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Title: Combining single- and repeated-visit occupancy models to make the best of monitoring surveys

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Abstract

1. A major challenge in applied ecology consists in integrating knowledge from different datasets to produce robust ecological indicators. To estimate species distribution, occupancy models are a flexible framework that can accommodate several datasets obtained from different sampling methods. However, repeating visits at sampling sites is a prerequisite for using standard occupancy models, which may limit their use. Under certain conditions, detection/non-detection data collected during single visit can be analysed with occupancy models. To date however, single-visit occupancy models have never been used to combine several different datasets.

2. Here, we developed an approach that combines multi-method and single-visit occupancy models. As a case study, we estimated the distribution of Bottlenose dolphins (*Tursiops truncatus*) over the North-western Mediterranean Sea by combining 24,624 km of aerial surveys and 21,464 km of at-sea monitoring. We compared the outputs of single- vs. repeated-visit multi-method occupancy models, and that of single-method occupancy models.

3. Multi-method models allowed a better sampling coverage in both coasts and high seas and provided a better precision for occupancy estimates than single-method occupancy models using aerial surveys or at-sea surveys in isolation.

4. Overall, single- and repeated-visit multi-method occupancy models produced similar inference about the distribution of bottlenose dolphins. This suggests that single-visit occupancy models provide robust occupancy estimates, which open promising perspectives for the use of non-standardized datasets.

5. *Synthesis and applications:* Single-visit multi-method occupancy models can help making the best out of ecological monitoring programs by optimizing cost effectiveness through the formal combination of datasets.

Keywords

Bottlenose dolphins, Ecological monitoring, Integrated species distribution models, Multi-method, Occupancy models, Single-visit

Introduction

Ecological monitoring (EM) is an inherent process of most ecology and conservation biology studies. EM produces important information for decision-making prior implementing management strategies, or for evaluating management efficiency (Lyons, Runge, Laskowski, & Kendall, 2008). With the proliferation of EM programs, concerns have been raised about the quality of sampling design (Bernhardt et al., 2005; J. Nichols & Williams, 2006; Yoccoz, Nichols, & Boulinier, 2001), and the sub-optimal use of collected data to inform wildlife management (Lindenmayer & Likens, 2010; J. Nichols & Williams, 2006). Some criticisms pointed out EM programs as being costly and wasteful, with few informative outcomes from collected data (Lovett et al., 2007), while studies in ecology and conservation are often performed in cost-constrained contexts that require making the best out of EM programs (Lindenmayer & Likens, 2010).

In applied ecology, several competing EM programs are often carried out to collect ecological data. EM programs are conducted by organizations operating across different time scales, geographic scales and funding initiatives (Lindenmayer & Likens, 2010). Some EM programs are performed at the local level, and provide highly detailed information over small spatial extents. On the other hand, institutional agenda of high-level policy-makers argue for large scale evaluation of environmental status (e.g. the EU Marine Strategy Framework Directive that requires a global assessment of European marine waters *Directive 2008/56/EC of the European Parliament*). Ideally, effective EM should address well-defined objectives using standardized sampling design, i.e. fixed protocols at known sampling locations (Lovett et al., 2007). However, in many cases, EM collect data under protocols in which the sampling locations, effort and methods are meant to change over time, therefore leading to what we will refer to as *non-standardized* data (Miller, Pacifici, Sanderlin, & Reich, 2019).

In this context, a major challenge consists in integrating knowledge from different EM programs (Fletcher et al., 2019; Lindenmayer & Likens, 2010; Miller et al., 2019) to produce robust ecological indicators that may be used to inform decision-making. Among others, species distribution is often required in ecology and conservation biology (Cabeza et al., 2004; Dorazio, 2014; Guillera-Arroita, Ridout, & Morgan, 2010). To this purpose, the IUCN introduced the Area Of Occupancy (AOO) as one of the main indicator of species distribution, defined as the area of suitable habitat occupied by the taxon (IUCN Standards and Petitions Subcommittee 2014). Recently, modelling tools have emerged to combine multiple data sources to estimate species distributions (Fletcher et al., 2019; Miller et al., 2019; J. D. Nichols et al., 2008). *Multi-method models* refer to the modelling approaches that combine different data sources (also known as *integrated species distribution models*, Miller et al. 2019). The main purpose of multi-method models is to improve the accuracy of ecological indicators (Bonnet-Lebrun, Calabrese, Rocamora, & López-Sepulcre, 2016; Jiménez et al., 2016). Species distributed over large scale areas could particularly benefit from multi-method models because they allow a global coverage of species occurrence by combining different data sources collected at different spatial scales (Haynes, Rosenberger, Lindberg, Whitman, & Schmutz, 2013; Miller et al., 2019).

