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Dealing with physical barriers in bottlenose dolphin (*Tursiops truncatus*) distribution

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ABSTRACT

Worldwide, cetacean species have started to be protected, but they are still very vulnerable to accidental damage from an expanding range of human activities at sea. To properly manage these potential threats we need a detailed understanding of the seasonal distributions of these highly mobile populations. To achieve this goal, a growing effort has been underway to develop species distribution models (SDMs) that correctly describe and predict preferred species areas. However, accuracy is not always easy to achieve when physical barriers, such as islands, are present. Indeed, SDMs assume, if only implicitly, that the spatial effect is stationary, and that correlation is only dependent on the distance between observations and not on the direction or a spatial coordinates. The application of stationary SDMs in these cases could lead to incorrect predictions and, consequently, to uninformed decision making. In this study, we identify vulnerable habitats for the bottlenose dolphin in the Archipelago de La Maddalena, Northern Sardinia (Italy) using Bayesian hierarchical SDMs that account for the physical barriers issue and provide a full specification of the associated uncertainty. The approach we propose constitutes a major step forward in the understanding of cetacean species in many ecosystems where physical, geographical and topographical barriers are present.

1. Introduction

Globally, the importance of cetaceans as keystone and umbrella species is being increasingly recognized as protected areas designed on top predator distributions have been demonstrated to be highly efficient, leading to higher biodiversity levels and more ecosystem benefits (Sergio et al., 2008). However, cetacean populations have been facing various threats including depletion of resources, habitat loss, interactions with commercial fisheries, diseases produced by pollution and physical and acoustic disturbances caused by vessel traffic (Pennino et al., 2017).

Among cetaceans the bottlenose dolphin (*Tursiops truncatus*) is a vulnerable species Bearzi et al. (2012) that is more susceptible to anthropogenic activities due to its occurrence in coastal waters where most threats occur. This species is protected by the EU Habitats Directive 92/43/EEC and its coastal ecotype is present in the ACCOBAMS (Agreement on the Conservation of Cetaceans in the Black Sea, Mediterranean Sea and contiguous Atlantic area) region Notarbartolo di Sciara (2002).

The protection of cetacean habitats, particularly those of bottlenose dolphins, should be a priority issue for marine conservation, given that protecting these areas constitutes an indirect measure toward global sea management (Pennino et al., 2016a). In order to achieve this goal, it is essential to have a solid understanding of the relationship that the species has with its habitat and apply robust analyses of existing information and databases to identify special areas of conservation (SAC) (Pennino et al., 2016a). SACs should be designed around specific sensitive areas, where local bottlenose dolphins are known to have their centers of distribution (Gnone et al., 2011).

In this context, species distribution models (SDMs) can be a useful tool to achieve these objectives given that they link spatial occurrence or species abundance data with multivariate environmental data that can estimate the relationship between the species and its habitat, and subsequently predict spatial occurrence or species abundance in unsampled locations or time-periods Martínez-Minaya et al. (2018). Nonetheless, environmental conditions alone may not sufficiently

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explain species distribution as spatially intrinsic ecological processes, such as competition or predation, can also contribute.

Therefore, SDMs that incorporate spatial random effects to account for unexplained spatial dependence in data have been gaining increasing interest in marine ecology. Indeed, spatial random components could account for the spatial correlation driven by unmeasured covariates. SDMs usually assume, if only implicitly, that the spatial random effect is stationarity, i.e. that correlation is only dependent on the distance between the points, and not on the direction or the spatial coordinates Bakka et al. (2019). However, this assumption could be erroneous in areas where there are physical barriers such islands, thus leading to potentially biased predictions of species distributions.

Consequently, biased estimations and predictions of species distribution can lead to both uninformed decision making and inefficient management of natural resources Bakka et al. (2019). This is a fundamental issue in marine ecology, where identification of vulnerable habitats (e.g., protected marine areas, nurseries, etc.) is one of the most common conservation management tools used to sustain the long-term viability of species populations.

