths between 200 and 600 m (Hernández-Molina et al., 2002; Palomino et al., 2011).

### 2.2 | Biological data

Species data were obtained from three ROV (Seaeye Falcon & Falcon DR) surveys conducted by OCEANA on board the *Oceana Ranger* from 2010 to 2012. An on-board altimeter continuously recorded the height above the sea bottom. Video footage greater than 1–2 m above the sea bed and video images from transects with poor visibility, as a result of sediment resuspension, were removed from the analysis. To record continuous depth and coordinate data, the ROV also hosted a depth sensor with a full-scale deflection (FSD) accuracy of ±0.5%, a navigation compass with a reliability of ±1°, and an underwater acoustic tracking position system (TrackLink 1500; LinkQuest Inc., San Diegao, CA). Fifty-five ROV video transects of both soft and hard bottoms were analysed, covering approximately 67.52 km of benthic imagery dispersed around the seamount from depths of 76 to 700 m (Figure 1). The use of these transects for scientific goals is opportunistic, as the sample design was not aimed at habitat mapping.

The sampling unit consisted of 1-minute continuous-movement ROV tracks at a speed of 0.2–0.4 knots, covering an average distance of ~13 m (mean ± SD = 13.16 ± 5.74 m). Each sample was characterized by the midpoint of the initial and final latitude and the longitude, depth, biological zone (circalittoral, < 200 m, or bathyal, ≥200 m), type of substrate (mud, detritic sand, maërl/rhodoliths, coral framework, and rock), and all megabenthic (>2 cm) invertebrate and sessile species

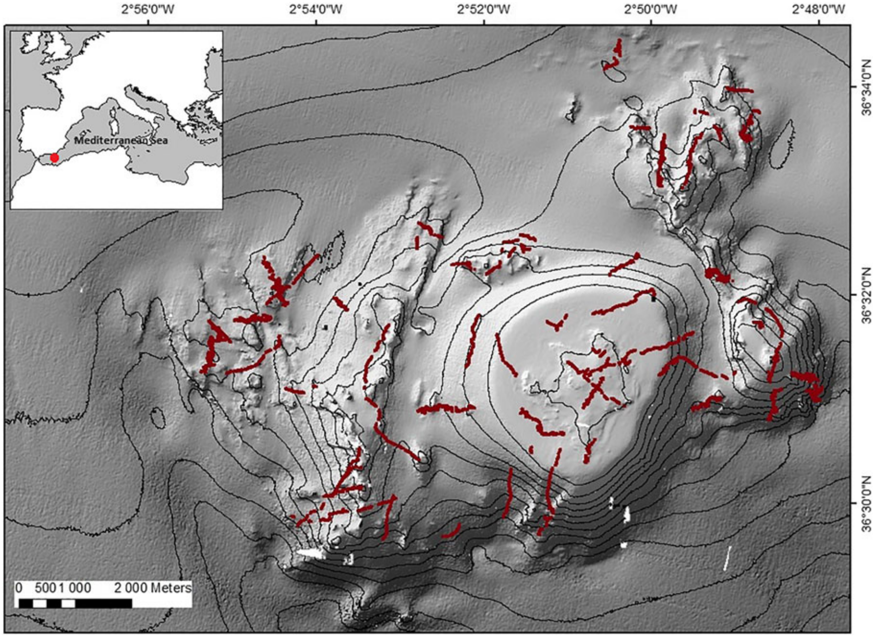

**FIGURE 1** Geographical setting of the study area. Red lines indicate remotely operated vehicle (ROV) transects carried out during the INDEMARES project. A 15-m resolution hill-shaded bathymetric grid depicts the submarine physiography of the Seco de los Olivos seamount. Bathymetric contour lines represent 50-m depth intervals. The inset shows the location of the seamount within the Mediterranean Sea (red dot), approximately 10 miles off the southern coast of Spain

that were found during that minute. For further details about the sampling design and data collection, see De la Torriente et al. (2018).

To identify the main benthic assemblages that occur at the Seco de los Olivos seamount, only video samples with five or more individuals or colonies of any habitat-forming species were considered in the analysis. Habitat-forming species are here defined as sessile and three-dimensional megabenthic invertebrates, regarded as substrate providers for other associated species (Jones, Lawton, & Shachak, 1994). The threshold of five individuals or colonies was determined based on the curve of mean species richness obtained as a function of the number of habitat-forming species (HFS): a marked change in species richness occurrs at abundances of 4.7 HFS individuals or colonies (De la Torriente et al., 2018). Data on 49 potential HFS from 720 samples were retained to conduct the habitat identification analysis. The benthic assemblages were obtained from a cluster analysis using the Bray–Curtis similarity index and by processing the distance matrix using the unweighted pair group method using arithmetic averages (UPGMA) algorithm. To identify the main taxa typifying each cluster group, similarity percentage analysis (SIMPER; Clarke & Warwick, 2001) and indicator value analysis (IndVal, Dufrêne & Legendre, 1997) were applied on the abundance data matrix as two complementary approaches. Only species identified as characteristic by both SIMPER and IndVal were considered as HFS that determined the various habitats on the Seco de los Olivos seamount (De la Torriente et al., 2018).

Habitats were described on the basis of sediment characteristics, water depth, and dominant benthic assemblages (Kostylev et al., 2001). Only benthic habitats with a clear biological component were identified. As a result, 13 distinct benthic habitats at European Nature Information System (EUNIS) level 4 were identified at the Seco de los Olivos seamount (Table 1). For more information about the habitat identification procedure, see De la Torriente et al. (2018).

## 2.3 | Environmental data

Bathymetric and backscatter data were obtained from a geophysical survey conducted by the Instituto Español de Oceanografía (IEO) on board the RV *Ángeles Alvariño* in 2012. Multibeam bathymetric data were gathered using a Simrad EM710 multibeam echo sounder (70–100 kHz; Kongsberg Maritime, Kongsberg, Norway) and processed using CARIS HIPS and SIPS software to produce 15 × 15-m bathymetric and backscatter grid models.

Four additional environmental datasets were derived from the bathymetric grid model using the SPATIAL ANALYST and BENTHIC TERRAIN MODELER extensions (Wright et al., 2012) within ARCGIS 10.3.1 (ESRI, 2015). These data included: (i) slope, in degrees of inclination; (ii) aspect, which reflects the orientation of the sea bed at any given location (this was split into two components: east-ness, computed as the sin(aspect), and northness, computed as the cos(aspect), to avoid

**TABLE 1** Main benthic habitats identified on the Seco de los Olivos seamount. The number of samples of each habitat recorded in each substrate type is also shown. Min *Z* and Max *Z*: minimum and maximum depths (m), respectively. Habitats indicated in grey were not modelled

| Habitat | Name | *n* samples | Mud | Detritic sand | Maërl/ rhodoliths | Coral framework | Rock | Min *Z* | Max *Z* |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Circalittoral maërl/rhodolites with *Alcyonium palmatum* and *Paralcyonium spinulosum* | 40 | - | – | 38 | – | 2 | 77.6 | 96.2 |
| 2 | Circalittoral vertical rocky walls with *Caryophyllia cyathus* and *Corallium rubrum* | 14 | – | – | – | – | 14 | 108.6 | 138.6 |
| 3 | Circalittoral rock with *Viminella flagellum and Chironephthya mediterranea* | 28 | – | – | – | – | 28 | 93.4 | 375.4 |
| 4 | Circalittoral rock with *Eunicella verrucosa* and *Paramuricea clavata* | 40 | – | – | 1 | – | 39 | 74.8 | 133.9 |
| 5 | Bathyal vertical rocky walls with *Neopycnodonte zibrowi* and cup sponges (*Phakellia* sp.) | 7 | – | – | – | – | 7 | 312.7 | 493.8 |
| 6 | Bathyal rock with *Dendrobrachia bonsai* | 14 | – | – | – | – | 14 | 410.9 | 454.5 |
| 7 | Bathyal rock with *Caryophyllia* sp. | 14 | – | – | – |  | 14 | 178.9 | 365.9 |
| 8 | Bathyal hard substrate with gorgonians (*Acanthogorgia hirsuta* and *Swiftia pallida*) and sponges (*Asconema setubalense* and other white sponges) | 357 | – | 3 | – | 28 | 326 | 131.9 | 462.9 |
| 9 | Bathyal hard substrate with corals (*Madrepora oculata*, *Savalia savaglia* and *Leiopathes glaberrima*) | 33 | – | – | – | 8 | 25 | 217.1 | 407.2 |
| 10 | Bathyal mud with pennatulids (*Kophobelemnon stelliferum*) | 72 | 72 | – | – | – | – | 365.3 | 561.1 |
| 11 | Bathyal mud with *Isidella elongata* | 56 | 55 | – | – | – | 1 | 411.7 | 461.2 |
| 12 | Bathyal detritic sand with solitary escleractinians *Caryophyllia smithii* | 22 | – | 22 | – | – | – | 247.8 | 334.7 |
| 13 | Circalittoral detritic sand with pennatulids (*Pennatula rubra*) | 23 | – | 23 | – | – | – | 123.7 | 137.2 |

