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Spatial conservation prioritization for mobile top predators in French waters: Comparing encounter rates and predicted densities as input

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ABSTRACT

EU member states have to develop their Natura 2000 networks in their national waters to fulfill their conservation obligations regarding species and habitats listed in the Birds and Habitats directives. In France, a coastal network of Natura 2000 areas exists since 2008 but it had to be completed in offshore waters for some marine megafauna species. The SAMM aerial surveys (Aerial Census of Marine Megafauna) which occurred in winter 2011 and summer 2011–2012 over a large area comprising the whole metropolitan French Economic Exclusive Zone produced sighting data for species listed in the Birds and Habitats directives. These data produced different types of species distribution data: encounter rates and predicted densities by kriging and habitat modelling. Using these species distribution data, the aim of the present study was to compare these different types of inputs in the same conservation prioritization process to complete the existing Natura 2000 network in French waters. We ran prioritization analyses using the encounter rates only (scenario 1) then using the predicted densities provided by kriging and habitat modelling (scenario 2). We then compared the outputs of the two prioritization processes. The prioritization outputs were different but not in contradiction, with similar areas appearing as important to reach the conservation targets. Habitat models were thought to provide better pictures of seasonal species distributions and informed scientists about the phenology and ecology of species. However, the use of encounter rates as input data for the prioritization process in the Natura 2000 program is acceptable provided that sufficient survey effort is available.

1. Introduction

In the last decades, Marine Protected Areas (MPAs) became cornerstones of marine conservation strategies (Halpern and Warner, 2002; Kelleher and Kenchington, 1992; Watson et al., 2014) and were considered to be an efficient way to reduce biodiversity loss (Claudet et al., 2008a; Lubchenco et al., 2003). MPAs, as a conservation tool, are proposed within different international treaties and conventions leading to international conservation objectives such as the Convention on Biological Diversity (CBD) 'Aichi Target' which recommends that 10% of marine and coastal areas should be covered by MPAs by 2020 (CBD, 2010). For a long time, protected areas design and locations relied mostly on social and political processes resulting in *ad hoc* Protected Areas (PAs) and opportunistic networks (Gronrud-Colvert et al., 2011; Halpern, 2003). To improve the balance between ecological and socio-

economic criteria, systematic conservation planning approaches have been developed in the last 25 years (Margules and Pressey, 2000). This planning process consists in using specific protocols and quantified conservation targets to identify networks of protected areas in order to protect biodiversity features (Margules and Sarkar, 2007). A key step of the process is the representation of the biodiversity component to be conserved (Knight et al., 2006; Margules et al., 2002). This biodiversity component can represent different levels of diversity organization like physical habitats, species distributions, functional or phylogenetic diversity but in most cases the used surrogates depend on data availability (Guilhaumon et al., 2014; Payet et al., 2010; Rondinini et al., 2006; Sutcliffe et al., 2015). However, it can be challenging to depict ecological processes and species movements occurring in the marine environment which are of utmost importance when the targeted species are performing large migrations and habitat shifts like marine

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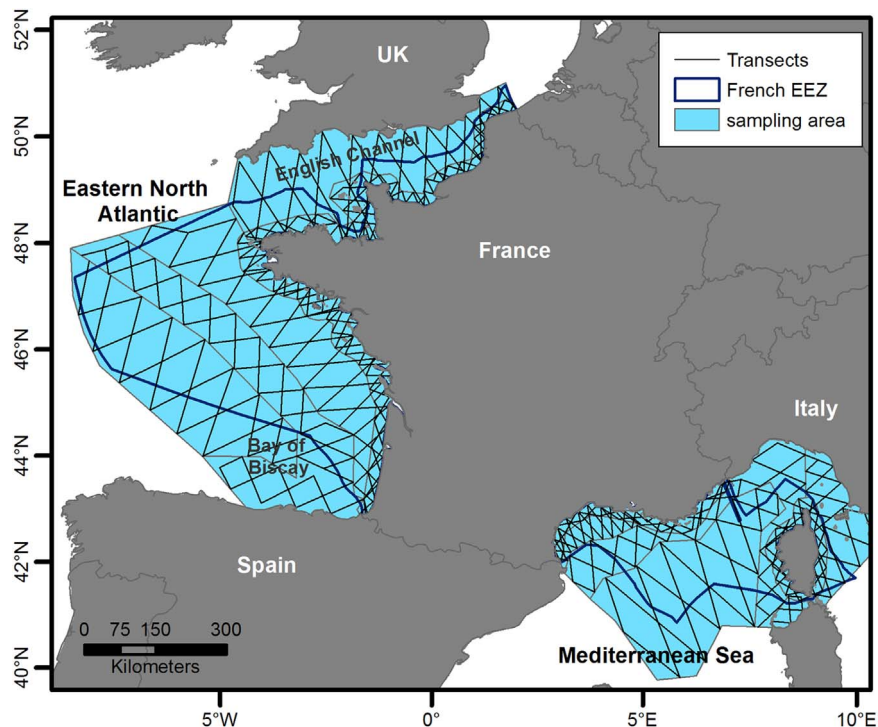


Fig. 1. Aerial surveys area and transects. The French Exclusive Economic Zone (EEZ) is in dark blue.

mammals or seabirds (Game et al., 2009; Possingham et al., 2009; Pressey et al., 2007; Wilson, 2016).