In this paper we identify sensitive habitats for the bottlenose dolphin in the Archipelago de La Maddalena, Northern Sardinia (Italy) using a hierarchical Bayesian approach for spatial SDMs that account for physical barriers. As a tool to approximate the posterior distributions, we use the integrated nested Laplace approximation (INLA) Rue et al. (2009). The spatial effect that accounts for the physical barriers is included and measured by the approximation to a system of stochastic partial differential equations proposed by Bakka et al. (2019).

The Maddalena Archipelago is included within the Pelagos Cetacean Sanctuary, which is the only pelagic marine protected area (MPA) for marine animals in the Mediterranean Sea. The bottlenose dolphin is one of the most common cetacean species in this area (Notarbartolo di Sciara, 2002), with a population of 71 photo-identified individuals (Pennino et al., 2013), of which 22 have been defined as residents (individuals sighted in all seasons during that one year and at least five times).

In line with all these, an improved understanding of the spatial distribution of the bottlenose dolphin in this area could contribute to management of this vulnerable species.

2. Materials and methods

2.1. Study area

This study was conducted in waters within 3 miles off the coast of Archipelago de La Maddalena, Northern Sardinia (Italy). This area is within a National Park located in the strait of Bonifacio, between the islands of Sardinia and Corsica, and is part of the Pelagos Cetacean Sanctuary that was established by Italy, France and Monaco in 1999.

The type of seabed of the inner shelf (from 0 to 70 m in depth) is mainly composed of rocky or sandy substrata covered with Posidonia seagrass (*Posidonia oceanica*, Delile, 1813) beds. A high hydrodynamism characterizes this area that, together with shallow depth and limited tidal range, generate very clean waters. The general aspect of the coast is indented, with small promontories, bays and narrow channels. The topography of the bottom is variable with large cracks, reefs and small islands.

2.2. Field and Study Methods

In order to equally monitor the area, random transects were performed from October 2007 to September 2008 on-board a zodiac boat with a speed of 8–10 knots. Surveys were conducted by experts during light hours from 6.00 A.M. to 8.00 P.M. To identify species, observers scanned with both the naked eye and binoculars (7 × 50 and 8 × 42). To ensure the same visibility across the study area, surveys were only performed when the sea-state was less than 3 (Douglas sea force scale) and in clear conditions with no precipitation. Data collected included sighting occurrence, date and geographical location. Geographical information were collected every minute using a GPS, logged to a computer equipped with "Mapsource" software (Garmin GPS device, 2010).

To avoid harassing the dolphins, sightings were performed from a respectful distance (no closer than 30 m), with binoculars or telephoto lenses to get a good view of the animals. If the dolphins approached the boat, the course was maintained to avoid sudden changes in direction or speed that could injure the animals.

2.3. Environmental variables

Bottlenose dolphin distribution was modeled using five environmental variables selected for being known to affect their habitat: three oceanographic variables—sea surface temperature (SST in °C), sea surface salinity (SSS in PSU) and chlorophyll-a concentration (CHL in mg/m^3)—and two topographic covariates—depth (in meters) and slope (in degrees)—. SST, SSS and CHL are strongly related to marine system productivity as they can affect nutrient availability, metabolic rates and water stratification. All these variables were derived from the aqua-MODIS sensor, as monthly values with a resolution of 2 km (https://modis.gsfc.nasa.gov/).

With respect to the importance of these selected variables, it is worth noting that these topographic covariates have frequently been used as predictors of cetacean species distribution (Panigada et al., 2008; Mannocci et al., 2014). Also, bathymetry-derived terrain variables, such as the slope of the seabed, are indicative of seabed morphology and have been widely used as predictors of cetacean distribution (Lauria et al., 2015; Fonseca et al., 2017; Pennino et al., 2016a). Usually low slope values correspond to a flat ocean bottom (areas of sediment deposition), while higher values indicate consolidate substrata (i.e., rocky substrate) Fonseca et al. (2017).