problems related to circular data ($0 \approx 360°$); (iii) rugosity, used as a measure of topographic unevenness; and (iv) the bathymetric position index (BPI), which measures whether the area is topographically high or low relative to the surrounding area. This variable was calculated using two different scales: BPIfine (inner and outer radius of one and 15 cells, respectively) and BPIbroad (inner and outer radius of 15 and 30 cells, respectively).

Before modelling and mapping, correlations between the explanatory variables were checked to eliminate highly correlated predictors and to avoid collinearity; this analysis was conducted using Spearman's rank correlations and variance inflation factors (VIFs) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). From the pairs of covariates that were considered to be highly correlated (Spearman rank values of >0.5 and VIFs of >3) and significant ($P < 0.05$), pairs that have been deemed as having a greater ecological relationship with species distribution were selected. Consequently, two environmental variables (ruggedness and BPIfine) were removed from the modelling process, and the final set of environmental variables used in the habitat modelling included: (i) depth; (ii) slope; (iii) backscatter; (iv) eastness; (v) northness, and (vi) BPIbroad (Figure S1). To avoid inflated error rates and substantial distortions of estimates, two outliers, which corresponded to two absence points (no habitat identified) with extreme values of slope and BPI, respectively, were removed from the dataset.

## 2.4 | Predictive modelling and mapping

From the 13 distinct benthic habitats identified on the Seco de los Olivos seamount (De la Torriente et al., 2018), only nine were modelled and mapped; of these, four habitats were on hard bottoms (coral framework and rock), four were on soft bottoms (mud and detritic sand), and one was on mixed substrate (rhodoliths on sand). The remaining habitats were considered to be unsuitable for modelling because of the low number of samples with presence (Table 1). For each habitat, a spatially explicit dataset of the presences and absences (2419 samples) was created, which was used as the response variable.

Generalized additive models (GAMs; Hastie & Tibshirani, 1990) were performed to link the presence of each benthic habitat with the local environmental conditions around the Seco de los Olivos seamount. Binomial distributions with a logit-link function were used to predict the mean presence probability of each of the selected habitats. The full binomial model for the nine habitats analysed was:

$$\mathrm{Ph_i} = \beta_i + \mathrm{s(depth)} + \mathrm{s(slope)} + \mathrm{s(backscatter)} + \mathrm{s(east)} + \mathrm{s(north)} + \mathrm{s(BPIbroad)} + \varepsilon_i,$$

where $\mathrm{Ph}_i$ is the probability of the presence of each modelled habitat $i$, $\beta_1$ is the intercept, s is an isotropic smoothing function (thin plate regression splines, one for each variable and model), and $\varepsilon_1$ is the error term. To select the explanatory variables for each model, a backwards/forwards stepwise procedure was based on Akaike's information criterion (AIC; Akaike, 1973); thus, the models with the best balance between bias and precision were selected. All the smoothers were constrained to 4 knots, which limited the degrees of freedom to a maximum of three to avoid overfitting. Modelling was performed using the 'gam' and 'predict.gam' functions of the package MGCV (Wood, 2011). Finally, to identify the relative importance of each environmental variable in each model, the targeted variable was removed from the final model, and the deviance variation was computed.

To check for spatial autocorrelation of the model residuals, variograms using the GSTAT package (Pebesma, 2004) and statistical tests using Moran's I, computed with the package APE (Paradis, Claude, & Strimmer, 2004), were performed. All of the models show observed Moran's I values significantly higher than the expected values ($P < 0.05$). The Moran's I value was low (<0.16) or very low (<0.1) for all habitats, meaning that the detected spatial autocorrelation was very weak in all cases. The effect of the spatial autocorrelation in habitats 8 and 9 (the two with the highest Moran's I observed values; Table 1) was explored including an autocovariate term in the null model (Crase, Liedloff, & Wintle, 2012; Rowden et al., 2017). This approach did not improve the models and did not change the main results; thus, the original approach (i.e. without the autocovariate term) for all the habitats was kept. The $P$ value used to determine whether the effect of an explanatory variable was significant was reduced to 0.01 in all habitats to compensate for possible inflation errors in the $P$ values (Fortin & Dale, 2005; Giannoulaki et al., 2017).

The predictive performance of the models was tested using cross-validation. The original presence–absence data for each habitat were randomly split into a calibration or training subset (80% of the total points) and a validation or test subset (the other 20%). The ability of the training subsample to predict the probability of presence was tested using the test subsample; thus, models were computed using the training data but evaluation statistics were calculated using the validation data. The accuracy of the models was measured using two different statistics: the area under the curve (AUC; Fielding & Bell, 1997) of the receiver operating characteristics (ROC; Fielding & Bell, 1997) and the Kappa statistics (Cohen, 1960). The process was repeated 10 times for each habitat and model, and the AUC and Kappa values were calculated each time based on a different random selection of training and test subsets. Both statistics were calculated using the 'evaluate' function in the R package DISMO (Hijmans, Phillips, Leathwick, & Elith, 2016). Based on the AUC values, which provided an indication of how well a model discriminates presence from absence, the following classification for the accuracy of each model was used: excellent, 0.90–1.00; good, 0.80–0.89; fair, 0.70–0.79; poor, 0.60–0.69; and fail, 0.50–0.59 (Gonzalez-Mirelis & Buhl-Mortensen, 2015). For computing the Kappa statistic, the threshold that provided the maximum Kappa values calculated each time was used; this was completed using the 'threshold' function in the same package. The classification used for Kappa values, which ranged from −1 to +1, was: excellent prediction, >0.75; intermediate-to-good prediction, 0.40–0.75; and poor prediction, <0.40 (Fleiss, 1991).

A continuous raster map of all presence probabilities for all habitats was obtained by merging the nine models. For each pixel, all the values lower than its habitat's prevalence were replaced by 0, and then, the habitat with the highest probability of presence was selected. Pixels with values of 0 for all nine habitats were classified as ‘no prediction’.

All data analyses were performed in R 3.2.4 (R Development Core Team, 2016).

## 3 | RESULTS

Based on a 15% Bray–Curtis similarity cut-off level, the hierarchical cluster analysis of habitat-forming species data separated 13 different assemblages (Figure S2; De la Torriente et al., 2018). The characteristic species for each assemblage revealed by the SIMPER and IndVal analyses are listed in Table S1 (De la Torriente et al., 2018).

### 3.1 | Performance of predictive models

The results obtained for each model using binomial GAMs for the nine distinct benthic habitats are summarized in Table 2. The models showed high values of explained deviance, i.e. above 30% in all cases. The predictive accuracy of all models ranged from ‘good’ to ‘excellent’ in terms of the AUC values and from ‘intermediate to good’ to ‘excellent’ in terms of the Kappa values, with the exception of habitats 3 and 9 (Table 2).

### 3.2 | Importance of predictor variables and habitat mapping

The relative importance of the predictor variables for each habitat is presented in Table 3. All variables were relevant for shaping benthic habitats as all of them were included as covariates in at least six models. Two of them, depth and BPIbroad, were included in all the models. Depth had the highest relevance as a predictor in eight of the nine models, whereas backscatter showed the highest explained delta deviance for one of the models. The findings of the relationship between habitat occurrence and significant predictor variables are given below and presented in Figure 2.