In the European Union, the Natura 2000 network of protected areas was designed to fulfill the CBD obligations and the Bern Convention in both terrestrial and marine ecosystems. The protected areas creation process started in 1992 to conserve valuable and threatened habitats and species enlisted in the Birds and Habitats directives (respectively BD and HD; EC, 2009, 1992). To extend the network at sea, coastal Natura 2000 areas were implemented in 2008 to protect marine habitats and species. All marine birds are trigger species for the Natura 2000 network and a few marine mammals are listed on annex 2 of the HD, such as the harbour porpoise *Phocoena phocoena* and the bottlenose dolphin *Tursiops truncatus*. In its latest evaluation in 2009, the European Commission concluded that for France, there was insufficient protection for the bottlenose dolphin in the Mediterranean Sea as well as a shortfall of knowledge for both species in offshore waters mainly because of a lack of knowledge about both habitat and species distribution (MNHN, 2009). To fill in the gaps of knowledge about offshore seabird and cetacean distributions, two aerial surveys, the SAMM surveys (*Suivi Aérien de la Mégafaune Marine - Aerial Census of Marine Megafauna*) were conducted in winter 2011–2012 and summer 2012 within the English Channel, the Bay of Biscay and in the Mediterranean sea to study seabird and marine mammal distributions. Raw sighting points were first integrated as encounter rates available in a grid of 40 by 40 km square (Pettex et al., 2013). In the second step, geostatistical analyses allowed interpolating the predicted densities in the whole study area and finally, habitat modelling procedures produced potential densities based on the environment characteristics (Pettex et al., 2014, 2017a, 2017b; Lambert et al., 2017a, 2017b; Virgili et al., 2017).

In most conservation planning studies, coarse biodiversity surrogates have to be chosen to face the lack of homogeneous data within the whole study area and this is especially true when targeted species are highly mobile such as marine mammals or seabirds (Lascelles et al., 2012; Rondinini et al., 2006; Williams et al., 2014). The SAMM surveys data and the different analyses based on them (encounter rates, kriging, habitat modelling) represented a unique opportunity to investigate the

effect of using different kind of distribution data as inputs in marine conservation planning analyses targeting mobile top predators. This paper focus on the step of prioritization of areas for conservation using MARXAN software, which has been developed to efficiently identify priority areas for conservation (Ball and Possingham, 2000). We implemented two scenarios to test the influence of the input data in the conservation prioritization process. A first scenario, hereafter named scenario 1, only used encounter rates as distribution data for seabirds and marine mammals targeted by the HD annex 2 (Pettex et al., 2013). The conservation prioritization outputs obtained with these data were then compared to the ones of a second scenario (scenario 2) where it was decided to use “the best available data”, defined as the distribution representation supposedly the most refined. Habitat model outputs produced with Generalised Additive Models (GAMs), representing the potential habitats of species, were considered as the best potential data to decide where to conserve target species. If habitat models were not available, we used kriging results which are a good representation of the distribution of the species. For species for which neither habitat modelling nor kriging were available, we used encounter rates as in the first scenario. The comparison between the two scenarios allowed us to discuss their benefits and flaws in a context of MPA designation constrained by regulatory time schedules like the Natura 2000 areas designation process.

2. Material and methods

2.1. Aerial Surveys and study area

The two aerial SAMM surveys (Aerial Census of Marine Megafauna) were conducted from November 3rd 2011 to February 15th 2012 and from May 15th to August 15th 2012. They both covered the English Channel, the Bay of Biscay and North-Western Mediterranean Sea with 46,205 km of sampled transect in winter and 52,315 km in summer (Fig. 1). A standardized observation protocol was used, with strip transect methodology for seabirds and line transect methodology for cetaceans (Buckland et al., 2001; Certain and Bretagnolle, 2008). Sightings were recorded at the lowest taxonomic level possible. As

Table 1
Seabird groups composition for the Mediterranean Sea region: group names refer either to the English name of a species/taxonomic group, or to a descriptive term for species morphologically similar from the air.

Family	Group names	Group composition	
Procellariidae	Small-sized shearwaters	Mediterranean shearwater <i>Puffinus yelkouan</i> Balearic shearwater <i>Puffinus mauretanicus</i>	
	Large-sized shearwaters	Scopoli's shearwater <i>Calonectris diomedea</i>	
Hydrobatidae	Storm petrels	European storm-petrel <i>Hydrobates pelagicus</i>	
Sulidae	Northern gannet	<i>Morus bassanus</i>	
Stercorariidae	Great skua	<i>Catharacta skua</i>	
Alcidae	Auks	Common guillemot <i>Uria aalge</i> Razorbill <i>Alca torda</i> Atlantic puffin <i>Fratercula arctica</i>	
Laridae	Terns	Common tern <i>Sterna hirundo</i> Little tern, <i>Sterna albifrons</i> Sandwich tern, <i>Thalasseus sandvicensis</i> Gull-billed tern <i>Sterna nilotica</i>	
		Little gull	<i>Larus minutus</i>
		Black-legged kittiwake	<i>Rissa tridactyla</i>
		Hooded gulls	Black-headed gull <i>Larus ridibundus</i> Mediterranean gull <i>Larus melanocephalus</i>
		Grey-backed gulls	Yellow-legged gull <i>Larus michahellis</i>
	Large-sized gull spp	All species from grey-backed gulls	

Table 2
Seabird groups composition for the North Eastern Atlantic region: group names refer either to the English name of a species / taxonomic group, or to a descriptive term for species morphologically similar from the air.

