Modeling sensitive elasmobranch habitats

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ABSTRACT

Basic information on the distribution and habitat preferences of ecologically important species is essential for their management and protection. In the Mediterranean Sea there is increasing concern over elasmobranch species because their biological (ecological) characteristics make them highly vulnerable to fishing pressure. Their removal could affect the structure and function of marine ecosystems, inducing changes in trophic interactions at the community level due to the selective elimination of predators or prey species, competitors and species replacement. In this study Bayesian hierarchical spatial models are used to map the sensitive habitats of the three most caught elasmobranch species (*Galeus melastomus*, *Scyliorhinus canicula*, *Etmopterus spinax*) in the western Mediterranean Sea, based on fishery-dependent bottom trawl data. Results show that habitats associated with hard substrata and sandy beds, mainly in deep waters and with a high seabed gradient, have a greater probability registering the presence of the studied species than those associated with muddy shallow waters. Temperature and chlorophyll-α concentration show a negative relationship with *S. canicula* occurrence. Our results identify some of the sensitive habitats for elasmobranchs in the western Mediterranean Sea (GSA06 South), providing essential and easy-to-use interpretation tools, such as predictive distribution maps, with the final aim of improving management and conservation of these vulnerable species.

1. Introduction

There is increasing concern worldwide over elasmobranch species because their K-selection life-history traits make them susceptible to population depletion as a result of anthropogenic activity, including unsustainable fisheries, by-catch, and habitat modification (Dell'Apa et al., 2012). Most elasmobranchs are predators at or near the top of marine food chains and thus, play an important role in marine ecosystems, potentially regulating the size and dynamics of their prey populations (Stevens et al., 2000). Their removal could affect the structure and function of marine ecosystems, inducing changes in trophic interactions at the community level due to selective removal of predators or prey species, competitors and species replacement.

In the Mediterranean Sea, this is of particular concern since sharks and rays make up an important percentage of the by-catch (Carbonell and Azevedo, 2003) and their mobile nature makes them potentially accessible to several fisheries at various bathymetric ranges (Ferretti et al., 2008). Bottom trawling is considered responsible for a large proportion of the by-catch of elasmobranch species in the Mediterranean Sea, and throughout the world in general (Maravelias et al., 2012). Evidence of changes in the number of elasmobranchs and the decrease in the abundance of several species (e.g. *Raja clavata* and *Dipturus batis*) over

the last decade has been reported for the whole of the Mediterranean Sea and in particular, for the highly exploited area of the Gulf of Lions (Abdulla, 2004). As a result cartilaginous fishes can be used as ecological indicators and their study and monitoring are considered essential for the conservation of the marine ecosystem (Stevens et al., 2000).

In 2009 the European Commission adopted the first Action Plan for the conservation and management of elasmobranchs (EU, 2009) with the aim of rebuilding their stocks under threat, and of setting down guidelines for the sustainable management of the fisheries concerned. Moreover, the implementation of an ecosystem approach to fisheries management (EAFM) and marine spatial planning (MSP) contemplates the protection of priority habitats, a policy of reducing by-catches and the study of current and expected impacts with a view to preparing efficient strategies for the preservation of the marine environment and in particular its living marine resources (Katsanevakis et al., 2009).

In order to achieve these purposes the prerequisites are a solid knowledge of species–environment relationships and the identification of priority areas using robust analysis of existing information and databases (Massutí and Moranta, 2003). Habitat and species mapping is essential for conservation programs because it provides a clear picture of the distribution and extent of these marine resources, and thus facilitates managing the marine environment (Barberá et al., 2012).

Following Soberón and Peterson (2005) and Soberón (2010) these objectives can be achieved by either using Species Distribution Models

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(SDMs; models containing biotic or accessibility predictors and/or being limited in spatial extent) or Ecological Niche based Models (ENMs; for forecasting an approximation to the species' niche) (Guisan and Zimmermann, 2000; Wiens et al., 2009). On the one hand, the theoretical framework of ENMs is based on the ecological niche concept which identifies a niche as a subdivision of the habitat containing the environmental conditions that enable individuals of a species to survive and reproduce, based on broad-scale variables (climate) that are not affected by species density (Sillero, 2011). On the other hand, SMDs aim to predict quantities of interest at unsampled locations based on measured values at nearby sampled locations, within the range of environments sampled by the training data and within the same general time frame as that in which the sampling occurred.

In line with the SMD context, our study aims to identify sensitive habitats of elasmobranch species and develop probabilistic spatial scenarios as effective tools for supporting decision-making within the conservation framework. To this end we have analyzed a group of georeferenced data of the presence/absence of the most common demersal cartilaginous species collected from fishery-dependent bottom trawl sampling carried out along the continental shelf and slope of the Western Mediterranean Sea (GFCM Geographical Sub Area 06) during a six-year period of time. In particular, we have modeled the occurrence data of the three most frequently captured species: smallspotted catshark (*Scyliorhinus canicula*, Linnaeus, 1758), blackmouth catshark (*Galeus melastomus*, Rafinesque, 1810) and velvet belly (*Etmopterus spinax*, Linnaeus, 1758), which comprise more than 80% of the total demersal elasmobranch abundance caught during the period 2006–2011. Cluster Analysis (CA) and Multi Dimensional Scaling (MDS) techniques have been applied to observers' data in order to verify whether the three species studied are in fact representative of the whole elasmobranch community of this area.

To accomplish spatial prediction, ordinary kriging can be used to obtain the best linear unbiased predictor. However, accuracy is not always easy to achieve because there is often a large amount of variability surrounding the measurements of response and environmental variables, and traditional prediction methods, such as ordinary kriging, do not account for an attribute with more than one level of uncertainty. This variability leads to uncertain predictions, and consequently to uninformed decision making. In order to solve this problem, we have chosen to use hierarchical Bayesian spatial models and Bayesian kriging has been used.

In our approach, one of the additional advantages is the possibility of integrating current modeling approaches (such as GLM and GAM) and uncertainty analyses into a more general hierarchical framework. Within the Bayesian framework, full inference about uncertainty, given what we have observed (the data) and what we know or assume about the process (the model), comes free with the model predictions (Banerjee et al., 2004). Spatial autocorrelation can be incorporated into a regression model through random effects that capture spatial dependence in the data (Latimer et al., 2006). Since the random effects are model parameters, they also emerge with a full posterior distribution that allows quantification of uncertainty. Hierarchical stages can describe conceptual but unobservable latent processes that are ecologically important, as well as error in the observation process or gaps in the data (Gelfand et al., 2006).

However, until recently, it was computationally quite expensive to calculate these Bayesian hierarchical models with this spatial structure. In this study we overcome this problem by using the integrated nested Laplace approximation (INLA) methodology and software (http://www.r-inla.org). INLA provides accurate approximations to posterior distributions of the parameters, even in complex models, in a fast computational way (Rue et al., 2009). In addition, INLA can be used through R software, providing a familiar interface with the programming of the model.