In addition to the challenge of combining several sources of information, EM faces uncertainties inherent to data collection. When monitoring elusive or mobile species, individuals can be missed even if present at the sampling site. The so-called imperfect detection issue (i.e. false-negative observations) leads to the underestimation of species distribution if not accounted for (Mackenzie et al., 2002). To deal with imperfect detection, occupancy models have been developed to estimate species distribution while accounting for false negatives in the observation process (Mackenzie et al., 2002). Estimating occupancy when species detection is less than 1 requires performing *repeated visits* (hereafter *RV*) to estimate the probability of detection (MacKenzie, 2006; Mackenzie et al., 2002). However, RV come with costs and logistical issues that make them not always feasible. There is a trade-off between i) investing in a reasonable sampling effort to perform RV, and ii) conducting monitoring at large scales without repeating visits at sample sites (Dénes, Sólymos, Lele, Silveira, & Beissinger, 2017).

In this context, two relevant developments of occupancy models have been recently proposed. First, multi-method occupancy models combine data from different monitoring programs to improve the estimation of species distribution (Fletcher et al., 2019; Miller et al., 2019; Nicol et al., 2019). Second, *single-visit* (SV) occupancy models allow estimating species distribution and detectability while having only one visit at the sampling site (Lele, Moreno, & Bayne, 2012; Miller et al., 2019). Therefore, we expect SV occupancy models to overcome some limitations that arise when using non-standardized data (e.g. lack of repeated surveys in occupancy modelling, Miller et al. 2019), hence being beneficial to cost-constrained EM programs (Dénes et al., 2017; Lele et al., 2012). Besides, RV occupancy models require that the ecological state of sampled sites remains unchanged between visits, which is not always the case, while SV models allow to relax this so-called closure assumption (Lele et al., 2012). An increasing number of studies suggest that under certain conditions, SV models produce robust estimates of occupancy without repeating visits at the sampling sites (Laran, Authier, et al., 2017; Lele et al., 2012; Peach, Cohen, & Frair, 2017; Sólymos & Lele, 2016).

In this paper, we develop an approach that combines multi-method and single-visit occupancy models. As a case study, we focus our analysis on the distribution of Bottlenose dolphins (*Tursiops truncatus*) in the North-Western Mediterranean Sea. We illustrate how two datasets of marine monitoring programs can be combined with multi-method SV occupancy models to estimate AOO indicator for biodiversity conservation. In the marine world, many species of conservation interest are elusive, and EM data can be costly (Aylesworth, Loh, Rongrongmuang, & Vincent, 2017; *Read "Marine Protected Areas*, 2001). In particular, the high seas are difficult to access and EM is often performed through aerial surveys (Authier et al., 2017). Coasts are another challenge that require detailed attention, and proximity to land allows to perform at-sea monitoring (Issaris et al., 2012; Pennino, Mérigot, Fonseca, Monni, & Rotta, 2017). Besides, many species such as marine megafauna are mobile and occur in both coasts and high seas (Authier et al., 2017; Laran, Pettex, et al., 2017). Combining monitoring programs that are carried out in each realm (i.e. coasts and high seas) has the potential to provide relevant information about these species (Waggitt et al., 2019). Here, we combine aerial surveys and at-sea monitoring into multi-method SV occupancy models. We compare the outputs of multi-method occupancy models to occupancy models using at-sea monitoring data only or aerial survey data only. We demonstrate that combining several datasets into multi-method SV occupancy models leads to accurate ecological estimation while relaxing the assumptions hampering the accommodation of non-standardized data. Last, we discuss the advantages of using complementary EM programs in applied ecology.

Methods

1. Study species and area

The North-Western Mediterranean waters represent an important biodiversity hotspot coexisting with intense human activities (Fraschetti, Terlizzi, Micheli, Benedetti-Cecchi, & Boero, 2002; Giakoumi et al., 2017; Lloret & Riera, 2008; Moullec et al., 2019).