Family	Group names	Group composition	
Procellariidae	Northern fulmar	<i>Fulmarus glacialis</i>	
	Small-sized shearwaters	Manx shearwater <i>Puffinus puffinus</i> Mediterranean shearwater <i>Puffinus yelkouan</i> Balearic shearwater <i>Puffinus mauretanicus</i>	
Hydrobatidae	Storm petrels	Great shearwater <i>Puffinus gravis</i> Sooty shearwater <i>Puffinus griseus</i> Cory's shearwater <i>Calonectris diomedea</i>	
		European storm-petrel <i>Hydrobates pelagicus</i> Leach's Storm-petrel <i>Hydrobates leucorhous</i> Band-rumped storm-petrel <i>Hydrobates castro</i>	
Sulidae	Northern gannet	<i>Morus bassanus</i>	
Stercorariidae	Great skua	<i>Catharacta skua</i>	
Alcidae	Auks	Common guillemot <i>Uria aalge</i> Razorbill <i>Alca torda</i> Atlantic puffin <i>Fratercula arctica</i>	
Laridae	Terns	Arctic tern <i>Sterna paradisica</i> Common tern <i>Sterna hirundo</i> Little tern <i>Sterna albifrons</i> Sandwich tern <i>Thalasseus sandvicensis</i>	
		Little gull	<i>Larus minutus</i>
		Black-legged kittiwake	<i>Rissa tridactyla</i>
		Hooded gulls	Black-headed gull <i>Larus ridibundus</i> Mediterranean gull <i>Larus melanocephalus</i>
		Black-backed gulls	Great black-backed gull <i>Larus marinus</i> Lesser black-backed gull <i>Larus fuscus</i>
	Grey-backed gulls	Herring gull <i>Larus argentatus</i> Yellow-legged gull <i>Larus michahellis</i>	

the observation from the air makes identification of species difficult, some seabird species were pooled into groups according to morphological criteria. Tables 1 and 2 detailed the species groupings for the eastern North Atlantic region (including the French part of the English

Channel and Bay of Biscay) and Mediterranean region. Concerning the cetaceans, harbour porpoise (*Phocoena phocoena*) and bottlenose dolphin (*Tursiops truncatus*), which were the only two species listed in the annex 2 of the HD, were identified at the species level.

2.2. From sighting data to habitat models as inputs for conservation planning

The sightings data obtained thanks to the SAMM surveys were used in a set of studies which produced three kinds of distribution maps for the seabirds and marine mammals in the whole study area, for winter and summer (Pettex et al., 2013, 2014, 2017a, 2017b; Lambert et al., 2017a, 2017b; Virgili et al., 2017, see details in Supplement A).

- 1) Encounter rates in number of sightings per 1000 km of transect, which were available as a grid of 40 by 40 km squares in the whole survey area (Pettex et al., 2013).
- 2) smoothed predicted densities in sightings.km⁻², using a “Poisson kriging” geostatistical model in a regular grid of 0.05° of longitude and latitude over the study area (Pettex et al., 2017a, 2017b).
- 3) smoothed predicted densities in individuals.km⁻² in a regular grid of 0.05° of longitude and latitude over the study area, using GAMs which establish relationship with environmental covariates (e.g., depth, slope, distance to coast, sea surface temperature or sea surface height) (Lambert et al., 2017a, 2017b; Virgili et al., 2017).

In the current study, we used these distribution maps as inputs representing the biodiversity, in a conservation prioritization process, using the software Marxan. To assess the effects of input data in Marxan, we defined two different scenarios. Scenario 1 only used encounter rates as species distribution data. Scenario 2 used the “best available data” to represent species distributions. In this second scenario, the choice was made to use habitat models predictions when available because they would represent potential habitats, i.e., areas where environmental conditions should allow the considered species to live. When habitat modelling was not available, we used the densities predicted by kriging. Finally for some species groups, encounter rates were the only available data, and were consequently also used in the second scenario (Table 3 and see supplement B for distribution maps).

Table 3
Distribution data used as inputs in Marxan in the scenario 2. OBS refers to Encounter rates, KRIG to kriging outputs and GAM to habitat model outputs.

species	WINTER		SUMMER	
	Atlantic	Mediterranean	Atlantic	Mediterranean
Northern fulmar	GAM	NA	GAM	NA
Small-sized shearwaters	OBS	GAM	GAM	GAM
Large-sized shearwaters	NA	OBS	KRIG	GAM
Storm Petrels	KRIG	NA	GAM	GAM
northern gannet	GAM	NA	GAM	NA
Great Skua	GAM	NA	GAM	OBS
Auks	GAM	KRIG	GAM	NA
Terns	GAM	GAM	GAM	GAM
Little gull	KRIG	KRIG	OBS	KRIG
Black-legged kittiwake	GAM	OBS	OBS	NA
Hooded gulls	GAM	GAM	GAM	GAM
Black-backed gulls	GAM	NA	GAM	NA
Grey-backed gulls	GAM	GAM	GAM	GAM
Harbour porpoise	GAM	NA	GAM	NA
Bottlenose dolphin	GAM	GAM	GAM	GAM

2.3. Conservation planning

2.3.1. Conservation planning process

Conservation planning can be described by a several stages process (Margules and Pressey, 2000). Here, these steps have been followed in order to identify priority areas able to protect targeted species of the Birds and Habitats directives (Table 1; EC, 2009, 1992):

- (i) Identifying biodiversity data. The seabird and cetacean distributions were used here: encounter rates in scenario 1 and a combination of habitat models, kriging outputs and encounter rates in scenario 2.
- (ii) Setting quantitative targets for each species or group of species. A 60% representation target was decided for every feature (60% of the abundance of each species), based on Natura 2000 designation guidelines advising that above 60% of representation, a habitat or a species distribution is considered sufficiently represented (EC, 1997). However, this 60% target is not an absolute threshold for conservation and species could be well covered by the network with less than 60% coverage (Evans, 2012).
- (iii) Dividing the study area in Planning Units (PUs) which will be the calculation unit for the next steps. The existing Natura 2000 coastal areas (either designed for the Birds or the Habitats directives) were considered ‘locked in the Protected Areas network’ hence, already participating in reaching the 60% target for each species. These PUs were joined to the 40 by 40 km grid cells of the encounter rates to create a Planning Unit theme (Fig. 2). The PUs were the same in both scenarios to allow comparisons. In scenario 1, for each PU and each species, a number of sightings was calculated from the encounter rates. In scenario 2, depending of the used distribution data, a number of sightings was predicted from kriging methods and a number of individuals was predicted from the habitat models for each PU. These numbers of sightings and individuals by PU were the ones used to calculate the 60% representation targets (How many PUs are needed to conserve for example 60 individuals on the total of the 100 individuals present

in the Mediterranean?)