But, more importantly to us, this methodology allows us both to estimate the processes that drive the distribution of elasmobranchs and also to generate predictive maps of the distribution of species in the study area, especially in non-observed locations.

The establishment of regional marine protected areas for protecting sensitive habitats would benefit from an improved understanding of the spatial distribution of vulnerable species, such as elasmobranchs, and could help towards the more efficient management and control of marine resources.

2. Material and methods

The study area was the Gulf of Alicante (Western Mediterranean), between 37° 15.6′ and 38° 30.0′ N, and 1° 0.0′ W and 0° 30.0′ E (Fig. 1). The Gulf of Alicante has a surface area of 3392 km² and an average shelf width of approximately 32 km. The largest fleet is the bottom trawl one, with 169 vessels landing an average of 8000 t per year. Seabed trawling usually takes place on the shelf, yielding a multispecific catch with European hake (*Merluccius merluccius*) as the main target species. The elasmobranch species most frequently caught are: *G. melastomus*, *S. canicula*, *E. spinax*, *R. clavata*, *Raja asterias* and *Squalus acanthias*. Their distribution and abundance vary according to depth.

2.1. Data

The data set includes 400 hauls of 25 different trawler vessels and has been provided by the Spanish Oceanographic Institute (Instituto Español de Oceanografía, IEO). The IEO provides the national input of the European Observers Programme for collecting fishery-dependent data. In particular, they collect samples from the commercial fleet with observers on board. This sampling has been carried out since 2003, usually involving about 2–3 observer samplings every month for the trawler fleet, accounting for an average of 10 hauls monthly. From this database we have used the geographical location and occurrence of the elasmobranch species for each haul. The fisheries were multispecies and none of the elasmobranchs were target species.

Extrinsic factors influencing the spatial distribution of elasmobranch species used were depth, which is often the main gradient along which faunal changes occur when analyzing shelf and upper slope assemblages (Kallianiotis et al., 2000), type of substratum (Demestre et al., 2000), slope of seabed and physical characteristics of the water masses (Maravelias et al., 2007).

For ocean processes, chlorophyll-α concentration and Sea Surface Temperature (SST) data can be used to locate thermal and productivity-enhancing fronts and marine productivity hotspots and thus determine the influence of such features on species distribution (Valavanis et al., 2008). In addition, SST and Chl-α are also strong functional links between surface primary productivity and biological activity at the sea floor through the episodic deposition of particulate material (Nodder et al., 2003, Leathwick2006). Previous studies have shown that the distributions of many demersal fish species are likely to be influenced by overall ecosystem productivity (Hopkins and Cech, 2003; Leathwick et al., 2006; Martin et al., 2012; Matern et al., 2000).

In particular, Chl-α concentration can be used as an index of primary production of an ecosystem (de Leiva Moreno et al., 2000). Obviously, primary production depends on a range of factors, including light, light penetration and temperature, which could not be taken into account here due to the absence of data. Nevertheless, the mean value of Chl-α concentration can be used as an independent index of primary production in the area of interest, since its variability could modify trophic conditions of the species' habitat from oligotrophic to mesotrophic (Katara et al., 2008).

Sea Surface Temperature (SST) is strongly related with primary productivity and is thus a possible candidate to explain the distribution of the species (Valavanis et al., 2004). Previous studies on
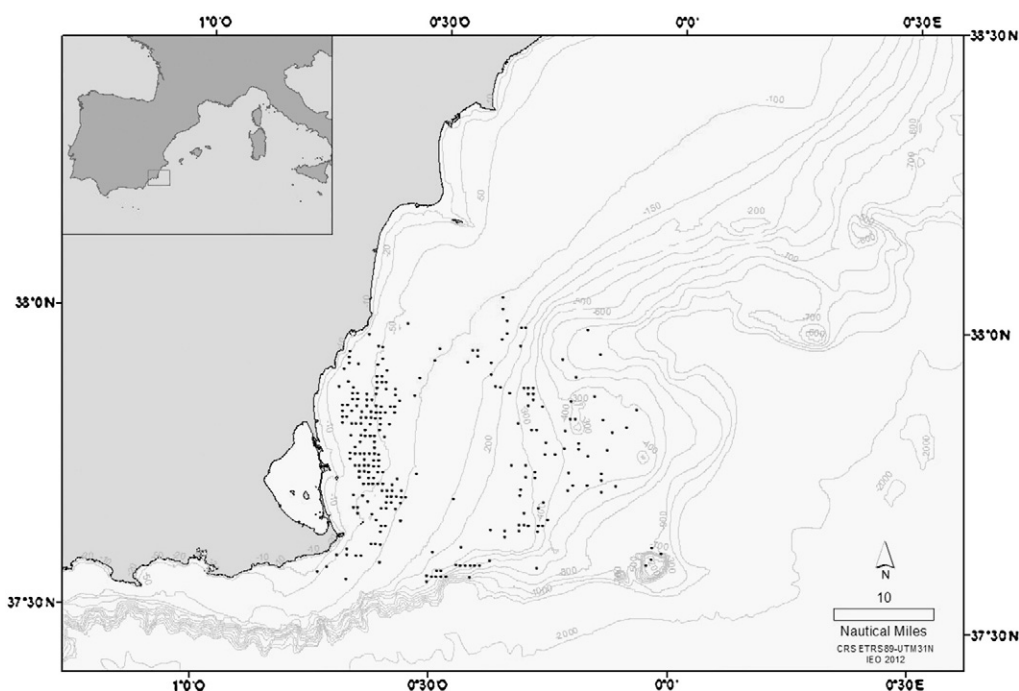
Fig. 1. Map of the study area with the sampling locations indicated by black dots.

elasmobranchs have implied that SST plays an important role in their distribution (Martin et al., 2012; Matern et al., 2000) from a physiological standpoint. The majority of coastal elasmobranchs are ectothermic and changes in the environmental temperature are rapidly transferred to the body of the animal, thus impacting most physiological processes (Hopkins and Cech, 2003).

The environmental satellite (SST and chlorophyll-α) data has been extracted as a monthly mean from the SeaWiFS (http: oceancolor.gsfc.nasa.gov). We have interpolated the raster surface of the SST and chlorophyll-α variables, using the *Spline* tool of ArcGIS 10. The *Spline* method is an interpolation method that estimates values using a mathematical function that minimizes overall surface curvature, resulting in a smooth surface that passes exactly through the input points. In particular, we have used the *Tension* method, which controls the stiffness of the surface according to the character of the modeled phenomenon. This method creates a less smooth surface with values more closely constrained by the sample data range (http://help.arcgis.com/en/arcgisdesktop/10.0/help/index.html//009z0000006q000000.htm) (Fig. 2A, B).