Bathymetric variables were derived from the MARSPEC database (available at http://www.marspec.org) with a spatial resolution of 1 km (Sbrocco and Barber, 2013). To maintain the same spatial resolution, all environmental data were gridded at 2 km using the raster package (Hijmans and van Etten, 2015) in the R software (Core Team, 2018).

Collinearity between explanatory environmental variables was checked using a Draftsman's plot and the Pearson correlation index. The variables were not highly correlated ($r = 0.6$), and thus were considered in further analyses. Finally, all explanatory variables were centered and standardized following the approach of Gelman (2008).

2.4. Statistical model

A hierarchical Bayesian spatial model that accounts for barriers (Bakka et al., 2019) was used to estimate and predict overall occurrence of bottlenose dolphins with respect to environmental predictors. This model has already been used in Krainski et al. (2018). In our case, as data are composed by the presences and absences of bottlenose dolphins, the response variable Y_i can be assumed to follow a Bernoulli distribution with a mean of π_i that can take on values of 1 or 0 depending on whether the habitat is suitable ($Y_i = 1$) or not ($Y_i = 0$) for the species. As usual in Generalized Linear Models, each π_i can be easily linked to a structured additive predictor η_i through a link function $g(\cdot)$, so that $g(\pi) = \boldsymbol{\eta}$. The structured additive predictor $\boldsymbol{\eta}$ accounts for the effect of various covariates and the spatial effect in an additive way:

$$\eta_i = \beta_0 + \sum_{m=1}^{M} \beta_m x_{\mathrm{mi}} + u(s_i), \tag{1}$$

where β_0 corresponds to the intercept; the coefficients $\boldsymbol{\beta} = \{\beta_1, \ldots, \beta_M\}$ quantify the effect of the possible factors and covariates $\boldsymbol{x} = (\boldsymbol{x}_1, \ldots, \boldsymbol{x}_M)$ on the response; and $u(s_i)$ denotes the spatial random effect.

SDMs usually assume stationarity in the spatial random effect $u(s_i)$. In other words, the spatial autocorrelation only depends on the distance between points Pennino et al. (2013, see, for instance), Paradinas et al. (2015), Rufener et al. (2017). Nevertheless, if there are physical barriers, such as islands, this assumption can be erroneous, thus prompting biased predictions. As a consequence, we suppose that the spatial random effect in the model depends also on the direction and the geographic coordinates, i.e., $u(\boldsymbol{s})$ is a non-stationary spatial random effect. Using the approximation presented of Bakka et al. (2019), it can be estimated as the continuous weak solution to the following system of stochastic differential equations:

$$
\begin{aligned}
u(s) - \nabla\cdot\frac{r^2}{8}\nabla u(s) &= r\sqrt{\frac{\pi}{2}}\sigma_u \mathcal{W}(s), \quad \text{for } s \in \Omega_n,\\
u(s) - \nabla\cdot\frac{r_b^2}{8}\nabla u(s) &= r_b\sqrt{\frac{\pi}{2}}\sigma_u \mathcal{W}(s), \quad \text{for } s \in \Omega_b,
\end{aligned}
\tag{2}
$$

where r and r_b are the ranges for the normal and barrier areas respectively, σ_u is the marginal standard deviation of u, $\nabla = \left(\frac{\partial}{\partial x}, \frac{\partial}{\partial y}\right)$, $\mathcal{W}(s)$ denotes the white noise, Ω_n is the normal terrain, Ω_b is the barrier, and their disjoint union gives the whole study area.

Unlike stationary spatial effects, the underlying idea is to construct a Gaussian Markov random field (GMRF) locally, with one governing equation for the normal area (sea), and another for the barrier area (earth). The prior spatial effect only depends on two unknown hyperparameters, the standard deviation (σ_u) and the range in the normal area (r), because the range in the barrier area (r_b) is fixed at close to zero. As a result, the system in (2) represents a local averaging of nearby values. If there are two points separated by a landmass, the very small range stops the local averaging on the barrier. It forces the dependency to focus on moving around the barrier, via local averages in the water area. The system of differential equations in (2) can be solved by constructing a Delaunay triangulation of the study area (Fig. 1) and then applying the finite element method as explained in Bakka et al. (2019).