- (iv) Assigning a cost to each planning unit. However, as the goal here was to identify priority areas for conservation independently of any socio-economic consideration, the cost was set to 1 for all PUs.
- (v) Using spatial prioritization software to identify near-optimal combinations of Planning Units which reach the conservation targets. Marxan is the most widely used decision-support tool in conservation planning (Moilanen et al., 2009). It uses a simulated annealing approach to identify the best combination of PUs that would allow reaching the targets at a minimum cost (Ball and Possingham, 2000). The cost is a combination of the summed PUs cost, and penalties for not meeting the targets. Here, each PU costed 1, then the summed PUs cost represented the number of selected PUs and we set a high penalty-cost to ensure every target is met. Marxan ran 100 times proposing 100 near-optimal solutions, *i.e.*, combinations of PUs reaching the targets, from which it selected the cheapest one and proposed it as best solution. In addition, a “summed solution” showed the selection frequency of each PU, meaning how many times each PU was part of the 100 near-optimal solutions. Hereafter, the summed solutions were referred to as “selection frequency” maps. They showed which PUs had a high selection frequency and hence were considered important to reach the conservation goals.

2.3.2. Marxan outputs comparison

In this paper, conservation planning analyses with MARXAN were first realised using encounter rates for every species group (‘scenario 1’ using encounter rates). Secondly, analyses were re-run considering the best available abundance indicators, *i.e.* encounter rates, kriged abundances and habitat modelling (‘scenario 2’ using best available data). In both scenarios, Marxan was used to obtain selection frequency maps for the conservation of either seabirds or cetaceans listed in the annex 2 of the HD or both groups together. Winter and summer data were considered separately and analyses were run independently for the eastern North Atlantic and Mediterranean regions. A Spearman rank coefficient was calculated to reveal if the selection frequency patterns

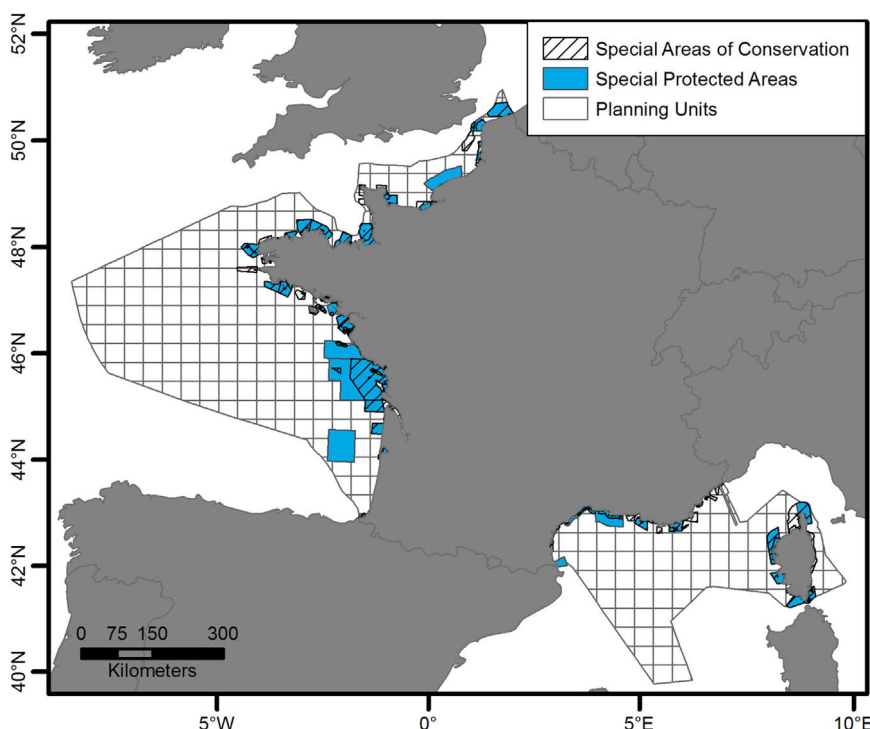


Fig. 2. Planning Units theme defined in the study area. They are composed of 40 × 40 km grid cells added to the existing Natura 2000 areas (each independent Natura 2000 area represents a planning unit). Special Areas of conservation are Natura 2000 areas under the Habitats Directive and Special Protected Areas are Natura 2000 areas under the Birds Directive.