Anthropogenic pressures and climatic vulnerability underline the critical position of Mediterranean Sea for biodiversity conservation (Giakoumi et al., 2017). We focused on the North-Western Mediterranean, an area of 255,000 km^2, which includes the Gulf of Lion and the Ligurian sea, the French coast, Corsica, and the Northern part of Sardinia (Fig. 1). For statistical analyses, we divided the study area in 5346 pixel/sites creating a 5'x5' Mardsen grid (WGS 84).

The North-Western Mediterranean Sea is a critical habitat for many cetaceans species (Bearzi, Piwetz, & Reeves, 2019; Labach et al., 2019; Laran, Pettex, et al., 2017). Due to its coastal behaviour, bottlenose dolphins (*Tursiops truncatus*) suffer from several threats due to anthropic pressures (e.g. collisions, fisheries bycatch, pollution, or acoustic perturbations), which raise concerns about their coexistence with human activities (Bearzi, Fortuna, & Reeves, 2009; Bearzi et al., 2019; Laran, Pettex, et al., 2017). Mediterranean population of Bottlenose dolphins is considered “vulnerable” by the IUCN Red List (IUCN, 2009) and is one of the two cetacean species listed on the Annex 2 in the European Habitats Directive (92/43/EEC). The protected status of this species within the French seas led to development of specific monitoring programs for its study in the Mediterranean Sea within the implementation of the European Marine Strategy Framework Directive (2008/56/EC; MSFD).

2. Data collection

We considered two large-scale monitoring programs developed for bottlenose dolphins in the North-Western Mediterranean Sea.

At-sea coastal monitoring program

We used data form the first large-scale study of Bottlenose dolphins in the French Mediterranean Sea. Four NGOs and one marine reserve performed at-sea surveys over 21,464 km of the French continental shelf including the Gulf of Lion, the French Riviera, and

Corsica. This program was performed all year long between 2013 and 2015 (see Labach et al. 2019 for details about the program).

Aerial pelagic and coastal monitoring program

Data were collected during aerial surveys targeting the main taxa of marine megafauna within the French Exclusive Economic Zone (EEZ) including the Pelagos Sanctuary. The survey covered 24,624 km of line-transect performed by scientific institutional partners of the French Biodiversity Agency between November 2011 and August 2012. This survey is repeated every six years to inform the MSFD.

Environmental data

We used two environmental covariates to estimate the area of occupancy of bottlenose dolphins: i) bathymetry, which is expected to have a negative effect on bottlenose dolphins' occurrence (Bearzi et al., 2009; Labach et al., 2019), and ii) sea surface temperature (SST, from Aqua/MODIS | NASA" 2019), which is locally related to dolphins' prey abundance and hence expected to affect local distribution of bottlenose dolphins (Bearzi et al., 2009; Giannoulaki et al., 2013; Passadore, Möller, Diaz-Aguirre, & Parra, 2018; Queiros, Fromentin, Astruc, Bauer, & Saraux, 2018). We checked for correlation between the two covariates and the Pearson coefficient was < 0.3.

3. Occupancy models

Occupancy models estimate spatial distribution while accounting for imperfect species detection (Mackenzie et al., 2002). In EM, a species may be not detected on a site even though it was present at that site – this is usually referred to as false negatives. The formulation of occupancy models as state-space models (SSM) allows distinguishing the latent ecological state process (i.e. species present or absent at a site) from the detection process (Royle & Kéry, 2007). We denote z_i the latent occupancy of site i ($z = 1$, presence; z

= *0*, absence). We assumed z_i is drawn from a Bernoulli distribution with Ψ_i the probability that the species is present at site *i*.

$$z_i \sim Bernoulli(\Psi_i).$$

In standard occupancy designs, each site is visited *J* times to estimate the rate of false-negatives. We denote $y_{i,j}$ ($y_{i,j} = 0$, no detection ; $y_{i,j} = 1$, detection) the observations corresponding to the data collected at site *i* during visit *j* ($j = 1,..,J$). Repeating visits at a site allows estimating species detectability, with $p_{i,j}$ being the probability of detecting the species at visit *j* given it is present at site *i*.