In addition to the environmental variables and the spatial effect, a factor representing the actual season was included in the model to account for temporal variability. Default priors were assigned for all fixed-effect parameters, which are approximations of non-informative priors designed to have little influence on the posterior distribution. PC priors Simpson et al. (2017) that followed the parametrization depicted in Fuglstad et al. (2018) were allocated for the only two hyperparameters in the model and define the covariance structure of $u(s)$: σ_u and r. We set the median of the prior range to 0.3 (the extent of the area in geographic coordinates) and the median for the marginal standard deviation to 1.

2.5. Bayesian inference with INLA

All the models were fitted, i.e. posteriors of the model parameters computed, using the Integrated Nested Laplace Approximation (INLA) methodology (Rue et al., 2009), implemented in the R package INLA (https://www.r-inla.org). In INLA, the Bernoulli likelihood is approximated by a Laplace approximation, and the posterior for all parameters, conditionally on the two hyperparameters σ, r for the spatial field, can be computed quickly by sparse matrix algorithms. The posterior for the hyperparameters are found by exploring this two-dimensional space, and is fast due to its low dimension. After representative values of the hyper-parameters have been chosen, these are integrated out to give a full posterior distribution for all the parameters and the spatial effect in the model.

Bayesian posterior distributions, unlike the mean and confidence intervals produced by classical analyses, enable simple probability statements about the unknown parameters. Thus, the region bounded by the 0.025 and 0.975 quantiles of the posterior distribution has an intuitive interpretation: for a specific model, the unknown parameter has a 95% chance of falling within this range of values.

As the interest was to analyze the probability of finding a dolphin in all the study area, a grid of prediction locations were included in the model fitting. At each grid, the posterior predictive distribution of the probability of observing the dolphin was obtained.

2.6. Model selection

Model selection was conducted based on choosing the best subset of covariates (see, for instance, Heinze et al. (2018) for a detailed revision of model selection procedures). This method evaluates all 2^k (k is the number of components of the model: covariates and random effects, such as the spatial effect) possible models and choose the best model according to an information criterion, in our case, the Watanabe Akaike Information Criterion (WAIC) (Watanabe, 2010) and the mean logarithmic of the approximated conditional predictive ordinate (LCPO) (Gneiting and Raftery, 2007). While WAIC values indicate the goodness of fit of the models, the LCPO evaluates the predictive capacity. Lower values for both WAIC and LCPO represent the best compromise between fit and parsimony. If the models are similar in terms of WAIC and LCPO,

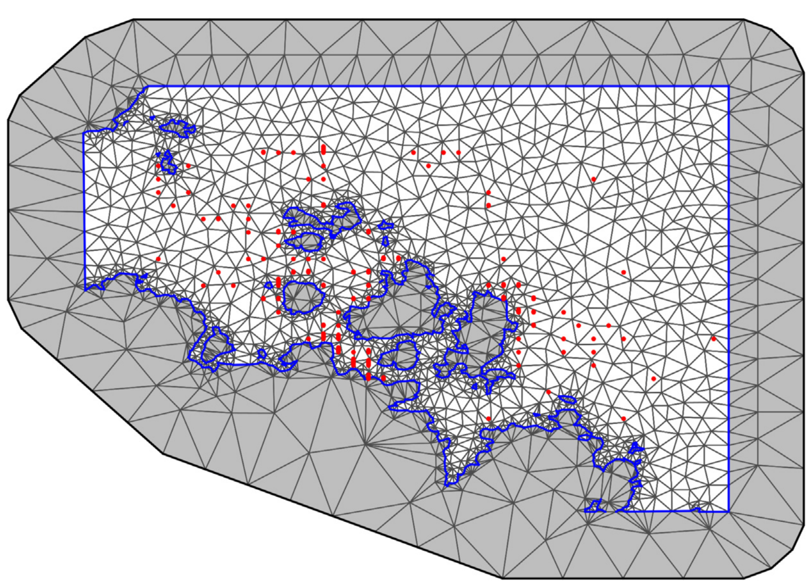

Fig. 1. Map of the study area with sightings locations (red dots). Triangulation used to calculate the GMRF for the SPDE approach. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Numerical summary of the survey effort and sighting rate by season.