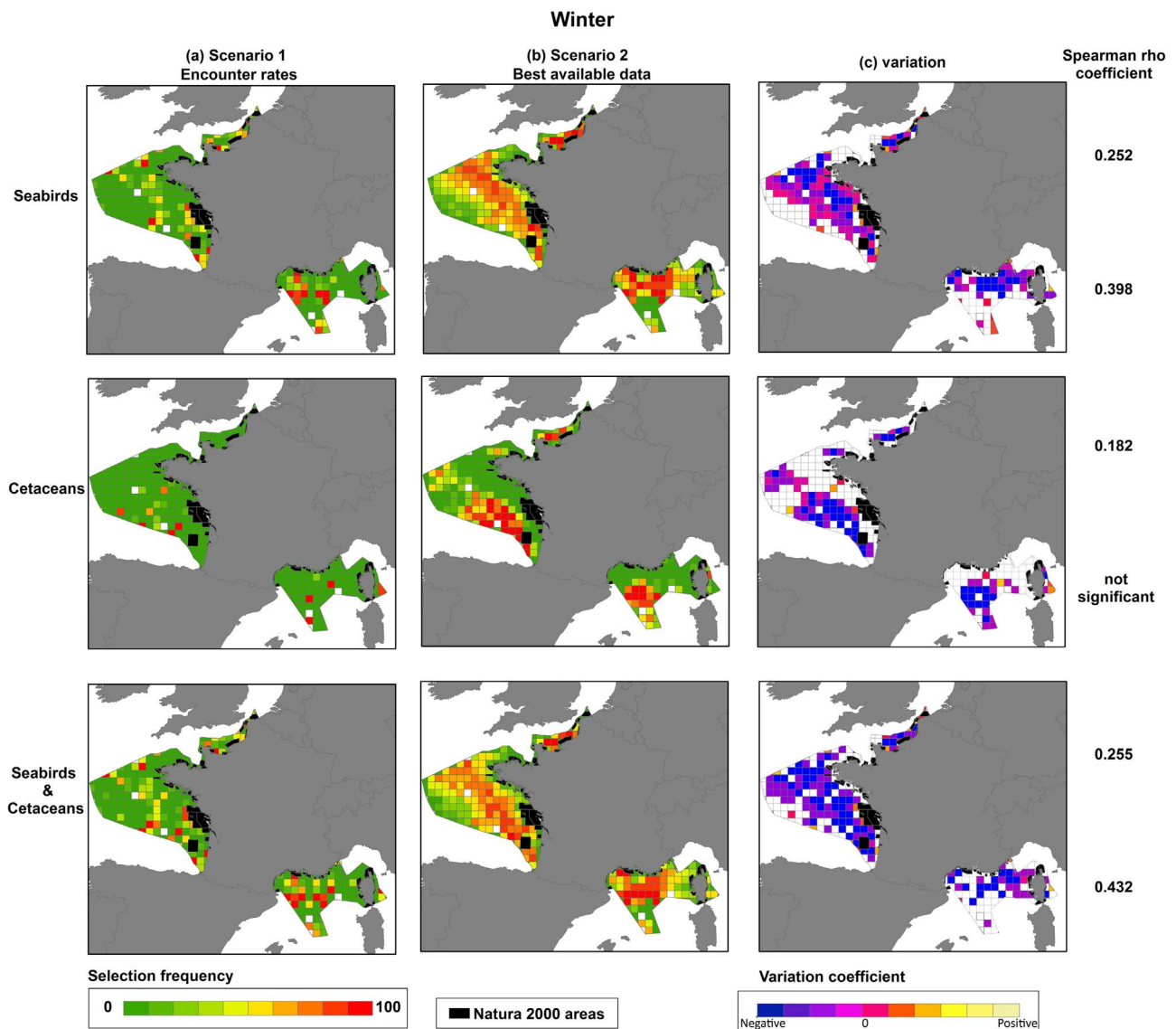


Fig. 3. Marxan selection frequency outputs for the winter period. (a) first scenario when species encounter rates were used as input layers, (b) second scenario when ‘best available data’ were used, (c) significant variation in selection frequency between (a) and (b). Results are presented for seabirds, cetaceans and seabirds and cetaceans together. 12 species or group of species are targeted for the seabird in Atlantic and 7 in the Mediterranean. Two cetaceans are targeted in the Atlantic and 1 in the Mediterranean. Negative values indicate a higher selection frequency in (b). Only significant ($p < 0.005$) Spearman rho coefficients are indicated to inform on the strength of the correlation between the two scenarios spatial patterns in selection frequency (the top value concerns the Atlantic region and the bottom value the Mediterranean region).

were significantly different between the two scenarios in each case (seabirds; mammals; both). Then, to investigate the differences between the patterns, a variation rate (1) was calculated for each PU.

$$\text{Variation rate} = \frac{X - Y}{\text{mean}(X, Y)} \quad (1)$$

with X the selection frequency in the first scenario and Y the selection frequency in the second scenario. It was tested against 1000 random permutations in Y. Only the variation rates outside the 95% confidence interval were shown on the maps (Figs. 3 and 4; within the confidence interval, variation is not higher than variation that could occur by chance in the permutations). A negative variation rate in the PUs would indicate that a large proportion of PUs were more often selected in scenario 2 than in scenario 1 and a positive variation rate in the PUs would show the opposite.

3. Results

Marxan selection frequency outputs varied with the nature of the input data but PUs with significant variations in selection frequency

represented less than 50% of the total in each scenario (Figs. 3 and 4). Comparisons between scenarios 1 and 2 showed that the high selection frequencies tended to be more frequent in scenario 2 (“best available data”), with more PUs having a null selection frequency in scenario 1.

3.1. Seabirds

3.1.1. North Atlantic region

In the eastern North Atlantic region for seabird data, the significant Spearman coefficient was higher in summer (0.389) than in winter (0.252) meaning that the selection frequency spatial patterns for the two scenarios were more correlated in summer (Figs. 3 and 4). In winter, 44% of the PUs had a significant selection frequency variation between both scenarios whereas only 31% of the PUs had a significant difference in selection frequency in summer. In summer, the variation rate map indicated an increase in the selection frequency on the continental shelf of the Bay of Biscay and in the English Channel in scenario 2 (Fig. 4c). In winter, the variations between the two scenarios showed a higher selection frequency in the eastern English Channel and