Bathymetry and type of substratum data were obtained from the IEO geoportal, accessible through the website of the Spanish Institute of Oceanography (http:www.ieo.es). In order to obtain the value of depth at any precise location of the study area we have interpolated the bathymetric map, using GRASS GIS (http://grass.fbk.eu), first rasterizing contours with a resolution of 500 m and then using the function *r.surf.contour*, following guidelines given in the website (http: grass.osgeo.org/wiki/Contourlines_to_DEM) (Fig. 2C). Log transformed bathymetry was included in the analysis for smoothing the effect and preserving the linearity of this variable.

The slope map has been derived by the bathymetry map, using the *Slope* tool of the ArcGIS 10. Slope values reflect the maximum rate of change (in degrees) in elevation between neighboring values derived with ArcGIS Spatial Analyst extension (http:\\webhelp.esri.com/arcgisdesktop/10/index.cfm?TopicName = How%20Slope%20works) (Fig. 2D).

The type of substratum polygon shapefile includes a classification of ten categories and a reduced version with four levels: Sand, Mud, Gravel and Rock. In order to reduce the level of variability in the analysis, since we have no observations in all categories, we have

used the simplified version (Fig. 2E). Moreover, in the study area there are no areas of gravel, so the categories have been reduced to the remaining three.

In order to make it possible to work in the R framework maps have been transformed into *SpatialPolygonsDataFrame* objects using the sp R package.

2.2. Multivariate analysis

Our data set includes 23 different elasmobranch species. We used multivariate analysis techniques in order to verify whether the three most captured species (*S. canicula*, *G. melastomus* and *E. spinax*) were truly representative of the whole elasmobranch community in this area. In particular, we applied Cluster Analysis (CA) and Multidimensional Scaling (MDS) techniques to analyze the 400 bottom trawl hauls. If results show a high degree of similarity in the species assemblage of the different hauls, we can assume that sensitive habitats identified for the three species studied are shared by the remaining elasmobranch species. Consequently, the conservation of these habitats would go a long way to protecting the entire community of elasmobranchs in this area.

Both multivariate analyses were performed on a Euclidean similarity matrix with the average method, considering the occurrence of each species to identify possible differences between the habitats studied.

2.3. Modeling sensitive habitats

The spatial variation in the probability of occurrence of the three most captured species (*S. canicula*, *G. melastomus* and *E. spinax*) was modeled by using a hierarchical Bayesian spatial approach, specifically a point-reference spatial model. These models are highly suitable for situations (such as that of the present study) in which data are observed at continuous locations occurring within a defined spatial domain (geo-referenced Bernoulli data). Note that these models can also be considered as a spatial extension of logistic regression models because the modeling process describes the variability in the response variable as a function of the explanatory variables, with the addition of a stochastic spatial effect, which models the residual spatial autocorrelation (Lindgren, 2012).
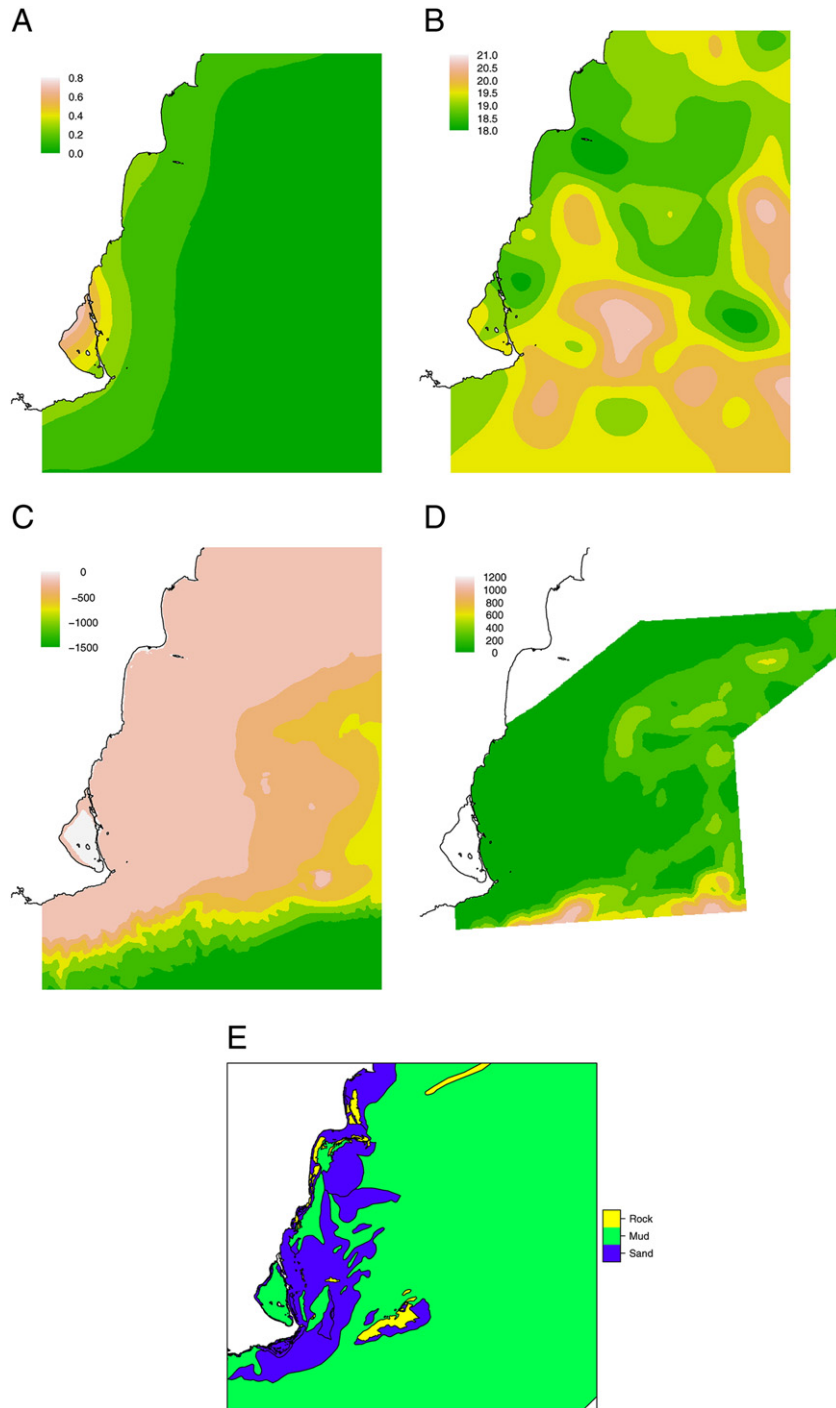
Fig. 2. The spatial patterns of the environmental variables used to map the habitat models, including (A) satellite derived Chlorophyll-α mean values; (B) satellite derived sea surface temperature mean values; (C) bathymetric map; (D) slope map; and (E) seabed sediment type map.