#### 3.2.1 | Habitat 1: Circalittoral maërl or rhodolites with *Alcyonium palmatum* and *Paralcyonium spinulosum*

This habitat showed a linear positive relationship with depth, indicating that its probability of occurrence was mainly associated with shallower zones. A linear negative relationship was found for BPIbroad, with higher preferences for areas with lower values (minimum confidence limits close to zero), which corresponded to constant slopes or flat areas.

#### 3.2.2 | Habitat 3: Circalittoral rock with *Viminella flagellum* and *Chironephthya mediterranea*

The probability of the presence of this habitat showed a positive relationship with depth, indicating a clear preference for shallower zones. In terms of BPIbroad, the occurrence of this habitat seemed to be associated with low values above zero, as indicated by the positive trend from −20 to 5, and therefore with flat or slightly elevated areas of the study area.

#### 3.2.3 | Habitat 4: Circalittoral rock with *Eunicella verrucosa* and *Paramuricea clavata*

A positive and linear relationship was shown with depth, indicating the occurrence of this habitat in the shallower zones of the study area.

#### 3.2.4 | Habitat 8: Bathyal hard substrate with gorgonians (*Acanthogorgia hirsuta* and *Swiftia pallida*) and sponges (*Asconema setubalense* and other white sponges)

This habitat showed a negative relationship with depth for values that ranged from −70 to −250 m, and a slightly positive trend for values

**TABLE 2** Summary of generalized additive model (GAM) results. Abbreviations: $Ph_i$, probability of presence of each modelled habitat *i*; $\beta_i$, intercept; *s*, isotropic smoothing function; $\varepsilon_i$, error terms. Area under the curve (AUC) and Kappa values are given as means ± standard deviations (±SDs)

| Habitat | GAM formula | Deviance explained | AUC | Kappa |
|---|---|---|---|---|
| 1 | $Ph_1 = \beta_1$ + s (depth) + s (east) + s (north) + s (BPIbroad) + $\varepsilon_1$ | 88.6% | 0.99 ± 0.00 | 0.93 ± 0.06 |
| 3 | $Ph_3 = \beta_3$ + s (depth) + s (slope) + s (backscatter) + s (east) + s (BPIbroad) + $\varepsilon_3$ | 30.7% | 0.83 ± 0.07 | 0.28 ± 0.10 |
| 4 | $Ph_4 = \beta_4$ + s (depth) + s (slope) + s (backscatter) + s (east) + s (BPIbroad) + $\varepsilon_4$ | 62.0% | 0.97 ± 0.03 | 0.64 ± 0.09 |
| 8 | $Ph_8 = \beta_8$ + s (depth) + s (slope) + s (backscatter) + s (north) + s (BPIbroad) + $\varepsilon_8$ | 30.9% | 0.86 ± 0.02 | 0.46 ± 0.03 |
| 9 | $Ph_9 = \beta_9$ + s (depth) + s (east) + s (north) + s (BPIbroad) + $\varepsilon_9$ | 88.6% | 0.89 ± 0.04 | 0.28 ± 0.13 |
| 10 | $Ph_{10} = \beta_{10}$ + s (depth) + s (slope) + s (backscatter) + s (east) + s (north) + s (BPIbroad) + $\varepsilon_{10}$ | 47.2% | 0.93 ± 0.02 | 0.50 ± 0.08 |
| 11 | $Ph_{11} = \beta_{11}$ + s (depth) + s (slope) + s (east) + s (north) + s (BPIbroad) + $\varepsilon_{11}$ | 53.0% | 0.96 ± 0.02 | 0.44 ± 0.10 |
| 12 | $Ph_{12} = \beta_{12}$ + s (depth) + s (slope) + s (backscatter) + s (east) + s (north) + s (BPIbroad) + $\varepsilon_{12}$ | 62.5% | 0.98 ± 0.00 | 0.55 ± 0.16 |
| 13 | $Ph_{13} = \beta_{13}$ + s (depth) + s (backscatter) + s (east) + s (north) + s (BPIbroad) + $\varepsilon_{13}$ | 73.8% | 0.99 ± 0.00 | 0.62 ± 0.07 |

**TABLE 3** Relative importance of each predictor in each model. Approximate significance of smoothing terms: Edf, estimated degrees of freedom; $\chi^2$, Chi-square statistic; $^{**}P < 0.01$

| | Model 1 | | | | Model 3 | | | | Model 4 | | | | Model 8 | | | | Model 9 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Predictor | Deviance | *P* | Edf | $\chi^2$ | Deviance | *P* | Edf | $\chi^2$ | Deviance | *P* | Edf | $\chi^2$ | Deviance | *P* | Edf | $\chi^2$ | Deviance | *P* | Edf | $\chi^2$ |
| Depth | −197.080 | ** | 1.000 | 12.789 | −36.233 | ** | 1.676 | 22.605 | −89.873 | ** | 1.000 | 22.567 | −131.88 | ** | 2.967 | 75.58 | −45.572 | ** | 2.968 | 19.935 |
| Slope | | | | | −13.652 | – | 2.863 | 11.700 | −11.662 | – | 1.883 | 9.171 | −14.676 | ** | 1.581 | 12.99 | | | | |
| Backscatter | | | | | −1.466 | – | 1.255 | 3.065 | −6.165 | – | 1.986 | 4.068 | −165.92 | ** | 2.200 | 132.38 | −14.051 | – | 2.736 | 8.513 |
| Eastness | −19.553 | – | 2.876 | 13.629 | −3.047 | – | 1.000 | 3.229 | −7.670 | – | 2.678 | 6.330 | | | | | −5.446 | – | 1.000 | 4.775 |
| Northness | −10.792 | – | 2.964 | 6.296 | | | | | | | | | −13.201 | ** | 2.800 | 12.44 | | | | |
| BPIbroad | −31.871 | ** | 2.876 | 13.629 | −7.024 | ** | 2.823 | 11.528 | −8.685 | – | 2.626 | 7.148 | −55.992 | ** | 2.521 | 49.00 | −31.512 | ** | 2.905 | 11.409 |

| | Model 10 | | | | Model 11 | | | | Model 12 | | | | Model 13 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Predictor | Deviance | *P* | Edf | $\chi^2$ | Deviance | *P* | Edf | $\chi^2$ | Deviance | *P* | Edf | $\chi^2$ | Deviance | *P* | Edf | $\chi^2$ |
| Depth | −136.19 | ** | 2.877 | 14.941 | −173.57 | – | 1.956 | 1.835 | −46.297 | ** | 2.083 | 11.025 | −102.13 | – | 1.898 | 3.305 |
| Slope | −6.865 | – | 1.990 | 5.043 | −61.731 | ** | 2.872 | 30.002 | −12.473 | ** | 1.000 | 8.223 | | | | |
| Backscatter | −7.045 | – | 2.900 | 7.244 | | | | | −3.983 | – | 2.840 | 6.358 | −22.598 | ** | 1.000 | 14.843 |
| Eastness | −23.747 | ** | 2.885 | 18.166 | −7.774 | – | 2.702 | 5.164 | −6.753 | – | 1.000 | 1.511 | −17.185 | – | 1.003 | 12.258 |
| Northness | −5.740 | – | 2.155 | 1.844 | −16.235 | ** | 1.000 | 15.184 | −6.258 | ** | 1.000 | 7.391 | −15.994 | ** | 1.000 | 13.796 |
| BPIbroad | −60.859 | ** | 2.918 | 27.349 | −45.709 | ** | 1.872 | 16.074 | −18.945 | – | 1.947 | 6.388 | −3.011 | – | 1.699 | 3.840 |