$$y_{i,j} \mid z_i \sim Bernoulli(z_i \, . \, p_{i,j})$$

An important assumption of occupancy models is that the latent ecological state of a site (the z_i's) remains unchanged between the repeated visits (MacKenzie, 2006). When monitoring highly mobile species, such as cetaceans, the closure assumption is likely to be violated because individuals moved into and out of the sampling sites. Occupied locations are used only temporary by individuals (MacKenzie 2006; Neilson et al. 2018). Then, occupancy is interpreted as the proportion of sampled sites *used* by the species, and AOO represents the *area of use* by the species. Subsequently, the occupancy estimator Ψ_i represents the probability that site *i* is *used* by the target species as opposed to the probability of occupancy (Kendall, Hines, Nichols, & Grant, 2013). The detection probability now accounts for both the probability of detecting the species and the probability that the species is present in the sampling unit, reflecting that the species might occupy the site but not during the sampling occasion (MacKenzie, 2006). MacKenzie (2006) showed that if individuals' movement in and out of the sampling sites is random, then the occupancy estimator is unbiased (Kendall et al., 2013).

We considered four sampling occasions ($J = 4$): winter (January, February, March), spring (Avril, May, June), summer (July, August, September), autumn (October, November, December). To estimate the sampling effort of the two monitoring programs, we calculated the transect length (in km) prospected by the monitoring method within each site at each occasion. Each sampling occasion *j* depicted a similar amount of sampling effort over the studied area.

We modelled Ψ as a function of the environmental covariates bathymetry and SST on a logit scale, and *p* as a function of sampling effort on the logit scale:

$$Logit(\Psi_i) = \beta_0 + \beta_1 * bathymetry_i + \beta_2 * SST_i,$$

$$Logit(p_{i,j}) = \alpha_0 + \alpha_1 * sampling\_effort_{i,j}$$

where regression parameters β_0, β_0, β_0, α_0, and α_1 are unknown and need to be estimated.

We considered that a covariate effect size was statistically significant when its 95% credible interval (CI) did not include 0.

4. Multi-method occupancy models

Although most occupancy studies use a single method to collect detection/non-detection data, it is possible to consider several detection methods (Miller et al., 2019; J. D. Nichols et al., 2008). Multi-method occupancy models account for several detection probabilities, therefore allowing to quantify the detection error of each sampling method (Clare, McKinney, DePue, & Loftin, 2017; Fisher & Bradbury, 2014; Pregler, Vokoun, Jensen, & Hagstrom, 2015). The Nichols et al (2008) multi-method approach considers two occupancy parameters to account for the different spatial scale of each detection methods. Bonnet-Lebrun et al., (2016) extended the multi-method framework for estimating multi-species abundance.

Here, we built a multi-method occupancy model using data from the two monitoring programs. For convenience, we drop the subscripts in the notation. The observation process takes four values with y = 0 for no detection, y = 1 for detection by aerial survey only, y = 2 for detection by at-sea survey, and y = 3 for detection by both monitoring programs. Assuming the detection methods are independent, the observation process can be written using detection probability by the aerial survey (p_a) and the detection probability by the at-sea survey (p_s):

$$y|z \sim Multinomial(1, z * \pi)$$

with

$$\pi = [p_0 \quad p_1 \quad p_2 \quad p_3] = [pr(y=0) \quad pr(y=1) \quad pr(y=2) \quad pr(y=3)]$$

$$\pi = [1 - p_a - p_s + p_a p_s \quad p_a(1-p_s) \quad p_s(1-p_a) \quad p_a p_s]$$

5. Single-visit occupancy models

SV occupancy requires that the set of covariates affecting occupancy includes at least one different covariate from the one affecting detection probability (Dénes et al., 2017; Lele et al., 2012; Sólymos & Lele, 2016). We applied SV occupancy models to both aerial surveys and at-sea dataset. As we considered a single visit (*J = 1)*, we calculated the total sampling effort and averaged the SST values over the 4 repeated visits.

6. Bayesian implementation

To assess the performance of multi-method SV occupancy models, we analysed separately aerial survey data models and at-sea data using both SV and RV occupancy models. We ran all models with three chains of Markov Chain Monte Carlo sampler with 20,000 iteration each in JAGS (Plummer & others, 2003) called from R (R Core Team, v 3.2.5 2019) using the *r2jags* package (Su & Yajima, 2015). We checked for convergence calculating the *R-hat* parameter (Gelman et al., 2013) and reported posterior means and 95% credible intervals (CI) for all parameters.