Specifically, the response variable is a binary variable that represents the presence (1) or absence (0) of the species in each fishing location sampled: Z_i represents the occurrence. Consequently, the conditional distribution of the data is $oxZ_i \sim Ber(\pi_{ij})$, assuming that observations are conditionally independent given π_{ij}, which is the probability of occurrence at location i ($i = 1,\dots, n$) and year j ($j = 1,\dots,6$). At the first stage of the hierarchical model, we model the observed data (occurrence of elasmobranchs) as a GLM by using the customary (for binary data) logit link function, but incorporating a spatial and a possible temporal effect. That is,

$$logit\left(\pi_{ij}\right) = X\beta + Y_j + W_i, \tag{2.1}$$

where β represents the vector of the regression coefficients, X is the matrix of covariates, W_i represents the spatially structured random effect, and Y_j is the component of the temporal unstructured random effect at year j, and the logit transformation is defined as $logit(\pi_{ij}) = log(\pi_{ij}/1 - \pi_{ij})$.

W_i is assumed to be Gaussian with a given covariance matrix $\sigma_W^2 H(\phi)$, depending on the distance between locations, and with hyperparameters σ_W^2 and ϕ representing respectively the variance and the range of the spatial effect:

$$W \sim N\left(0, \sigma_W^2 H(\phi)\right). \tag{2.2}$$

2.4. Bayesian inference

Once the model has been determined, the next step is to estimate its parameters. Following Bayesian reasoning, the parameters are treated as random variables, and prior knowledge has to be incorporated via the corresponding prior distributions of the said parameters. In particular, for the parameters involved in the fixed effects, we use the Gaussian distribution $\beta \sim N(0, 100)$. In this second stage of the hierarchical model the uncertainty about the parameters used in the first level is incorporated and propagated across model stages to more accurately reflect overall inferential uncertainty.

In the third, and final, level of hierarchy, prior knowledge about the hyperparameters is expressed. For the temporal effect we assume, following Rue and Held (2005), LogGamma prior distribution on the log-precision λ_y ($a = 1$, $b = 5e-05$). The choice of the priors of the hyperparameters of the spatial effect will be described in the following section.

As usual in this context, the resulting hierarchical Bayesian model has no closed expression for the posterior distribution of all the parameters, and thus numerical approximations are needed. Here, due to speed of computational processing, we use the integrated nested Laplace approximation (INLA) methodology and software (http://www.r-inla.org) as an alternative to the Markov chain Monte Carlo (MCMC) method.

2.5. The INLA framework

To better understand the idea behind this modeling, the key is to think of these models as a particular case of the *Structured Additive Regression* (*STAR*) *models* called *Latent Gaussian models* (Rue et al., 2009). In these models the mean of the response variable Z_i is linked to a structured predictor that accounts for the effects of various covariates in an additive way. Gaussian prior distributions are assigned to all the components of the additive predictor which is the latent Gaussian model.

Here, the latent models represent the elasmobranch occurrence phenomena that exist independently of whether species are observed in a given location or not. Thus, we are not building hierarchical models solely for discretely observed data, but for approximations of entire processes defined on continuous domains. Until recently, the problem was the infeasibility of fitting the particular case of continuously indexed Gaussian models, as is the case with our spatial component W.

Lindgren et al. (2011) have proposed a solution to this problem: the Stochastic *Partial Differential Equation* (*SPDE*) approach. This alternative solution is an explicit link between Gaussian models and the Gaussian Markov Random model (Rue and Held, 2005). The benefits are that the Markov property makes the covariance matrix sparse, enabling the use of efficient (and faster) numerical algorithms and the use of the Matérn covariance function, which is a highly flexible and general family of functions in spatial statistics.

Under this perspective, Eq. (2.2) changes as follows:

$$W \sim N(0, Q(\kappa, \tau)). \tag{2.3}$$

Now the spatial effect depends on two different parameters: κ and τ, which determine the range of the effect and the total variance, respectively. Hyperpriors for κ and τ are centered in values such that the range is about 20% of the diameter of the region and the variance is equal to 1 (Lindgren et al., 2011).

Here, the two major bonuses are that INLA can be used through R, providing a familiar interface with the model specification (see Lindgren, 2012 for a detailed explanation of the INLA syntax) and that inference and prediction in unsampled locations could be performed simultaneously.

INLA provides a variety of approximation strategies for the posterior distributions. In this study we have used the default ones: the simplified Laplace approximation for marginalization, and the Central Composite Design for the numerical integration of the hyperparameters. These are the default and recommended settings providing reasonable accuracy with maximum computational efficiency (Held et al., 2010).

2.6. Model prediction

Once the inference has been carried out, the next step is to predict the occurrence of elasmobranchs in the rest of the area of interest, especially in unsampled locations. Here, we adopted a Bayesian kriging, which allows for the incorporation of parameter uncertainty into the prediction process by treating the parameters as random variables.

A common method for performing prediction with a Bayesian kriging is to take observations and construct a regular lattice over them. In this study, we have considered a more computationally efficient approach. Using the INLA SPDE module we created a triangulation around the sampled points in the region of interest (Fig. 3). As opposed to a regular grid, a triangulation is a partition of the region into triangles, satisfying constraints on their size and shape in order to ensure smooth transitions between large and small triangles. Initially, observations are treated as initial vertices for the triangulation, and extra vertices are added heuristically to minimize the number of triangles needed to cover the region subject to the triangulation constraints. These additional vertices are used as prediction locations.

The triangulation approach has a number of advantages over a regular grid. Firstly, the triangulation is denser in regions where there are more observations and consequently there is more information, and more detail is needed. Secondly, it saves computing time, because prediction locations are typically much lower in number than those in a regular grid. And thirdly, it is possible to take boundary effects into account by generating a mesh with small triangles in the domain of interest, and using larger triangles in the extension used to avoid boundary effects.

After obtaining the prediction in the selected location, there are additional functions that linearly interpolate the results within each triangle into a finer regular grid. As a result of the process, for each point of the area we obtain a predictive posterior distribution of elasmobranch occurrence for the whole study area. This means that for each posterior distribution, unlike the mean and confidence interval produced by classical analyses, we are able to make explicit probability statements about the estimation of elasmobranch occurrence.

2.7. Model selection

Models were compared considering two criteria: the Deviance Information Criterion, usually denoted as DIC (Spiegelhalter et al., 2002), which is computed routinely by INLA as the default criterion for comparing hierarchical models; and the Conditional Predictive Ordinate (CPO), which has been used as a predictive measure (of the models). In particular, as indicated by Roos and Held (2011), we computed the mean logarithmic CPO (LCPO). Lower values for both DIC and LCPO represent the best compromise between fit and parsimony.