Season	Sightings	N. surveys	Sighting rate (%)	Seasonal effort (%)
Winter	34	35	97.14	16.99
Spring	29	91	31.86	44.17
Summer	8	42	19.04	20.39
Autumn	22	38	57.89	18.45
Total	93	206	45.14	100

following the parsimony criterion, the model with less amount of covariates is selected.

3. Results

Between October 2007 and September 2008, bottlenose dolphins were sighted in 93 of the 206 surveys of the study area. More specifically, 34 sightings occurred in winter, 29 in spring, 8 in summer and 22 in autumn. The total sighting rate was about 0.45, 0.97 for the winter season, 0.32 in spring, 0.19 in summer and 0.57 in autumn (Table 1). Due mainly to atmospherically reasons the survey effort was not homogeneous in all the seasons, recording is maximum during the spring and summer period (Table 1).

Regarding the hierarchical Bayesian SDMs, in addition to the five environmental variables, the season factor and the non-stationary spatial effect were considered to select the best model. A total of 128 models were fitted. Table 2 displays the best 20 models and their WAIC and LCPO ordered by LCPO. As noticed, the presented 20 models were very similar in terms of WAIC and LCPO, and so these models can be considered equivalent. Thus, the parsimony criterion was employed in order to select the best model among those having equivalent values of WAIC and LCPO. The final selected model was the one with only one covariate, the seasonal effect.

After selecting this model we also investigated the importance of the covariates not selected. In particular, Bayesian estimation of the regression coefficients associated to the covariates not selected was negligible, in the sense that all the posterior distributions of the regression parameters were centered around zero and with variances smaller that the ones provided in the priors. This was a clear proof that those covariates should not be part of the final selected model.

Table 2
Model comparison. The acronyms are: seasonal factor (S), sea surface temperature (SST in °C), sea surface salinity (SSS in PSU) and chlorophyll-a concentration (CHL in mg/m^{-3}), two topographic covariates—depth (in meters) and slope (in degrees) and the non-stationary spatial effect (u). Models are ordered by LCPO.

	Models	WAIC	LCPO
1	1 + S + SST + u	185.33	0.453
2	1 + S + SSS + SST + u	185.57	0.454
3	**1 + S + u**	**186.43**	**0.455**
4	1 + S + SSS + u	186.37	0.456
5	1 + S + CHL + SSS + u	185.71	0.456
6	1 + S + CHL + SSS + SST + u	185.11	0.456
7	1 + S + SST + slope + u	186.57	0.456
8	1 + S + SSS + SST + slope + u	185.68	0.456
9	1 + S + SST + depth + u	186.59	0.456
10	1 + S + SSS + SST + depth + u	186.49	0.457
11	1 + S + CHL + SSS + slope + u	185.97	0.458
12	1 + S + SSS + slope + u	186.87	0.458
13	1 + S + CHL + SSS + SST + slope + u	184.52	0.459
14	1 + S + CHL + u	185.75	0.459
15	1 + S + slope + u	187.86	0.459
16	1 + S + CHL + SSS + SST + depth + u	186.05	0.459
17	1 + S + SSS + depth + u	187.91	0.459
18	1 + S + CHL + SSS + depth + u	187.13	0.459
19	1 + S + SSS + SST + depth + slope + u	187.28	0.460
20	1 + S + SST + depth + slope + u	188.04	0.460

Table 3
Mean, standard deviation, quantiles and mode for the parameters and hyperparameters of the best model. Summer, spring and winter are the three levels of the factor Season (the remaining one being the reference level autumn). σ_u represents the standard deviation of the spatial effect and r the range of the normal (non-barrier) area.