Results

Between summer 2013 and summer 2015, at-sea surveys produced 1,670 dolphins' detections located in 89 sites. The sampling effort of at-sea surveys was heterogeneous over the study area (between 1 and more than 20 visits per site, Fig. 1). Sampling effort for aerial surveys was homogeneous over the studied area with three or four replicates per line-transect between November 2011 and August 2012. The aerial survey produced 170 detections located in 87 sites.

Multi-method occupancy models had a better precision than aerial survey or at-sea occupancy models to estimate effect size of environmental covariates on Ψ (see 95% CI in Fig. 2). Aerial survey had a better precision than at-sea survey. SV occupancy models produced similar estimates to RV occupancy models although with lower precision to estimate the effect size of bathymetry and SST on Ψ (Fig. 2). Estimates of SST and bathymetry effects were similar between all occupancy models. Parameter Ψ increased when bathymetry decreased. Bathymetry ranges from 0 m to 3,488 m deep, hence a negative influence of the bathymetry referred to a preference for a low seafloor (e.g. 0-200m depth). SST effect size was null for all models (Fig. 2).

All maps displayed higher Ψ values on the continental shelf than on the high seas although intensities of Ψ were different between occupancy models (Fig. 3). At-sea surveys produced the most contrasted maps, with the highest estimation of Ψ in the high-seas and the lowest in the continental shelf. Maps from multi-method occupancy models displayed moderate contrast of Ψ compared to maps from at-sea and from aerial surveys (Fig. 3). SV models displayed higher Ψ in sea shelf compared to RV occupancy models.

Discussion

Combining datasets improves parameter estimates of occupancy models

When the species of interest displays a large range of occurrence (such as bottlenose dolphins), considering multiple sampling methods is effective to monitor the entire population making the best of each device (Haynes et al., 2013). In the marine world, aerial surveys allow to monitor the pelagic area while at-sea surveys provided coastal information with a higher concentration of sampling effort, which results in maximizing spatial and temporal coverage of marine megafauna (Waggitt et al., 2019). In our case study, ecological estimates from multi-method occupancy models ranged between the estimates obtained with each dataset separately, and combining data increased precision of covariates effect size on AOO (i.e. Ψ, Fig. 2).

Across all occupancy models, the effects of environmental covariates were similar and consistent with other studies. Bottlenose dolphins are more likely to use low depth seafloor (Bearzi et al., 2009; Labach et al., 2019), and depth had a higher effect than SST on the use of space by bottlenose dolphins (Derville, Torres, Iovan, & Garrigue, 2018; Torres, Read, & Halpin, 2008). However, the probability of area used by bottlenose dolphins was spatially different between models (Fig. 3). Because at-sea occupancy model assigned more importance to bathymetry than aerial survey occupancy models, at-sea data occupancy models predicted a lower presence of bottlenose dolphins in the high seas than aerial surveys occupancy models (Figs 2-3). These spatial differences in the intensity of AOO could affect the allocation of conservation funding for future monitoring or management of this species. For example, assuming the species makes little use of the high seas compared to the continental shelf might lead to unbalanced conservation effort discarding the high seas. Multi-method occupancy models accounted for bottlenose dolphins' detections from aerial surveys in the high seas and produced a map closer to aerial survey occupancy models than that of at-sea occupancy models. Our results support the well-known benefit of combining datasets into multi-method occupancy models (Clare et al., 2017; Haynes et al., 2013; Miller et al., 2019). The flexibility of occupancy models provided a relevant framework to combine monitoring programs (Miller et al., 2019; J. D. Nichols et al., 2008). Also, if detection methods are not independent, bias in parameter estimates may occur. Then, explicitly accounting for dependence can overcome this issue (Clare et al., 2017; J. D. Nichols et al., 2008). Because at-sea and aerial surveys were performed during different years (see Methods section), we considered them as independent in our case study.

Using SV occupancy models to make the best of EM

Here, RV multi-method occupancy model provided the highest precision in effect size estimation of AOO, but implementing multiple methods combined with RV also led to the highest sampling effort. Monitoring agencies do not always have the resources to conduct RV and to implement multiple sampling methods (Pregler et al., 2015). In applied ecology, monitoring is often performed in a cost constrained context (Lindenmayer & Likens, 2010; J. D. Nichols et al., 2008). SV occupancy models produced similar estimates to those obtained with RV occupancy but with lower precision on the covariates' effect size (Fig. 2). Because at-sea sampling effort was heterogeneous among sampled sites, many sites were sampled only once by at-sea monitoring program. We underlined the capacity of SV occupancy models to use datasets obtained from sampling protocols that did not perform replicated surveys, which was the case for the at-sea dataset. In this way, Miller et al. (2019) encouraged further developments of methods mixing standardized and non-standardized frameworks. In this spirit, we illustrate the flexibility of the state-space modelling framework by building a multi-method occupancy model mixing RV occupancy for aerial surveys and SV occupancy for at-sea surveys (see Appendix I for details).