2.8. Model evaluation and calibration

The dataset was randomly split into two main subsets: a training dataset including 70% of the total observations, and a validation dataset containing the remaining 30% of the data. The relationship between occurrence data and the environmental variables was modeled by using the training dataset and the quality of predictions was then assessed by using the validation dataset. We repeated validation 10 times for the best model for each species and results were averaged over the different random subsets.

We performed a validation procedure to formally evaluate overall model prediction using the area under the receiver-operating
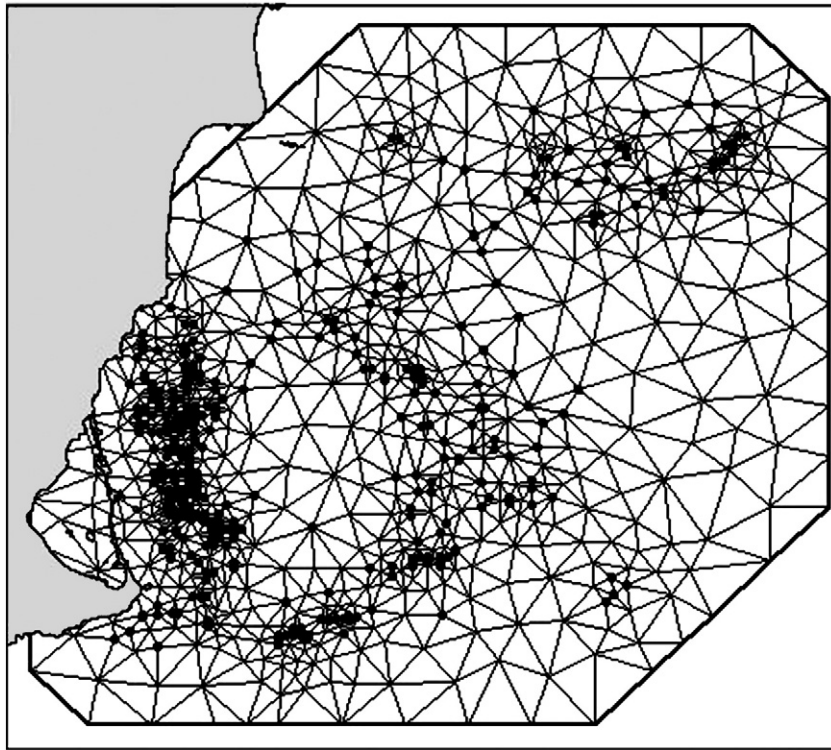
Fig. 3. The triangulation of the Gulf of Alicante. The (●) marks the fishing locations.

characteristic curve (AUC) (Fielding and Bell, 1997), specificity, sensitivity and kappa.

AUC measures the ability of a model to discriminate between those sites where a species is present and those where it is absent, and has been widely used in the species distribution modeling literature (Elith et al., 2006). AUC ranges from 0 to 1, with values below 0.6 indicating a performance no better than random, values between 0.7 and 0.9 considered as useful, and values > 0.9 as excellent. AUC is tabulated through the confusion matrix indicating the true positive (TP), false positive (FP), false negative (FN), and true negative (TN) predictions. We can summarize that there are two types of prediction errors: false positive (FP) and false negative (FN). FP leads to an over-prediction while FN or omission error, leads to an under-prediction. From the confusion matrix we calculated the specificity, sensitivity and kappa criteria.

Specificity is the proportion of TN correctly predicted and reflects a model's ability to predict an absence given that a species in fact does not occur at a location. Sensitivity is the proportion of TP correctly predicted and reflects a model's ability to predict a presence given that a species in fact occurs at a location.

Kappa measures the proportion of correctly classified units after accounting for the probability of chance agreement. It requires a threshold to be applied to the predictions in order to convert them to presence–absence predictions. Kappa provides an index that considers both FP and FN errors. In this study, a maxKappa is used for each model generated.

All the analyses described in this paper were carried out using the R 2.15 software (R Development Core Team, 2012).

3. Results

The similarity dendrogram for the bottom trawl hauls revealed the existence of three different assemblages for the elasmobranchs, which were confirmed by the MDS analysis (Fig. 4).

Picked dogfish (*S. acanthias*) and common eagle ray (*Myliobatis aquila*) form a separate group, bull ray (*Pteromylaeus bovinus*) is in a group of its own, and all the other elasmobranch species are included in one single group. This latter group includes 20 out of the 23 of elasmobranch species caught in the study area, including the three most caught species which are the ones used in this study.

A total of 400 trawl fishery operations were observed during a period of six years. In the case of the smallspotted catshark (*S. canicula*), its presence was recorded in 204 of these hauls, that of the blackmouth catshark (*G. melastomus*) in 135 and that of the velvet belly (*E. spinax*) in 54. The main predictors of elasmobranch habitats in the western Mediterranean Sea were depth, slope and type of substratum.

SST and chlorophyll-α concentration show a negative relationship with species occurrence but affect only the distribution of *S. canicula* (Table 1). The final models with the best fit for *G. melastomus* and *E. spinax* do not include SST and chlorophyll-α concentration as relevant variables (Table 1).

No important yearly differences were found in this area for the occurrence of these species. All the models that include the temporal effect, show higher Deviance Information Criterion (DIC) than those without it.

The model selected for its best fit (based on the lowest DIC and LCPO) with *S. canicula* has log-transformed bathymetry, type of substratum, slope, SST and chlorophyll-α concentration as covariates, and a stochastic spatial component that accounts for the residual spatial autocorrelation. Table 1 presents a numerical summary of the posterior distributions of the fixed effects for this final model. This summary contains the mean, the standard deviation, the median and a 95% credible interval, which is a central interval containing 95% of the probability under the posterior distribution.