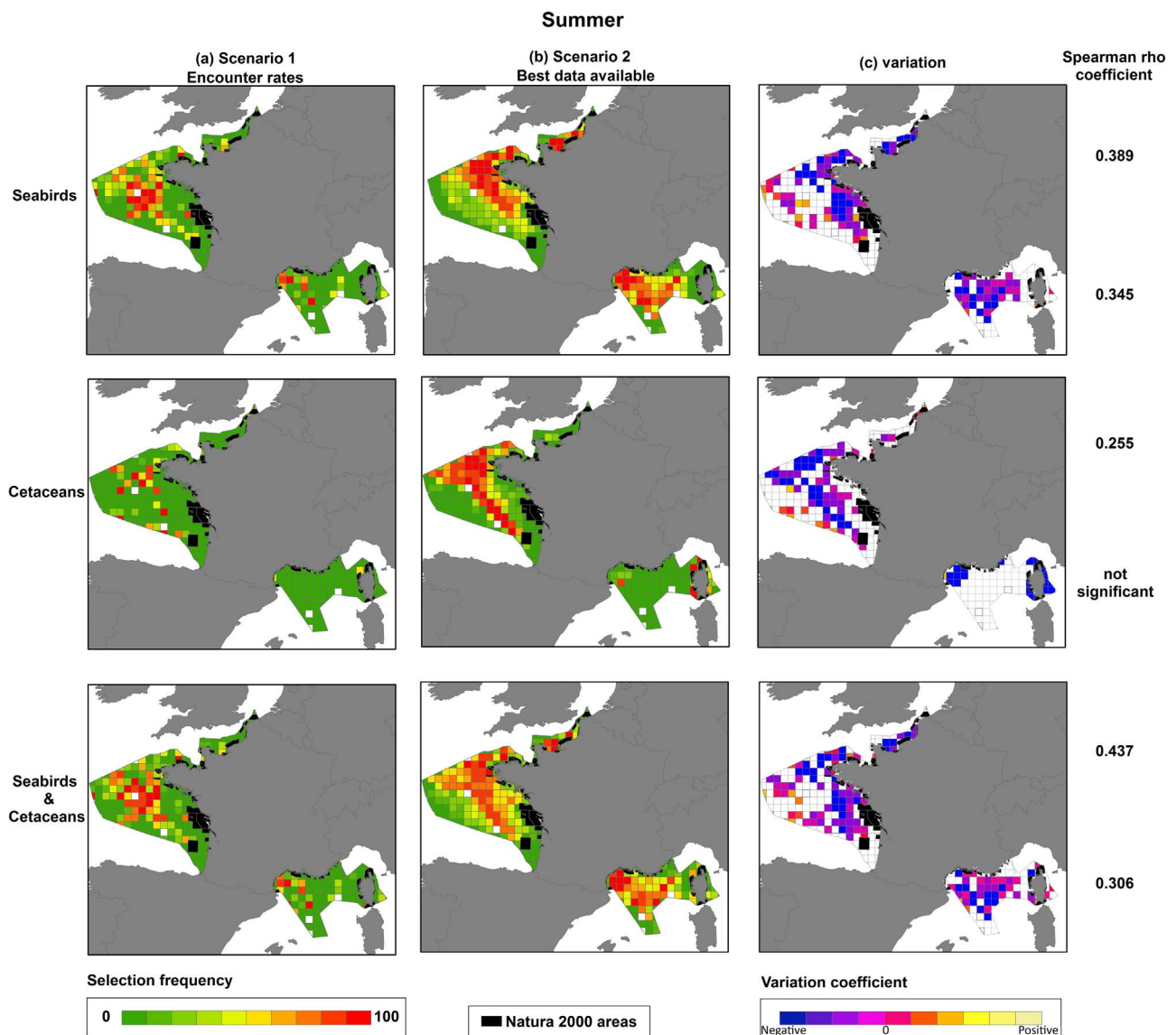


Fig. 4. Marxan selection frequency outputs for the summer period. (a) first scenario when species observation rates were used as input layers, (b) second scenario when ‘best available data’ were used, (c) significant variation in selection frequency between (a) and (b). Results are presented for seabirds, cetaceans and seabirds and cetaceans together. 13 species or group of species are targeted for the seabird in Atlantic and 8 in the Mediterranean. Two cetaceans are targeted in the Atlantic and 1 in the Mediterranean. Negative values indicate a higher selection frequency in (b). Only significant ($p < 0.005$) Spearman rho coefficients are indicated to inform on the strength of the correlation between the two scenarios spatial patterns in selection frequency (the top value concerns the Atlantic region and the bottom value the Mediterranean region).

on a large part of the Bay of Biscay in the scenario 2 (Figs. 3c). Moreover, in winter in scenario 1, 73% of the PUs had a selection frequency equal to zero.

3.1.2. Mediterranean region

The selection frequency patterns in the Mediterranean varied between the two scenarios (Figs. 3 and 4). The areas showing high selection frequencies in scenario 1 also showed high selection frequencies in scenario 2, but in scenario 2, much more PUs showed non null selection frequencies leading to a wider selection frequency spatial pattern. The Spearman coefficient was equal to 0.398 in winter and 0.345 in summer (significant in both cases) with respectively 34 and 33% of PUs with significant selection frequency variations.

3.2. Cetaceans

3.2.1. North Atlantic region

North Atlantic region results for cetaceans concerned only bottlenose dolphins and harbour porpoises. In the North Atlantic region

during winter, 75% of the PUs had a null selection frequency in scenario 1 and 48% in scenario 2 (Fig. 3). In scenario 2, the highest selection frequencies were in offshore areas of the Bay of Biscay and in the English Channel (Fig. 3). This pattern was different in scenario 1 where no PU was selected in the Channel. In summer, 55% of PUs displayed a null selection frequency in scenario 1 while 45% of PUs had a null frequency selection in scenario 2. The variation map indicated an increase in selection frequency when the best available data were used in Marxan (scenario 2). The variation was significant for 24% of the PUs in winter and 27% in summer. The spatial pattern of high selection frequency also differed between the two scenarios with a clear concentration of high selection frequencies on the continental slope of the Bay of Biscay. Finally, the selection frequency pattern also differed between seasons mainly in the second scenario.

3.2.2. Mediterranean region

In the Mediterranean region, only bottlenose dolphin data were used, as harbor porpoise is absent from the region. Regarding the results in the Mediterranean region in winter, there was no significant

correlation between the summed solutions produced in scenarios 1 and 2 (Spearman test p -value > 0.1 ; Fig. 3). Bottlenose dolphin encounter rates showed a few grid cells with densities higher than the others (Pettex et al., 2013). These PUs were selected in priority by Marxan and have been sufficient to reach the 60% target, hence 73% of the PUs had a zero selection frequency in scenario 1 (Fig. 3a). The predicted densities used in scenario 2 allowed Marxan to try more combinations of PUs to reach the 60% target leading to less PUs with a zero selection frequency (Fig. 3b).