	Mean	SD	$Q_{0.025}$	$Q_{0.5}$	$Q_{0.975}$	Mode
Parameters						
Intercept	0.455	2.237	−3.942	0.424	5.049	0.397
Summer	−2.375	0.643	−3.708	−2.351	−1.182	−2.304
Spring	−0.794	0.480	−1.744	−0.792	0.141	−0.788
Winter	4.460	1.263	2.315	4.342	7.253	4.098
Hyperparameters						
σ_u	2.254	1.408	1.165	2.242	4.470	2.199
r	0.157	1.624	0.065	0.152	0.434	0.137

Results in Table 3 showed that winter is the season with the highest estimated dolphin occurrence (posterior mean = 4.46; 95% CI = [2.32, 7.25]) with respect to the reference level (autumn season). Conversely, summer and spring seasons show lower estimated dolphin occurrence than the reference level (respectively, posterior mean = −2.37; 95% CI = [−3.71, −1.18] and posterior mean = −0.79; 95% CI = [−1.74, 0.14]).

The median for the posterior predictive distribution of the probability of occurrence showed higher values in the whole area during the winter season (Fig. 2d). Conversely, in autumn and spring, a higher probability of occurrence (close to 1 in line with the high sighting rate observed) was found in the Northwest area (Fig. 2a and c). Similarly, in summer, the most frequented area was the Northwest, but with probabilities of presence close to 0.5 (Fig. 2b).

The spatial effect that indicates the intrinsic variability of the distribution of bottlenose dolphins after excluding environmental variables was consistent with the probability maps (Fig. 3). Moreover, the mean of the range of the spatial effect of the normal area was about 0.157 geographical degrees, that are equivalent to 17.48 km. The physical meaning of this value is that sightings of dolphins that are this distance or greater apart are not spatially correlated. It is worth noting that this range value is in line with the one that biologists consider as the distance that observed dolphins are from different groups.

4. Discussion

Seasonal sensitive habitats for the bottlenose dolphin in the Archipelago de La Maddalena were identified using hierarchical Bayesian SDMs that account for physical barriers. The proposed model showed that dolphin occurrence in the Archipelago de La Maddalena is influenced by a seasonal effect in the area. Our findings agree with those obtained by Brotons et al. (2008) in the Balearic Islands, Campana et al. (2015) in the Western Mediterranean Sea, and Pennino et al. (2015) and Pennino et al. (2016a) in our study area. Indeed, estimated dolphin occurrence is higher during the winter season and especially compared to spring and summer. Several possible reasons, either isolated or combined, could explain this seasonal variation. Natural seasonal movement of dolphins could be related to prey availability or reproduction patterns. Moreover, the intense nautical traffic in summer that characterizes this area could encourage these animals to move to areas where there are fewer pleasure boats and where the risk of collision and the noise is lower (Pennino et al., 2016b).

Another important factor driving dolphin occurrence is the spatial component, which is highest in the western zone. In this area, bottlenose dolphins show a residential attitude with their center of distribution in the identified favourable areas. The spatial effect usually captures the impact of important missing predictors and accounts for ecological processes (e.g., predation or competition) that may affect the