Results showed a positive relationship between bathymetry and the presence of *S. canicula* (posterior mean = 1.06; 95% CI = [−0.32, 2.05]). Conversely, chlorophyll-α concentration showed a negative relation with respect to the presence of this species (posterior mean = −13.96; 95% CI = [−29.96, 1.24]). For low SST values, the occurrence of *S. canicula* is higher (posterior mean = −0.52; 95% CI = [−0.22, 1.05]). Rock substratum is the type of seabed that shows the lowest estimated probability of occurrence (posterior mean = −1.91; 95% CI = [−3.87, −0.12]) with respect to the
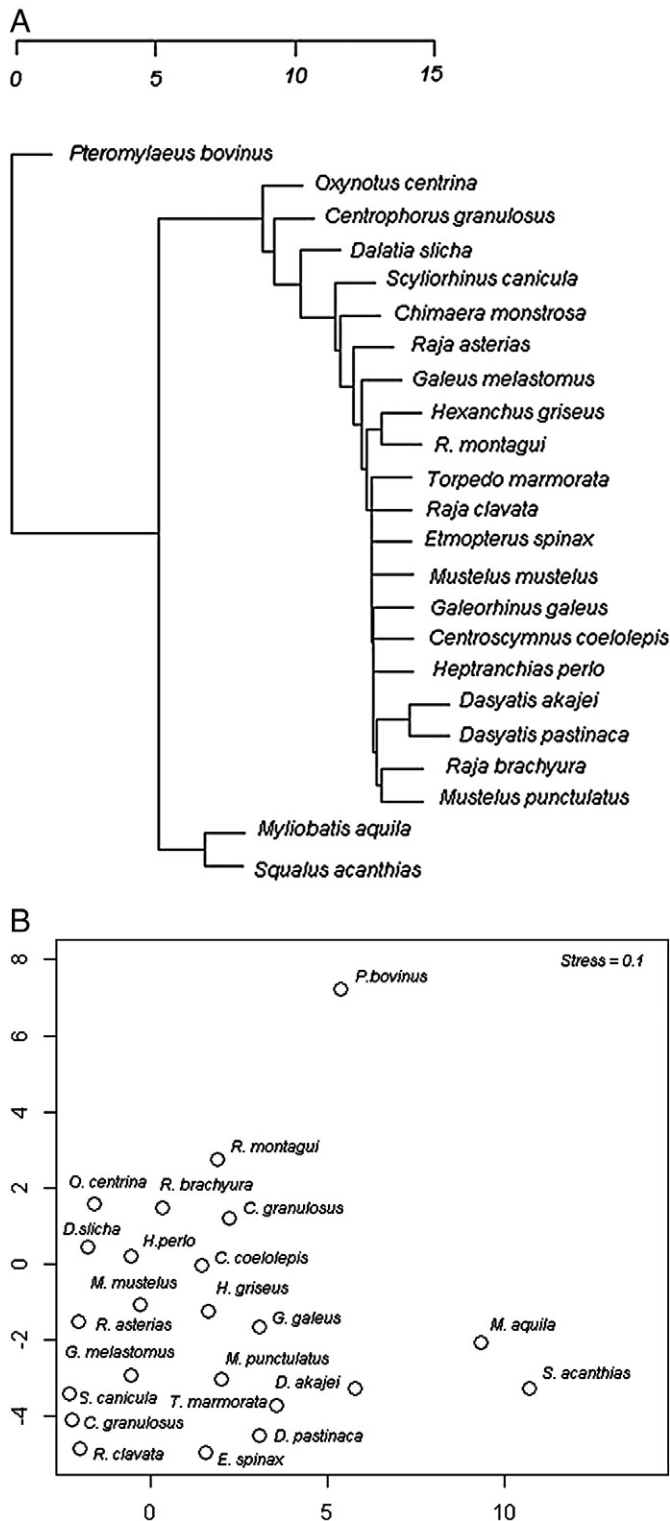
Fig. 4. Analysis Cluster dendrogram (4A) and MDS ordination (4B) of elasmobranch species caught during bottom trawl commercial hauls carried out in the Gulf of Alicante.

Table 1
Numerical summary of the posterior distributions of the fixed effects for the best model of the three species studied. This summary contains the mean, the standard deviation, the median and a 95% credible interval, which is a central interval containing 95% of the probability under the posterior distribution.

Species	Predictor	Mean	sd	$Q_{0.025}$	$Q_{0.5}$	$Q_{0.975}$
S. canicula	Intercept	0.23	2.14	−4.23	0.73	4.32
	Log depth	1.06	0.63	−0.32	1.04	2.05
	Seabed (mud)	−0.32	0.42	−1.16	−0.33	0.51
	Seabed (rock)	−1.91	0.95	−3.87	−1.88	−0.12
	Slope	0.21	0.11	−0.51	0.22	0.74
	Chlorophyll-α	−13.96	7.83	−29.96	−13.82	1.24
	SST	−0.52	0.27	−0.22	−0.51	1.05
G. melastomus	Intercept	−1.72	2.91	7.53	−1.89	4.94
	Log depth	0.33	−0.27	0.25	0.35	0.85
	Seabed (mud)	0.41	−0.50	0.40	0.42	1.29
	Seabed (rock)	−0.72	1.28	−3.36	−0.68	1.69
	Slope	0.19	0.02	−0.06	0.20	0.33
E. spinax	Intercept	−2.35	12.76	−32.34	−2.72	28.65
	Log depth	5.45	3.63	2.70	5.35	10.39
	Seabed (mud)	0.08	0.85	−1.61	0.09	1.73
	Seabed (rock)	−0.73	1.28	−3.36	−0.68	1.70
	Slope	0.09	0.03	−0.06	0.08	0.10

(posterior mean = 0.21; 95% CI = [−0.51, 0.74]) of S. canicula. As can be appreciated in Fig. 5(A), the median posterior probability of the occurrence of S. canicula in the Gulf of Alicante, is greater over a high slope gradient, in deeper waters where chlorophyll-α and SST values are higher, and where there are sandy seabeds.

Habitats associated with hard substrata and sandy beds, mainly from deeper waters and with a high slope gradient, show a greater probability of the presence of G. melastomus than those associated with mud from shallow waters and low slope gradient (Table 1 and Fig. 5(B)). Table 1 showed a positive relation between log-bathymetry and the presence of G. melastomus (posterior mean = 0.33; 95% CI = [0.25, 0.85]). Rock substratum is the type of seabed that shows the highest estimated probability of occurrence (posterior mean = −0.72; 95% CI = [−3.36, 1.69]) with respect to the reference level (sand substratum). Muddy substrata showed a lower estimated coefficient than the reference level (posterior mean = 0.41; 95% CI = [0.40, 1.29]). High slope gradient positively influences the probability of the occurrence of G. melastomus (posterior mean = 0.19; 95% CI = [−0.06, 0.33]). Fig. 4(B) shows high median posterior probability of the occurrence of G. melastomus over steeper slopes, in deeper waters and where there are rocky and sandy seabeds.

The results for E. spinax are very similar to those for G. melastomus. The best model fit for this species included depth, slope of seabed and type of substratum as relevant covariates. Table 1 shows a positive relation between log-bathymetry (posterior mean = 5.45; 95% CI = [2.70, 10.39]), slope (posterior mean = 0.09; 95% CI = [−0.06, 0.10]) and E. spinax occurrence. Habitats associated with hard substrata (posterior mean = −0.73; 95% CI = [−3.36, 1.70]) show the highest estimated probability of occurrence with respect to the reference level (sand substratum), the lowest corresponding to muddy beds (posterior mean = 0.08; 95% CI = [−1.61, 1.73]).