In summer, the same number of PUs with null selection by Marxan was observed in both scenarios (Fig. 4). Giving the very low proportion of PUs with a selection frequency higher than 0 in both scenarios, no correlation was found and the Spearman coefficient was not significant in this case ($p > 0.1$). In scenario 1, the existing Natura 2000 network already covered more than 50% of the bottlenose dolphin distribution, hence only a few additional PUs were necessary to reach the 60% target. In scenario 2, the predicted densities were also higher in coastal waters (Lambert et al., 2017b), leading to globally low or null selection frequencies in most of the Mediterranean Sea.

3.3. Seabirds and cetaceans

3.3.1. North Atlantic region

In the North Atlantic region, differences in spatial patterns obtained for seabirds and cetaceans together were similar to those found for seabird data with a correlation between the selection frequency patterns of the two scenarios. The Spearman coefficient was equal to 0.255 ($p < 0.005$) in winter. The variation in selection frequency was significant for 45% of the PUs (Fig. 3). In summer the correlation between the two scenarios also existed with a Spearman coefficient of 0.437 ($p < 0.005$), and a significant difference of selection frequency was found for 30% of the PUs (Fig. 4).

3.3.2. Mediterranean region

In winter, a significant correlation was found between the two scenarios in the Mediterranean region. The Spearman coefficient was equal to 0.432 ($p < 0.005$) with 29% of the PUs with a significant difference between selection frequencies (Fig. 3). In summer, the coefficient was a bit lower (0.306; $p < 0.005$) meaning a less important correlation between the two scenarios (Fig. 4). Hence, 45% of the PUS had a selection frequency varying significantly between the two scenarios (Fig. 4).

4. Discussion

The SAMM surveys represented a unique opportunity to develop a conservation planning process for offshore MPAs identification in French waters without relying on range maps or expert knowledge only as it is often the case in study cases with marine top predators (Pompa et al., 2011; Williams et al., 2014). The present analyses showed that the nature of species distribution data has an influence on the spatial prioritization but lead to spatially correlated conservation priority areas in more than 80% of the cases.

4.1. MPAs and conservation prioritization methods for mobile megafauna

MPAs are an efficient conservation tool when responding to some criteria like sufficient surface or an efficient legal enforcement (Edgar et al., 2014). Most of the time, evaluated MPAs were designed to reduce fishing effort and conserve coastal benthic habitats of fishes (Claudet et al., 2008b; Hobday et al., 2011). Their effects could be assessed because the targeted species were found in the MPA at least at one stage of their development even if it is not always easy to take into account larval dispersal or mobility. However, the evaluation of the MPA efficiency to sustain populations of mobile megafauna is more complicated, particularly in offshore MPAs when the targeted species are not

area faithful species like some populations of harbour porpoises (Wilson, 2016). Hence, the efficiency of MPAs to conserve highly mobile megafauna is still discussed in the scientific community (Hooker et al., 2011; Wilson, 2016). They are certainly not sufficient to preserve marine megafauna but they help mitigate spatially restricted threats or protect species that use discrete areas for some vital functions (Halpern et al., 2008; Hooker et al., 2011; Hooker and Gerber, 2004). Moreover, international, regional and national regulations like the Habitats and Birds Directives ask for MPAs designation targeting mobile megafauna. Hence, the best data available should be used to design them in order to create a potentially efficient MPA network.

The SAMM surveys provided the first datasets of seasonal species distributions with estimated densities for species targeted by the Habitats and Birds Directives in the whole French EEZ and represented an interesting case study for the use of Marxan in an example of MPAs designations directed towards marine mammals and seabirds (Williams et al., 2014). If Marxan is increasingly used to design MPAs, it has rarely been implemented for mobile megafauna (see Pompa et al. (2011) for an example at global scale and Williams et al. (2014) for a regional study). Conservation prioritization for a multi-species scenario has the potential to propose networks which should be efficient for all targeted species (Hooker et al., 2011).

4.2. Differences between the two conservation prioritization scenarios

We compared Marxan outputs when using two types of species distribution resulting from different analyses steps of aerial survey data (Pettex et al., 2013, 2014). Differences in the summed solutions of both scenarios relied on the nature of distribution data. In scenario 1, encounter rates showed, depending on the concerned species, a succession of cells without sightings and cells with a low to high encounter rates (see supplement B). For some species which have not been sighted over a large part of the EEZ, the PUs were not interchangeable to reach the 60% target, leading to selection frequency patterns where some PUs had high selection frequencies while the majority of the remaining PUs had a null or low selection frequency. In scenario 2, kriging and habitat models led to predicted densities, evaluated from observations for kriging while habitat models relied on continuous environmental parameters like the sea temperature or depth (Lambert et al., 2017a, 2017b; Virgili et al., 2017). The predicted species densities were smoothed over the study area with low to high density zones with few blank cells, offering a longer continuum to Marxan in its optimization process among all targeted species. This led to summed solutions where less PUs had a null selection frequency and more PUs were interchangeable to reach the 60% target for every species. Hence, the summed solutions showed a smoother pattern than in scenario 1. This pattern was well illustrated in the Mediterranean Sea for the bottlenose dolphin where the optimization process was at its simplest level with only one species to take into account. The encounter rates were null in most of the area, except in some PUs in a quite discontinued pattern whereas the habitat model predicted the highest densities in the southern part of the Mediterranean EEZ (supplement B). These two types of data led to different selection frequencies in Marxan. In scenario 2, with these predicted numbers of individuals distributed over a wide area, Marxan had more choice in PUs selection to reach the 60% target and the number of PUs with a zero selection frequency decreased to 41% compared to 73% in scenario 1. The same kind of pattern was also found when looking at the analyses on seabirds in the eastern North Atlantic region. The variation maps revealed strong spatial differences in the selection frequency patterns. For example, the eastern English Channel had low scores in the first scenario and high selection frequencies in the second one due to predicted densities differing from the encounter rate patterns and a larger choice for Marxan to reach the conservation target.