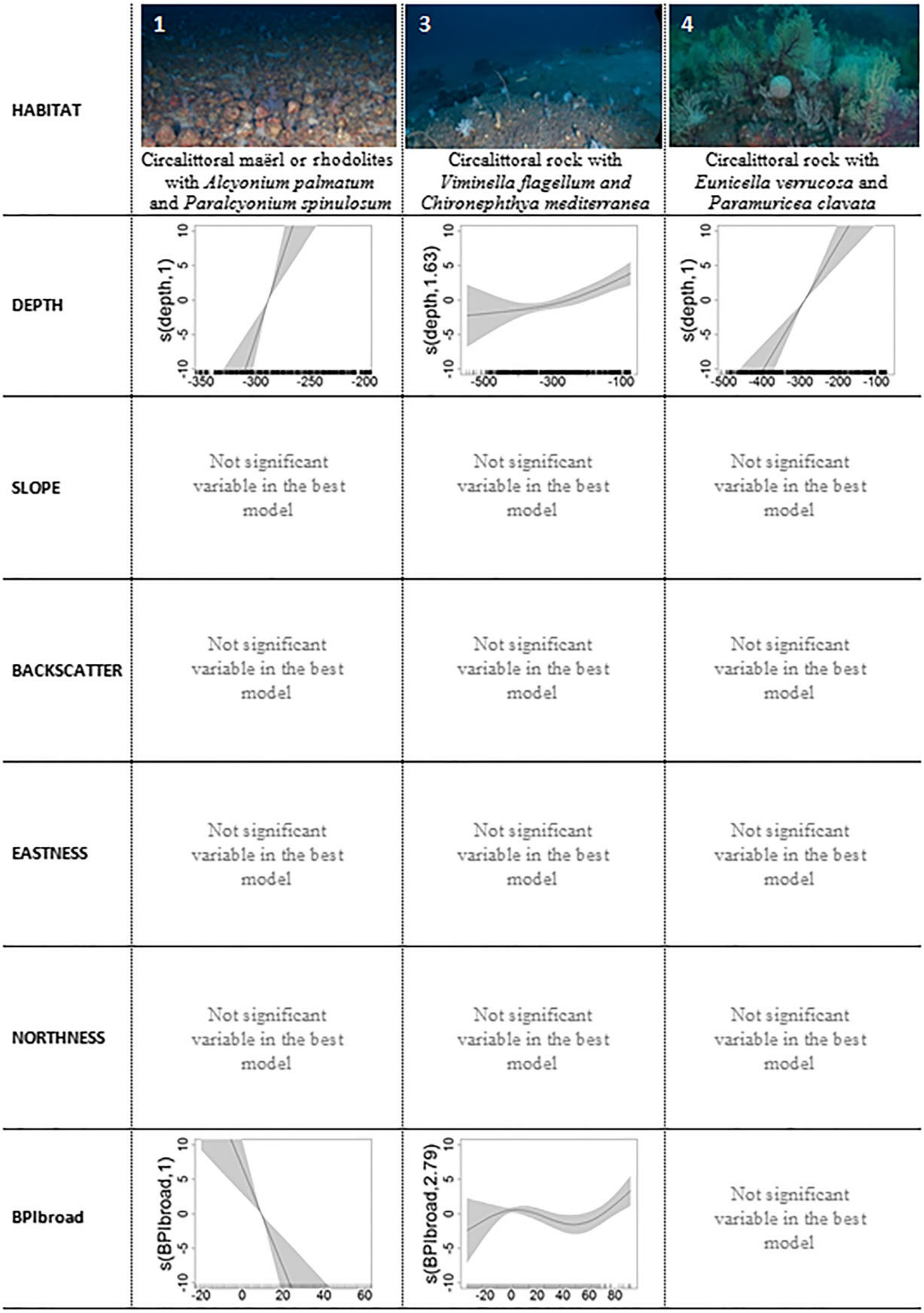

**FIGURE 2** Generalized additive model (GAM) curves for the nine models, showing the significant response variable shapes in relation to the probability of the habitat occurrence. The fitted smoothing functions (solid lines) obtained with the models are shown. Estimated degrees of freedom (edf) are displayed on the *y*-axes. Shaded areas denote the approximate 95% confidence bands. Blank spaces indicate variables that are not included in the best model