Although RV occupancy models remain statistically more efficient (Lele et al. 2012, Fig. 2), there are benefits in using SV to relax the closure assumption inherent in the ecological behaviour of mobile species like bottlenose dolphins (Kendall et al., 2013; Lele et al., 2012). Overall, when financial or logistical costs are an issue, SV occupancy models provide robust estimates while accounting for imperfect detection (Lele et al., 2012). Multi-method SV sampling design combines the benefit of a large spatial coverage due to the integration of several datasets with a reduced cost associated to SV. As EM often suffers from a lack of well-articulated design (Lovett et al., 2007), multi-method SV occupancy modelling opens perspectives for the use of non-standardized data collected through different sampling designs.

Implications for EM programs

We acknowledge the importance of planning monitoring programs according to clearly stated objectives (Lindenmayer & Likens, 2010; J. Nichols & Williams, 2006). We showed that even with non-standardized datasets, using information from different monitoring programs is beneficial. Multi-method occupancy modelling has been used to evaluate EM programs prior to their implementation (i.e. comparing detection probabilities between devices, Otto & Roloff 2011; Haynes et al. 2013). In contrast, we emphasized the benefit of considering multiple methods after data collection. Even if at-sea dataset was not designed for occupancy modelling because of the lack of RV, its use into multi-method SV occupancy models improved precision in ecological estimates compared to analyses of aerial surveys only. Despite their crucial role in the conservation process, EM programs are often perceived as costly and wasteful when compared to management (Lovett et al., 2007). Maximizing their ecological outcomes through data combination and SV approaches will be beneficial for the support and cost effectiveness of EM program.