Fig. 5(C) shows a map of the median posterior probability of the occurrence of E. spinax, with a marked influence of depth. High probabilities appear in deep water, and low probabilities in coastal waters.

Model prediction performance statistics of all models are presented in Table 2. All models have achieved AUC values greater than 0.80, which indicates an excellent degree of discrimination between those locations where a species is present and those where it is absent. All maxKappa values are between 0.55 and 0.70, which represent a good degree of similarity between the occurrence of the species and the available real evidence. Specificity and sensitivity also show high values (>0.8), reflecting a high ability of the model to predict true negative and true positive predictions correctly.
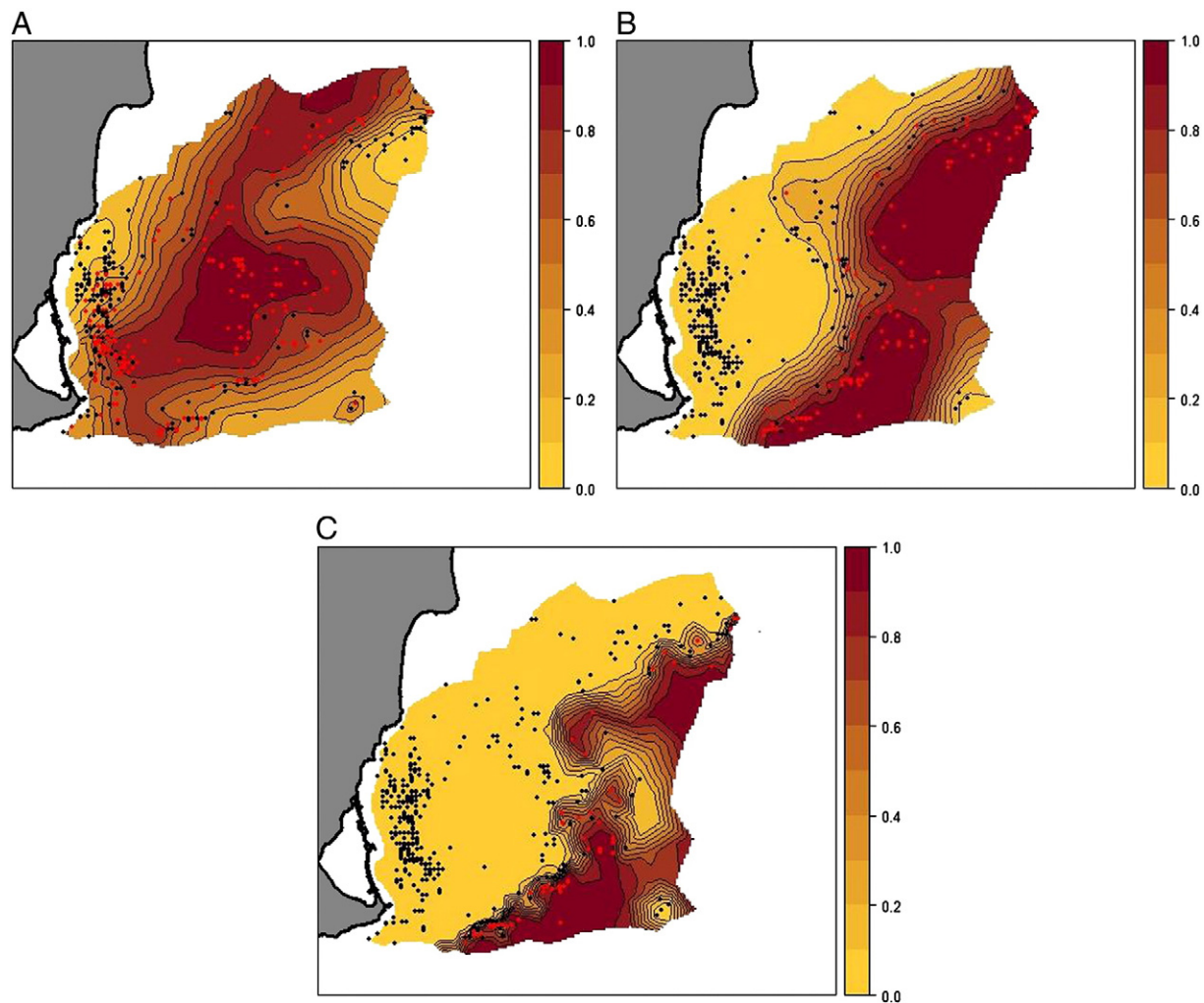
reference level (sand substratum). Muddy substrata also showed a lower estimated coefficient than the reference level (posterior mean = −0.32; 95% CI = [−1.16, 0.51]), leaving sandy substrata as the kind of sediment granulometry category with the highest probability of the presence of S. canicula. A positive correlation is characterized by a high slope gradient and the probability of occurrence

Fig. 5. Median of the posterior probability of the presence of the studied elasmobranchs: *S. canicula* (A); *G. melastomus* (B); and *E. spinax* (C). Sampling locations for the presence (●) and the absence (●) were plotted.

4. Discussion

4.1. Biological conclusions

Fishery-dependent data were used to improve our understanding of habitat utilization by elasmobranchs in the western Mediterranean Sea. In this study we used data from observers on board commercial trawlers, which represent one of the most important, but often underestimated, sources of data for the study of demersal fish. The methodology used is a Bayesian spatial hierarchical model that makes possible to assess the influence of the covariates on the presence/absence of species, as well as to predict the probability of occurrence in non-sampled areas. We have also introduced the spatial-temporal component into the study, an important effect which is commonly overlooked in most fishery studies that use traditional methods.

The estimated parameters have contributed to quantify habitat use and reveal important relationships of environmental variables with each species' habitat. With the available data, the main predictors of elasmobranch habitats in the western Mediterranean were found to be depth, slope of seabed and type of substrate.

Elasmobranch species from the Gulf of Alicante show different optimum depths, which may indicate certain of fine-tuned bathymetric segregation, although they were in fact found to coexist on shelf and slope bottoms.

However, the direct effect of depth on species occurrence is expected to be relatively small in relation to the indirect effects of bathymetry due to its correlation with many crucial environmental and biological parameters. Due to this, in the absence of such data (e.g. CTD data for oceanographic characteristics in the near bottom), a good knowledge of the bathymetric distribution of species could explain the spatial pattern and it is essential for fisheries management.

From our results, we can summarize that, in our study area, *E. spinax* inhabits the deepest stratum, *G. melastomus* the middle and upper slope and *S. canicula* the shelf and the middle slope. On the upper slope, maps show a habitat overlap between *G. melastomus* and *E. spinax*, and on the middle slope a slight overlap between *G. melastomus* and *S. canicula*. Habitat overlap does not necessarily imply competition, except when resources are in short supply. Otherwise, on rich shelf bottoms, species that are spatially segregated are not driven to differentiate their diets and may easily converge in the use of resources in overlapping areas.