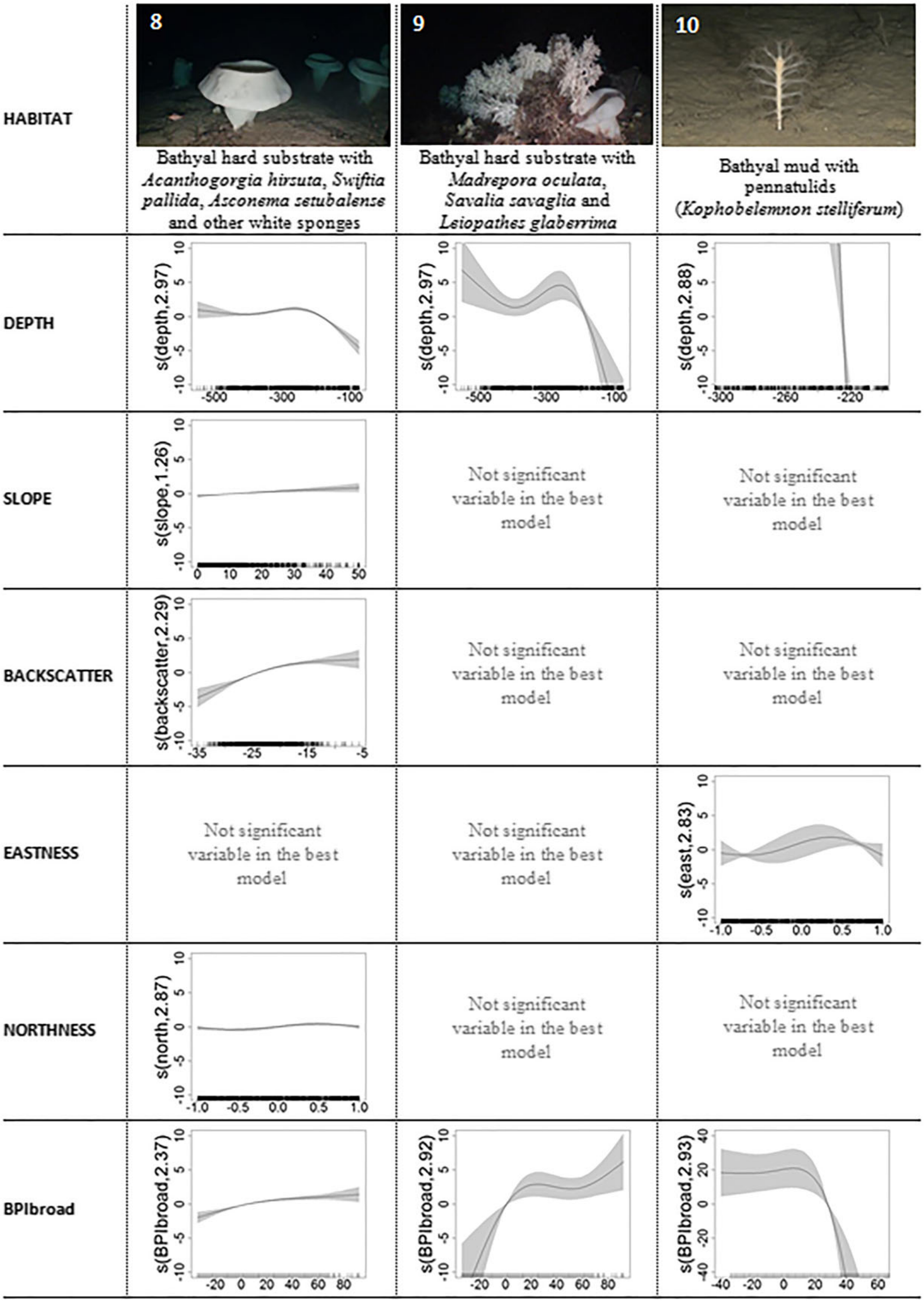

**FIGURE 2** Continued.

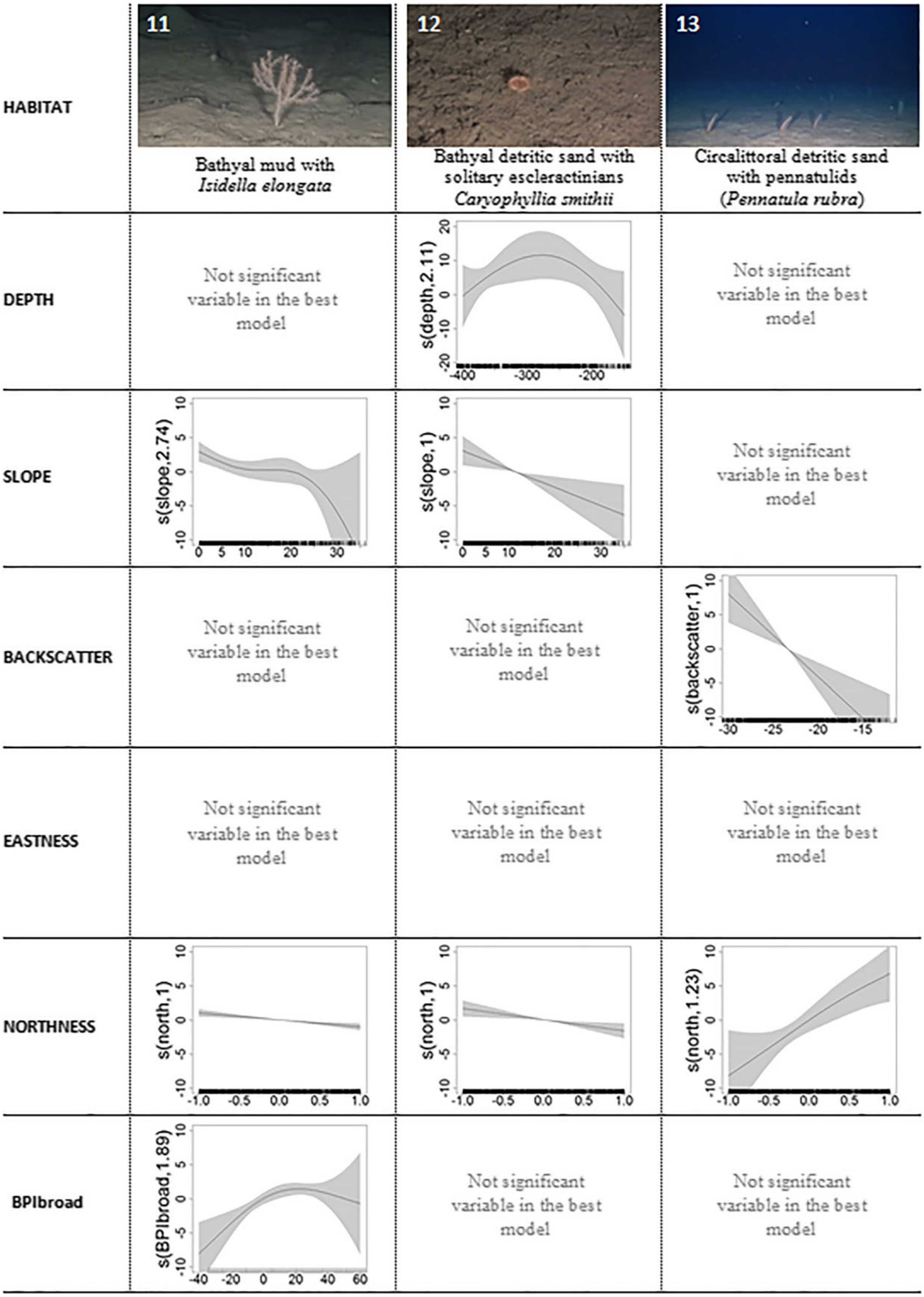

**FIGURE 2** Continued.

from −250 to −400 m; however, the trend for deeper values was unclear (with a very wide error interval). Positive nonlinear relationships, which were slightly pronounced, were shown with slope, BPIbroad, and backscatter. These results suggested a preference for areas located at intermediate depths of the study area and characterized by low–medium values of slope. Its occurrence seemed to be associated with high-relief features that are higher than their surroundings and with harder types of substrate, which was supported by the higher values of backscatter than that for the rest of the habitats. The trend for northness was not clear, and therefore no orientation was suggested.

### 3.2.5 | Habitat 9: Bathyal hard substrate with corals (*Madrepora oculata*, *Savalia savaglia*, and *Leiopathes glaberrima*)

The effect of depth on the probability of the presence of this habitat peaked in value around −250 m, with a clear negative relationship for shallower values and a positive relationship for nearby deeper values. These results suggest that the occurrence of this habitat was mainly associated with intermediate depths. Positive nonlinear relationships were shown for BPIbroad, indicating higher preferences for steep or high-relief areas.

### 3.2.6 | Habitat 10: Bathyal mud with pennatulids (*Kophobelemnon stelliferum*)

This habitat showed a linear and negative relationship with depth, indicating that its occurrence was mainly associated with deeper zones. For BPI, the wide range of values (including negative, zero, and small positive values) for this habitat seemed to be associated with its occurrence on more diverse seafloor types, i.e. from depressions, to flat areas, to constant slopes, to small crests, whereas the clear negative relationship for values greater than 15 indicated that the presence of this habitat was not associated with steep or high-relief areas. The shape of the smoothed fitted function line for eastness suggested a certain preference for slopes with a north-east or south-east orientation.

### 3.2.7 | Habitat 11: Bathyal mud with *Isidella elongata*

This habitat seemed to occur on areas characterized by low–medium slope values. A negative linear relationship was shown for northness, suggesting a preference for south-facing slopes. The BPI showed a positive trend: this trend was particularly clear for values from −20 to +25, which indicated a higher probability of occurrence of this habitat in flat areas, constant slopes, and small crests.

### 3.2.8 | Habitat 12: Bathyal detritic sand with solitary scleractinians (*Caryophyllia smithii*)

The effect of depth on the probability of the presence of this habitat peaked in value around −270 m, with a clear negative relationship for shallower values and a positive relationship for deeper values. This habitat seemed to be mainly associated with areas at intermediate depths in the study area. Negative linear relationships were shown for the slope and northness aspect, suggesting a preference for flat areas or areas with low slopes that faced south.

### 3.2.9 | Habitat 13: Circalittoral detritic sand with pennatulids (*Pennatula rubra*)

Negative relationships were found for backscatter and positive relationships were found for northness aspect, suggesting that an increase in its probability of occurrence was associated with softer bottoms in areas with slopes orientated to the north.

The nine final models of each habitat resulted in nine different prediction maps (Figure 3). The distribution patterns of these benthic habitats were rather different: whereas some habitats had clear and highly localized geographical locations (e.g. habitats 1 and 13), others had widely dispersed distribution patterns across the study area (e.g. habitats 8 and 10). The final map that showed the highest probability of presence of each habitat in each pixel is shown in Figure 4. Habitats 1, 3, 4, and 13 are restricted to the summit of the central guyot, whereas habitats 8 and 9 are bound to the surrounding ridges, and habitats 10, 11, and 12 appeared to be associated with deep flat areas all around the seamount.

## 4 | DISCUSSION

The high predictability of models based on habitat occurrences characterized by habitat-forming species resulted in a fine-scale map with full coverage showing the potential distribution of benthic habitats on the Seco de los Olivos seamount. Based on this map and the environmental variables used, five different geomorphological features that host a great diversity of vulnerable habitats present on this seamount were identified, which can be used to inform the spatial management of the benthic habitat of this seamount. The robustness of this methodological approach leads us to propose it as a blueprint for other areas of the Natura 2000 marine network.