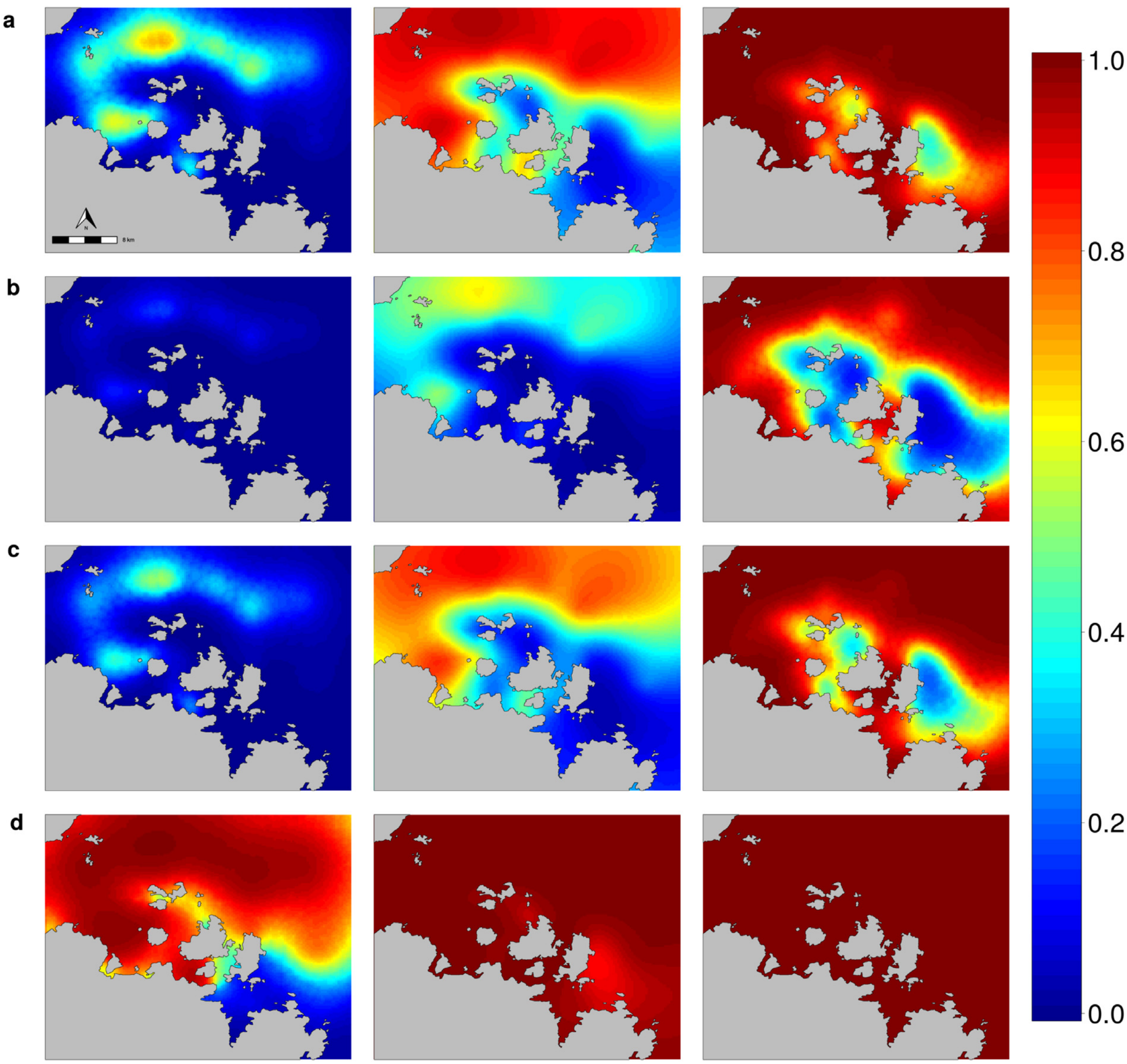

Fig. 2. Posterior predictive distribution of the probability of presence: 95% credible intervals (first and third panel respectively) and the median (central panel) for the different seasons. (a) Autumn, (b) summer, (c) spring and (d) winter.

spatial arrangement of a species (Roos et al., 2015). In our case, the spatial effect was not directly related to any environmental variable included in the final model but it could be reflecting disturbance from pleasure boating.