These differences in priority areas identified by prioritization software, caused by the type of data, confirmed the results of previous

studies where discrepancies between MPAs identified with different type of distribution data were observed (Elith and Leathwick, 2009; Grand et al., 2007; Hermoso and Kennard, 2012; Rondinini et al., 2006; Underwood et al., 2010; Williams et al., 2014). Rondinini et al. (2006) highlighted the risks associated with the type of distribution data in conservation planning, like strong omission errors (false absence) when using point data or higher commission/inclusion errors (false presence) when using predicted distribution data. Quantity and quality of data are known to impact results (Grand et al., 2007; Underwood et al., 2010). Here, we did not compare two datasets of different quality levels but two datasets with different representations of species distributions based on the same set of survey observations. In the first scenario, we used encounter rates while in the second scenario densities predicted from kriging and habitat modelling were used as input data. All datasets may contain commission errors: encounter rates because of their representation in 40 by 40 km cells and kriging and habitat modelling outputs because of prediction uncertainties. In addition, due to the high mobility of the considered species, their small size for seabirds or their low availability at the surface for the cetaceans, determination at the species level can be difficult in aerial surveys and their abundance estimation may be underestimated.

4.3. SAMM surveys to inform conservation prioritization: Methodological considerations

The main limitation in our approach to prioritize conservation areas based on SAMM survey data is the lack of inter-annual distribution data. For mobile species, MPA designation should consider the variability of their habitats at different scales: seasonally (breeding and foraging areas are often different) and annually because some species such as the harbor porpoise can show long term changes in their distribution patterns (Heinänen and Skov, 2015; Wilson, 2016). To overcome the lack of long term considerations in the study, other data sources could be used to confirm their distributions over several years or new surveys should be conducted to confirm their presence in the designated Natura 2000 areas (Hammond et al., 2013; Wilson, 2016). The SAMM surveys were deployed over the French EEZ; such surveys cannot be organized every year so inter annual variability have to be approached with less expensive studies such as observer programs conducted from fisheries surveys vessels for example or other platforms of opportunity.

The PU size and shape are also known to impact Marxan outputs (Hermoso and Kennard, 2012; Nhancale and Smith, 2011; Smith et al., 2009). Mostly, the PU size must be adapted to data resolution and to study area scale (Hermoso and Kennard, 2012). Here, the 40 by 40 km PU matched the resolution of encounter rate maps (Pettex et al., 2013). Scenario 2 also used encounter rates for some species (see Table 3); hence the choice was made to keep the PU dimensions when treating the best available data. Moreover, it facilitates the comparison between the two scenarios. As we were treating highly mobile species distribution data, we consider that large PUs were appropriate to identify large areas to be designed as MPAs for these type of species (Hooker et al., 2011; Pichegru et al., 2012).

4.4. Spatial conservation prioritization and experts opinions in the conservation planning process

Systematic conservation planning is not only about the conservation prioritization step, it also has a large part devoted to stakeholders consultations and experts feedbacks (Knight et al., 2013; Margules and Pressey, 2000). After the European evaluation of the network in 2009, the new Natura 2000 designation process was tightly scheduled and experts meeting aiming at deciding about the creation of new offshore sites, called Large Sectors, were convened rapidly, before full analyses of survey data had been completed. The conservation prioritization analyses were computed using the encounter rates data alone and the

outputs produced in scenario 1 were used as the basis for discussions among experts in birds and cetaceans who had a great knowledge of the ecology and distributions of the species in French waters (Delavenne et al., 2014). In the designation process, most areas arising as essential for Marxan were clearly confirmed by biologists like the shelf edge but some areas with low selection frequencies arose as important for a consistent Natura 2000 network from the discussions among experts. Interestingly, some of these areas like the western English Channel effectively appeared as important in the second scenario showing the undeniable value of the experts' knowledge in the species biology and ecology.

Conservation prioritization software are now increasingly being used in MPA identification but these types of analyses are just a step in a conservation planning process and are not a sufficient condition for an effective implementation and management of MPAs or MPA networks (Knight et al., 2009; Smith et al., 2009). Conservation scientists advocate for conservation planning process based on a stakeholder centered approach (Smith et al., 2009) and in some cases, MPA managers complained about the lack of consideration for the opinions of experts in the process (Keppel, 2014; Klein et al., 2014a, 2014b). During the Natura 2000 designation procedure, experts and stakeholders were consulted at different steps of the process and their opinions were always considered valuable.

5. Conclusions

Our objective was to compare Marxan outputs considering different type of species distribution data used as inputs. These types of datasets resulted from the different steps in analyzing the SAMM surveys data. Results showed that the nature of the species distributions data influenced the selection frequencies with more options for prioritization when using predicted abundances than encounter rates.

Habitat models are accurate pictures of seasonal species distributions and helped scientists to develop knowledge about the biology, phenology and ecology of cetacean and seabirds species in the area. They are produced through a complex quantitative process and are scientifically defensible for MPA design. However, the use of encounter rates associated to experts' knowledge for the Natura 2000 program is highly defensible too. Conservation prioritization based on sightings is more likely to indicate priority areas in zones where species were actually present provided that survey effort is sufficient to ensure that false absences are minimized; whereas outputs based on species distribution models may favor areas where species should be present based on the environmental conditions but were not necessarily seen. However inter-annual variability in the distribution of the targeted species should also be considered.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2017.05.003>.

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