### 4.1 | Performance of predictive models

Most of the models have a high predictability (AUC > 0.8 and Kappa > 0.40), indicating that predictions based on habitat occurrence (i.e. presence or absence) data can be sufficiently accurate to be used in management and conservation planning. All these habitats are characterized by habitat-forming taxa, which are located in an area with optimal conditions for their occurrence. Our results are consistent with the statement by Gonzalez-Mirelis and Buhl-Mortensen (2015), who proposed that habitat-forming species are easier to model than non-habitat-forming species. Only two models (habitats 3 and 9) have Kappa values of <0.40. This lower performance could be explained to some extent by the low number of samples (with presence records of these habitats) recorded from the ROV transects and by their greater heterogeneity. These habitats encompassed a suite of different species with a wide

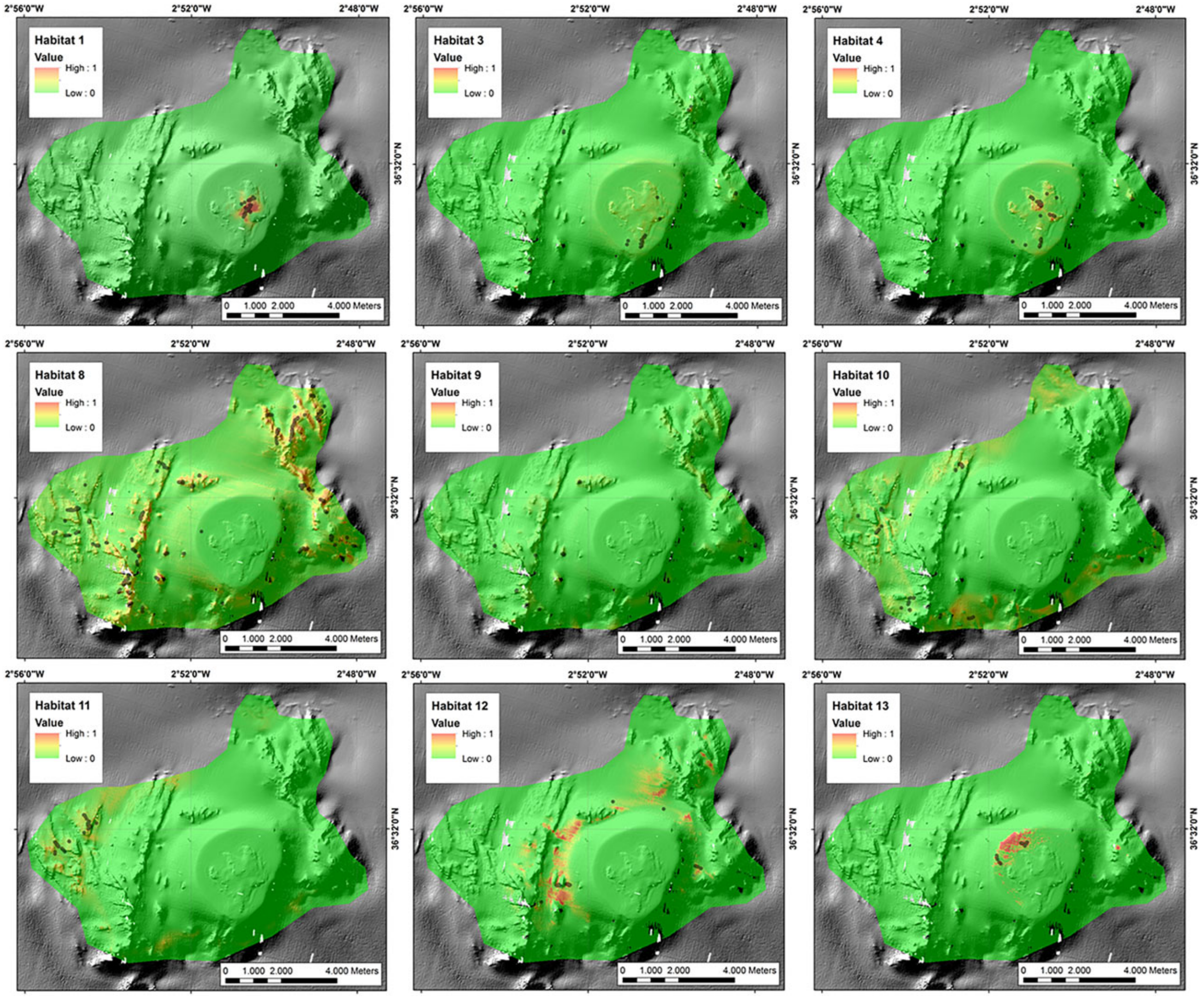

**FIGURE 3** Maps of probability of the presence of every benthic habitat modelled. The presence points for each habitat are superimposed in grey

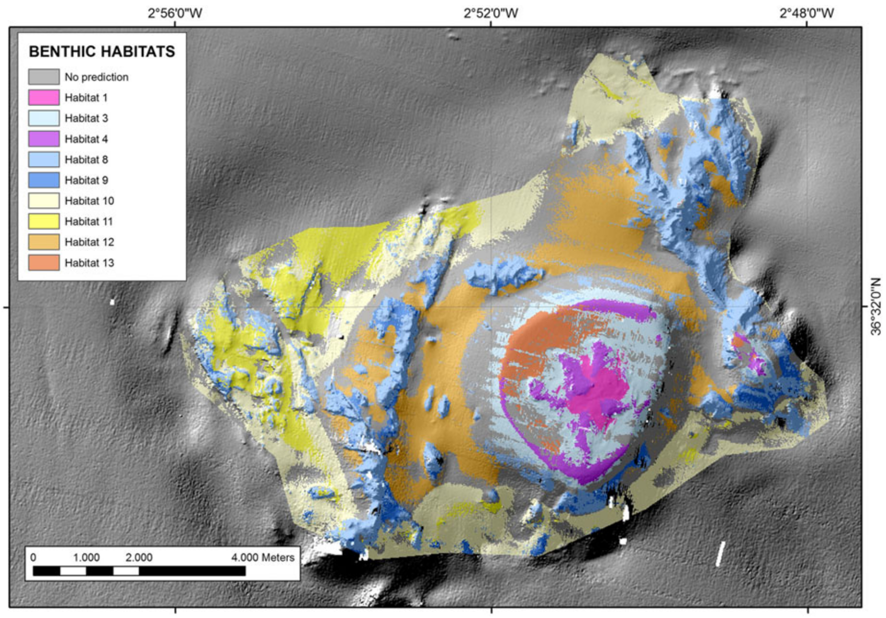

**FIGURE 4** Benthic habitat map (i.e. indicating highest probabilities of presence) of the Seco de los Olivos seamount

range of responses to environmental conditions. Zimmermann and Kienast (1999) found similar results and stated that ubiquitous species that possess a high tolerance to environmental variability, eurioic species with a wide range of responses to environmental variables, and multi-specific habitats composed of several representative species, may explain, among other factors, the lower performance of the models. Conversely, the high performance of some of their models was a result of dealing with a single species and, thus, a uniform response.

## 4.2 | Main environmental predictors associated with benthic habitat distribution

Distribution models (DMs) are commonly used to provide insights into the environmental drivers that control species or habitat distributions (e.g. Fournier, Barbet-Massin, Rome, & Courchamp, 2017; Stirling, Scott, & Wright, 2016). Depth and slope have been cited among the main environmental predictors associated with the zonation of benthic communities on seamounts (De la Torriente et al., 2018; Du Preez, Curtis, & Clarke, 2016; McClain & Lundsten, 2015; Serrano et al., 2017). Distributed as depth-regulated bands, these assemblages or habitat structure patterns are likely to be a combination of suitable ecological conditions and local recruitment processes (De la Torriente et al., 2018). Low slope values are associated with rocky flat areas of high hydrodynamism, or with areas of sediment deposition, whereas higher values indicate potentially rocky outcrops and ridges. Our results, together with these two variables, highlighted the importance of BPI in habitat distribution, which contributes to the amplification of the local currents and changes in the sedimentation processes (Mohn & Beckmann, 2002), with both physical processes being relevant for filter-feeding fauna (Gage & Tyler, 1991). All the habitat-forming species of the modelled habitats were sessile filter-feeding species, such as cold-water corals and other solitary scleractinians, bamboo corals, and other gorgonians, black corals, sea pens, and large sponges. These species rely on the aggregation of organic particles and the low rates of sedimentation generated by medium–strong currents to feed, and to avoid being smothered (e.g. DeVogelaere et al., 2005; Gori et al., 2011; Teichert, 1958; Wagner, Luck, & Toonen, 2012). This effect is particularly evident for species located on elevated features both at the summit of the guyot (e.g. habitat 4) and in the surrounding ridges (e.g. habitats 8 and 9).