An effective conservation programme should take into account these findings: favourable areas for bottlenose dolphins should be identified and protected as SACs (special areas of conservation). Indeed, bottlenose dolphins are listed in Annex II of the Habitats Directive that specifically requires the identification of the SACs (Cañadas et al., 2005). SACs should be designed around special sensitive areas, such as

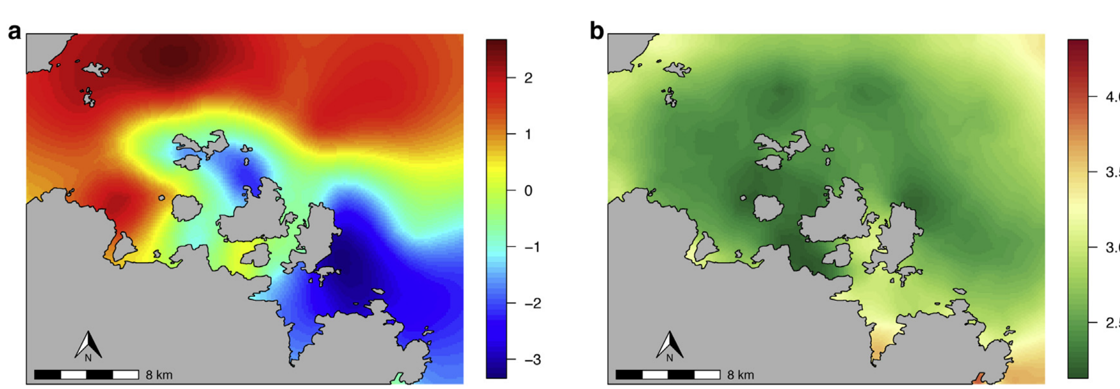

Fig. 3. Mean and standard deviation for posterior distribution of the spatial effect u.

the ones identified in this study. Protection measures should be devoted to limiting the disturbance from recreational boats, which is probably the main threat for this species in the area.

Spatial ecology has a direct applied relevance to cetaceans management, but it also has a broad ecological significance. Although it may be complicated to define the boundaries of habitats of these highly mobile species, it represents the first step towards facilitating effective spatial management. However, using a non-accurate approach could culminate in misidentification in both the posterior distributions of the fixed and random effects and in species habitat predictions, therefore leading to inappropriate management measures that can sometimes be irreversible Bakka et al. (2019).

In line with this, we have used here a hierarchical Bayesian spatial model that simultaneously deals with the presence of physical, geographical and topographical barriers, spatial autocorrelation issues and different sources of uncertainties. Our modeling is based on the novel approach by Bakka et al. (2019), and allows us to analyze sparsely binary spatial data. Some advantages result from using our proposal. The first is a result of the Bayesian methodology itself, that is, that all multiple sources of uncertainty associated with both the observed data and ecological process can be included in the analysis, thus resulting in more robust statistical inference. Moreover, the posterior predictive distribution of the probability of finding the species turns out to be a very suitable tool that allows us to express our uncertainties associated with the entire species habitat prediction phenomenon and to explicitly describe the associated spatio-temporal variability. The second advantage is that the proposal provides an accuracy that would not be easy to achieve when physical barriers are present. The application of stationary models in these cases could lead to uncertain predictions, and consequently to uninformed decision making. The third advantage is that we can present a map of the spatial effect along with its corresponding uncertainty. The final advantage is the computational gain from the use of the INLA approach, which allows us to easily make inferences and predictions within a highly structured model.

Finally, regarding the database used in this study, it is worth to be mentioned that it has some flaws, especially due to the non-standardized sampling effort and limited field quantitative information (i.e. total and seasonal nautical mileage traveled). This can probably have affected the sighting rate per season, and so, the resulting predictive maps. Nevertheless, it is well known that collecting data at sea presents many logistic and financial challenges in particular due to find suitable seagoing vessels for data collection and atmospherically and oceanographic reasons. However, determining cetacean distribution is essential for proposing conservation policies and any advance in this sense is an improvement of the management and conservation of their populations. In conclusion, this approach constitutes a major step forward in the understanding of species in many aquatic ecosystems where physical, geographical and topographical barriers are present.

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