Table 2
Model prediction performance statistics for the three species studied. AUC (Area Under the receiver-operated characteristic Curve), maxKappa, sensitivity and specificity.

	AUC	maxKappa	Sensitivity	Specificity
S. canicula	0.88	0.63	0.87	0.81
G. melastomus	0.84	0.69	0.95	0.90
E. spinax	0.90	0.72	0.84	0.92

Our spatial results are in accordance with a recent trophic study of these species in the Balearic Islands (Valls et al., 2011). *S. canicula* and *G. melastomus* both prey mainly on euphausiids and share the habitat. However, in our study, *G. melastomus* expressed a wider and deeper distribution trend with respect to *S. canicula*. A possible explanation for this could be a phenomenon of competitive exclusion due to the exploitation of similar resources. Based on the competitive exclusion principle, other species are forced to retreat to the bathymetric and/or geographic range to which they are most highly adapted in relation to the other potential inhabitants. In this case *G. melastomus* retreats to a depth interval of between 400 m and 700 m, usually home to the biomass peak of decapod crustaceans, which constitute an important part of the diet of this species. *E. spinax* feeds preferentially on cephalopods, while euphausiids are only a small part of the diet. This different trophic pattern with respect to *G. melastomus* would be a mechanism for reducing competition in the deepest stratum.

In general, our results show a negative relationship between all the elasmobranch species studied and depth, and high slope gradient values. In addition, for *S. canicula*, the probability of their presence is higher where SST and chlorophyll-α concentration values are lower. This may be explained by the fact that shallow sunlight waters above the continental shelf are usually areas of high productivity and SST mean values, while the deeper waters away from coastlines usually lack sunlight and nutrients, and present low values of chlorophyll-α concentration and SST.

This study confirms the importance of the type of substratum in the patterns of elasmobranch spatial distribution, as substrate type was included among the best models for all species. Our analysis shows that elasmobranchs prefer hard and sandy substrates while muddy ones affect their occurrence negatively. This preference has already been documented (Skjæraasen and Bergstad, 2000) and probably it is partly attributable to the distribution of their preferred prey, which as mentioned earlier, is crustaceans (Holden and Tucker, 1974).

These patterns were also consistent with those from other studies reporting on habitat utilization by various species (e.g. *Raja brachyura*, *Raja montagui* and *Scyliorhinus stellaris* in Ellis et al., 2005; *R. clavata* in Hunter et al., 2005; *S. canicula* in Vaz et al., 2008).

Although the present study was limited to three species, multivariate analysis of elasmobranch assemblage shows that 20 out of 23 species of elasmobranchs caught in this area are always fished jointly with one of the species examined. These results indicate that sensitive habitats identified for the three species studied are shared by the other, less frequently caught elasmobranchs. The preservation of these habitats may be useful for protecting the majority of the species of the elasmobranch community in this area. However a more thorough analysis should be done to verify with which of the species studied a given elasmobranch species is usually fished and what kind of habitat shared.

Finally, it should be noted that although the fishery-dependent data that we used were collected with a systematic sampling design, Bayesian spatial models may also aid analyses of data with geographically uneven levels of survey effort because such bias can be incorporated within the spatial random-effect term, thereby reducing its influence on estimates of the effects of environmental variables. By treating spatial effects as a variable of interest, hierarchical Bayesian spatial models can suggest the identity of additional environmental covariates that may improve model fit or the existence of area effects that may limit population viability.

However, some other data are available for elasmobranch species from online databases, such as Fishbase and the Global Biodiversity Information Facility (GBIF). These databases include presence-only data and provide probability maps on a more extensive spatial scale. Macro-scale studies allow for a broader and more complete view of ecosystem status, but their use often leads to a compromise in the analysis, because the quality and quantity of data available for large ecosystems and long time-series are often lower. Mapping sensitive

habitats of vulnerable species within a region for conservation planning requires the highest level of accuracy. Here, Bayesian interpolations are sufficiently reliable for the purpose of effective decision making and a range of evaluation criteria demonstrated the good predictive performance and properties of this approach as well as its advantages in term of ecological interpretability.

4.2. Applicability of the results for fisheries management

Improved knowledge of the spatial distribution of commercially important fish species and their relationships with the marine environment could form an integral aspect of a precautionary approach (Thrush and Dayton, 2010). There is growing worldwide support for the argument that fisheries should be conducted in a way that is robust to environmental change, and thus that fish stocks should never be exploited to a point where they cease to be resilient to environmental change.

In order to achieve this purpose, the European Marine Strategy Framework Directive has specifically requested the incorporation of any existing knowledge about environmental drivers in the assessment of ecosystems and fisheries and in advice (Wiegand et al., 2011).

Implementing plans and control schemes that would target specific species assemblages, based on a good knowledge of the species' spatial distribution in relation to the environment, could serve as a sustainable approach to fisheries management and also for other marine activities and uses (Martin et al., 2012). The establishment of marine protected areas for protecting sensitive habitats, in line with the recent trends for a holistic ecosystem-based approach to management and Marine Spatial Planning, would also benefit from an improved understanding of the spatial distribution of vulnerable species such as elasmobranchs.

To achieve these objectives, predictive habitat maps, such as those generated by the approach presented here, could be a useful source of information in the selection of areas for improved regional management or technical measure adoption.

We believe that the use of this approach for constructing maps of the spatial distribution of vulnerable species may help the design of integrated programs for the more efficient management and control of marine resources.

5. Conclusions

Species habitat analysis should be able to identify those areas within the distribution of a species that contribute most to sustain the long-term viability of a population. Although it may be complicated to define the boundaries of sensitive habitats, the definition of these areas, combined with an efficient fishery management that recognizes the importance of such areas, represents the first step towards facilitating an EAFM approach (Valavanis et al., 2008). However, accuracy is not always easy to achieve because there is often a large amount of variability surrounding the measurements of response and environmental variables (Latimer et al., 2006). This variability leads to uncertain predictions, and consequently to uninformed decision making. It is therefore important to develop tools which account for measurements with significant variability. Here, we have shown a Bayesian spatial hierarchical model that makes it possible to identify sensitive habitats together with a full specification of associated uncertainty. In our study we have improved knowledge of the habitat utilization of elasmobranchs in the Gulf of Alicante and provided practical tools for conservation planning and resource management. However, as both species and environmental data are sampled over a limited period of time and area of space, the models fitted can only reflect a snapshot view of the expected relationship. Future studies should compare the spatial distribution of these species from a fishery-independent scientific survey, which is often considered as being a more reliable abundance index because of its scientifically rigorous design (Cao et al., 2011).

However, this first approximation could serve to promote a greater effort in data collection and to identify the areas on which future research attempts should concentrate.

Acknowledgments

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