The complex hydrodynamics, derived from the complex geomorphology of the area, may partially explain the patchy distribution of the benthic habitats (Palomino et al., 2011). Although the Atlantic Water of the Alboran Sea flows eastwards, affecting only the summit of the guyot (habitats 1, 3, 4, and 13), the Levantine Intermediate Water flows towards the west in a deeper layer, influencing the sea floor of the rest of the modelled habitats (habitats 8, 9, 10, 11, and 12). The meeting of this Mediterranean water mass with the seamounts located in this area splits the water mass into strands flowing on either side around the seamount (Hernández-Molina et al., 2006). As topographical barriers, seamounts affect the pathway and velocity of currents and the sedimentary processes (Hernández-Molina et al., 2006; Howe et al., 2006; Owens & Hogg, 1980), producing morphological features that range from moats, excavated by stronger areas of flow, to depositional tails on leeward sides (Palomino et al., 2011).

Not all of the predictors were equally significant for all of the modelled habitats. Even though benthic habitats are highly dependent upon the type of substrate, it was remarkable that our results did not note backscatter as one of the most important predictors. The backscatter intensity provides indications on the nature of the substratum, i.e. its roughness and hardness, and indirectly provides information related to fauna, flora, and biodiversity (e.g. Brown & Blondel, 2009; Brown, Smith, Lawton, & Anderson, 2011). Consequently, backscatter is a valuable parameter as a high-resolution proxy for benthic habitat identification (Collier & Brown, 2005; Serrano et al., 2017). Furthermore, some authors have obtained clear correlations between backscatter and grain size (Collier & Brown, 2005; De Falco et al., 2010; Goff, Olson, & Duncan, 2000), and the reflective strengths on the Seco de los Olivos seamount were used to identify the occurrence of carbonate coral mounds, well-sorted bioclastic coarse sands, and coarser sediment fractions (Lo Iacono et al., 2008). Although the results showed a slight correlation between the backscatter values and the type of substrate (Figure S3), the correlation was not strong enough to clearly distinguish between the soft and hard bottom values for all transect lines in the study. This, in part, could be caused by sedimentary depressions that may contain a sediment veneer above the rocky bottom, with a thickness that is sufficient to host some habitat-forming species that are typical of soft benthic habitats. Despite the signal intensity that was reflected by the rocky sea floor (backscatter data), the visual examination of the ROV images revealed the dominance of soft bottoms. Additionally, the highly patchy distribution of benthic habitats on this seamount may generate disassociation between the scales of the backscatter and the ROV data that were used. In some areas, some habitats only extended for a few metres, but a larger scale was used to obtain the backscatter data than that used for the biological component.

## 4.3 | Distribution patterns of the modelled benthic habitats

The main environmental drivers of habitat distribution were depth, slope, and BPI. Based on this result, five different geomorphological areas were distinguished: (i) top of the central guyot, where habitats were characterized by lower values of depth and slope; (ii) crests of the two surrounding ridges, where habitats with a clear preference for deeper areas and higher BPI values appeared; (iii) flat bottoms or depressions in the terrain, where the only habitat identified was characterized by areas with low slope values at intermediate depths; (iv) slight slopes on deep-sea bottoms, where habitats occupied areas with intermediate and higher depths and with lower values of slope and BPI; and (v) channels or transitional bottoms, where no biological components were found to characterize the habitats (Figure 5; for a 3D video showing the potential pattern of habitat distribution see Video S1). The general pattern of distribution predicted by the models agrees with expectations from previous research on this seamount, in which the occurrences of highly diverse patchy habitats were

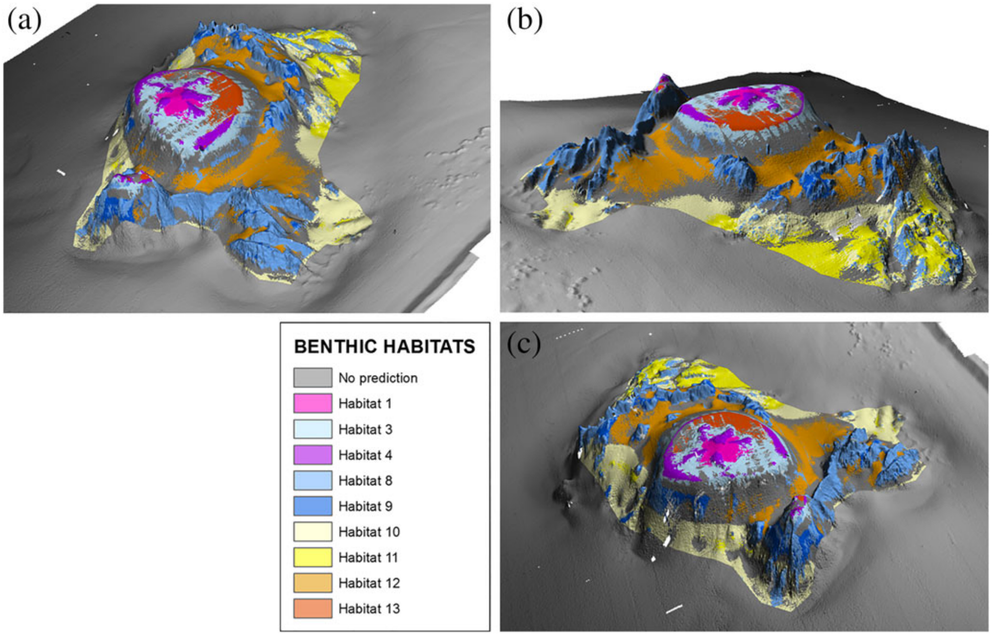

**FIGURE 5** Benthic habitat 3D maps of the Seco de los Olivos seamount: (a) viewed from the north-east; (b) viewed from the north-west; and (c) viewed from the south-east

associated with a specific combination of environmental characteristics (De la Torriente et al., 2018).

### 4.3.1 | Top of the central guyot

The probability of the presence of four habitats were restricted to the summit of the flat-top main elevation: habitat 1 was clearly localized on depressions found on the central area of the summit, whereas habitats 3 and 4 showed a preference for slightly elevated rocky areas; and finally habitat 13 showed a preference for the soft bottoms of the north-western area.

In line with the distribution recorded for habitat 1, large concentrations of living rhodoliths have been found in other regions from the low-intertidal zone to depths of 150 m, typically in areas with sufficient light for growth, and with high enough water motion to inhibit burial by sediment but not so high or unidirectional to cause mechanical destruction or the rapid transport of individuals away from favourable growing conditions (Ballesteros, 1988; Foster, 2001). The occurrence of habitat 4, which was linked to dense coralligenous communities, was also mainly determined by light exposure (Casas-Güell, Teixidó, Garrabou, & Cebrian, 2015), and therefore this habitat was limited to the shallowest bottoms of the study area. One of the main singularities of this seamount is that its summit is within the photic zone; therefore, communities that included algae could develop. Classified as a 'shallow seamount', this peculiarity makes the development of unusual shallow-water habitats that considerably differ from the surrounding deep ocean possible (Ramos et al., 2016).

The distribution of the habitat-forming species that characterized these habitats at the top of the guyot was also consistent with previous descriptions of their distributions in other areas: *Alcyonium palmatum* was found on soft bottoms of the Atlantic Ocean and Mediterranean Sea, at depths from 20 to 200 m, fixed to shells, pebbles, or small stones (Gili & Pagès, 1987; Weinberg, 1977). *Chironephthya mediterranea* was found at a depth range of 115–200 m, although most of the colonies were present between 150 and 185 m. Colonies were mainly observed growing on rocky bottoms and boulders, covered by a fine sediment veneer, and most colonies were observed growing on slight and intermediate inclinations. In areas that were exposed to currents, the species could reach high densities (López-González, Grinyó, & Gili, 2015). Both *Eunicella verrucosa* and *Paramuricea clavata* also dwelled on circalittoral bottoms, with distributions mainly driven by the requirement for hard bottom substrates, as their basal holdfast requires a stable substratum upon which to attach. These species were mainly associated with more vertical slopes (Gori et al., 2011; Hiscock, 2007). Finally, *Pennatula rubra* also occurs in the shallow waters of the Atlantic and Mediterranean, but has adapted to live on silty, sandy/silty, and sandy/muddy bottoms (Chimienti, Angeletti, & Mastrototaro, 2018; Chimienti, Maiorano, & Mastrototaro, 2015; Gili & Pagès, 1987), with an anchoring muscular peduncle (Bayer, 1956; Williams, 2011).

### 4.3.2 | Crests of surrounding ridges

Suitable areas for the occurrence of two bathyal habitats, habitats 8 and 9, were restricted to the crests of the two surrounding ridges. Both habitats appeared on hard bottoms, although they showed different values of backscatter. This finding is probably related to the diverse typologies recorded for habitat 9, which appeared on two different types of substrate: as reef on a coral framework in areas with high levels of sedimentation and as discrete colonies on rocky areas. These different morphologies of the same habitat have also been described from the Galicia Bank, which is another seamount that is part of the Spanish Natura 2000 network (Serrano et al., 2017).

The filter-feeding species characterizing these habitats are typical of rocky areas with strong hydrodynamism. The occurrence of cold-water corals, such as *Madrepora oculata*, on exposed areas may be related to a compromise between protection from the sediment and exposure to the water flow, which ensures feeding (Gori et al., 2013). The black coral *Leiopathes glaberrima* has also been cited as a species that thrives especially on exposed, steep rocky bench terraces or platforms (Bo et al., 2014; Mytilineou et al., 2014), or among white coral reefs (Angeletti et al., 2014; D'Onghia et al., 2010; Mastrototaro et al., 2010). Similarly, the occurrence of gorgonian species, such as *Acanthogorgia hirsuta* and *Swiftia pallida*, have been previously described on exposed rocks and boulders, showing a distribution ranging from circalittoral to bathyal zones (Grinyó et al., 2016; Raimundo et al., 2013; Wilding & Wilson, 2009). On the other hand, habitat 8 was the only habitat that was typified by sponges. Consistent with other studies on seamounts, sponges dwell close to steep escarpments (Davies et al., 2015; Serrano et al., 2017).

### 4.3.3 | Flat bottoms or depressions in the sea bed

The distribution of habitat 12 was restricted to soft substrates at intermediate depths around the central guyot. Two different forms of the habitat-forming species *Caryophyllia smitthi* have been described, i.e. a cylindrical robust shallow-water form (*Caryophyllia smithii* var. *smithii*) and a smaller and delicate deep-water form with an inverse cone shape (*Caryophyllia smithii* var. *clavus*) (Manuel, 1988). Sometimes the narrow base of this latter form becomes detached from the substrate, and it lives freely on the sea bed, generally in less turbulent waters than the more robust shallow-water form (De Kluijver & Ingalsuo, 2014; Manuel, 1988). On the Seco de los Olivos seamount, *Caryophyllia smitthi* was recorded as half-buried free-living corals, which corresponded to the deep-water form. Generally, this smaller form is taller in height to escape smothering (Bell & Turner, 2000). Its high probability of occurrence is associated with areas with low backscatter values (see Figure S1), where hard bottoms are not present, and this suggests that the species is transported by water currents far from their point of dislodgement.

### 4.3.4 | Slight slopes on deep-sea bottoms

The presence of habitats 10 and 11 were restricted to soft substrates located in deeper areas along the outer flanks of the seamount. The two habitat-forming species of these habitats, *Kophobelemnon stelliferum* and *Isidella elongata*, have been observed on soft bottoms at similar depths or at even deeper depths in other regions of the Mediterranean Sea (Gili & Pagès, 1987; Lauria et al., 2017). These two filter-feeding species that live on mud bottoms depend on medium–strong currents for the local enrichment of food availability, but they generally occur in less turbulent waters than the other more robust coral forms to avoid high sedimentation rates (De Kluijver & Ingalsuo, 2014; Lauria et al., 2017).

### 4.4 | Methodology approach and recommendations on zoning activities for the design of management plans for MPAs

The modelling and mapping techniques used in this study provide insights into the potential distribution of benthic habitats at the EUNIS level 4 and VMEs on a seamount located in an MPA. This information is crucial for promoting the development of a suitable zonation plan that can protect ecosystem functions and biodiversity on the Seco de los Olivos seamount.

Eight of the nine habitats modelled and mapped in this study are priority conservation habitats, according to the EU Habitats Directive and the Barcelona Convention, and only habitat 12 is not listed on any conservation reference list. The presence of this wide range of habitats with high ecological importance has important implications for biodiversity conservation in the area. The final map supports the high probability of the presence of VMEs over the entire extent of the seamount, as only areas located on 'flat bottoms or depressions in the sea bed' and in 'channels or transitional bottoms' showed a low probability of occurrence of any of the vulnerable benthic habitats that were modelled and mapped.

Habitat 1, although not considered to be a specifically protected habitat in the Habitats Directive, is included under 'Habitat 1110: Sandbanks which are slightly covered by sea water all the time' together with other habitats such as sand bottoms and *Cymodocea nodosa* meadows, or under 'Habitat 1170: Reefs', together with other habitats such as cold-water coral reefs or mixed facies of gorgonians, depending on the specific criteria adopted. The same problem applies to habitats on rocky bottoms that are characterized by corals and sponges (habitats 3, 4, 8, and 9): because they are not a specifically protected habitat, all are included under 'Habitat 1170: Reefs'. This is even more problematic in the case of habitats on soft bottoms that are characterized by pennatulids (habitats 10 and 13) or gorgonians (habitat 11), which are not considered by the directive at all. Adopting such broad definitions for the habitats may, however, lead to some confusion (Barberá, Moranta, Ordines, & Ramón, 2012), highlighting the need for their review and improvement, as previously recognized by other authors (Dotinga & Trouwborst, 2009; Evans, 2006). Conversely, the eight priority conservation habitats modelled in this study have already been proposed for integration within the Habitats List of the Barcelona Convention in the framework of the Mediterranean Action Plan of the United Nations Environment Programme (UNEP/IUCN). There are two differences, however: *Viminella flagellum* on bathyal rock instead of circalittoral rock and *Savalia savaglia* on circalittoral rock instead of bathyal rock.

By knowing the spatial distribution and the extent of the main benthic habitats in the area, a proper multiple-use zoning approach can help to protect biodiversity and separate conflicting activities, providing high levels of protection for specific areas whilst allowing for reasonable use, including certain fishing activities, in other specially designated areas. Similarly, the main activities that occur in this area should be considered during the design of the management plan for the entire MPA. Maritime traffic and fisheries (including purse-seine fishing, bottom trawling, gill nets, longline fishing, and sport fishing) have been described as the main threats facing biodiversity in the Seco de los Olivos seamount

(De la Torriente et al., 2014). Specifically, demersal fishing has a great impact on benthic habitats through erosion and breakage of the substrate and habitat-forming species, causing a loss of biodiversity and long-term shifts in the community structure. This zoning approach should be implemented in conjunction with other management tools and represents one more step towards fulfilling the main European policies, such as the Marine Strategy Framework Directive (2008/56/CE), the Habitats Directive (92/43/CEE), and the Directive on Establishing a Framework for Maritime Spatial Planning (2014/89/EU).

The methodological approach of 'ensemble first – predict later' used in this study was previously applied to marine ecosystems by Moritz et al. (2013) in the Gulf of Saint Lawrence (Canada). The process involves two different steps: first to identify the different benthic habitats present in the study area using multivariate techniques, and then assign each sampling point to each specific habitat; and second to apply DMs to the resultant presence/absence points in order to predict the habitat distribution in the whole area. This technique has been criticized by Baselga and Araújo (2010) for producing the simultaneous occurrence of different habitats that do not co-occur in reality, and consequently new modelling techniques with a different approach in which both steps are carried out at once are being developed (Dunstan, Foster, & Darnell, 2011; Foster, Givens, Dornan, Dunstan, & Darnell, 2013). In this study, however, there is not any significant overlap between habitats and the results presented prove to have a high predictability, probably linked to the fine scale used to define the habitat concept. Adopting broad definitions for assemblages or habitats may lead to a greater degree of overlapping, which underlines the need of developing a clear definition of habitat in the context of modelling and mapping. The clear zonation of the benthic habitats obtained in the area of study, and the robustness of the methodological approach used, leads us to propose it as a blueprint for other areas of the Natura 2000 marine network.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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