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Tables & Figures

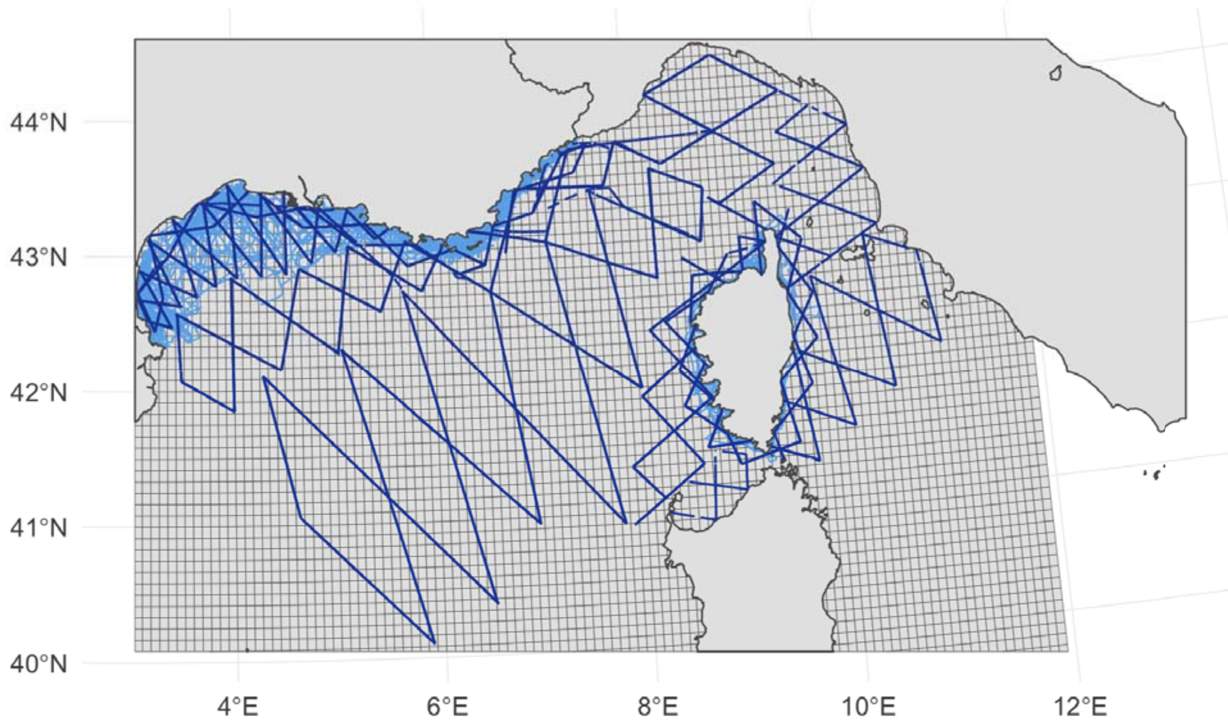

Figure 1: Sampling design of the two monitoring programs studied. The aerial surveys (SAMM program; dark blue) prospected 24,624 km of both sea shelf and high seas. At-sea surveys (GDEGeM program; light blue) prospected 21,646 km of the French continental shelf.

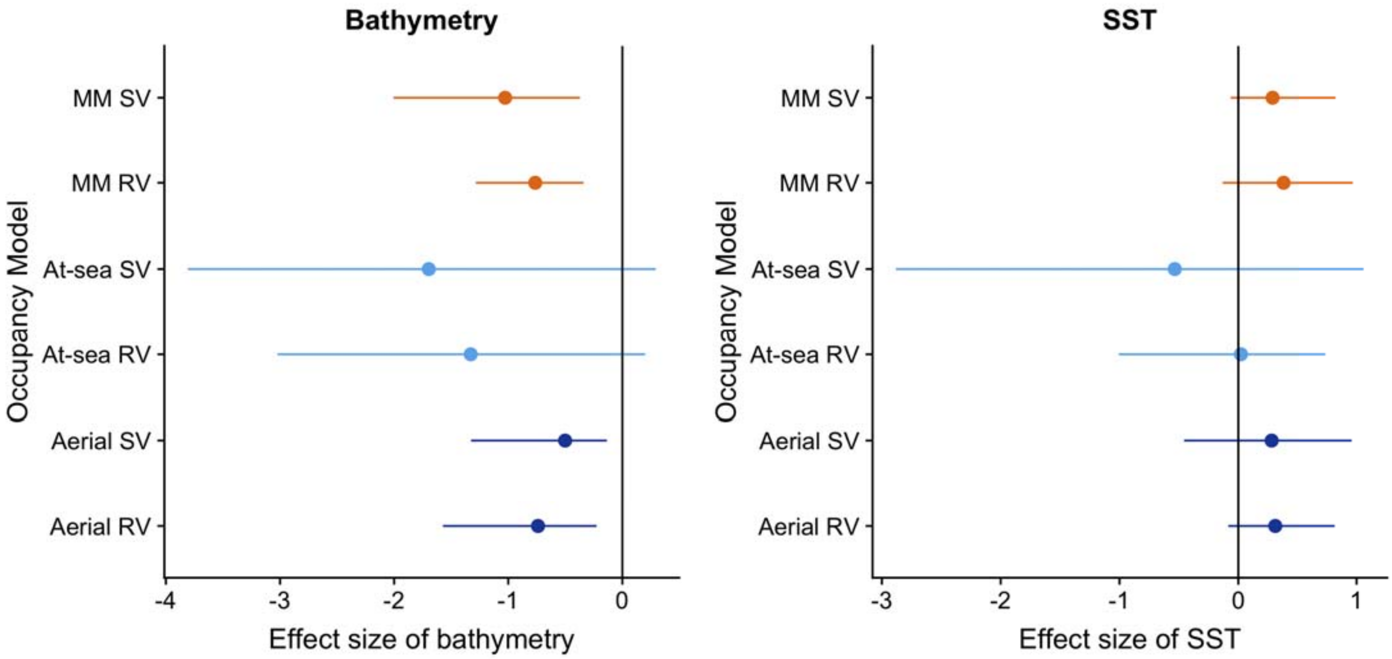

Figure 2: Effect size of bathymetry and sea surface temperature (SST) on the probability Ψ that a site is used by Bottlenose dolphins (*Tursiops truncatus*) obtained with different monitoring programs. The posterior mean is provided with the associated 95% credible interval. “SV” refers to *single-visit* occupancy models, “RV” to *repeated visits* occupancy models, and “MM” stands for *multi-method* occupancy models, in which aerial surveys and at-sea surveys are combined. Estimates are given on the logit scale.

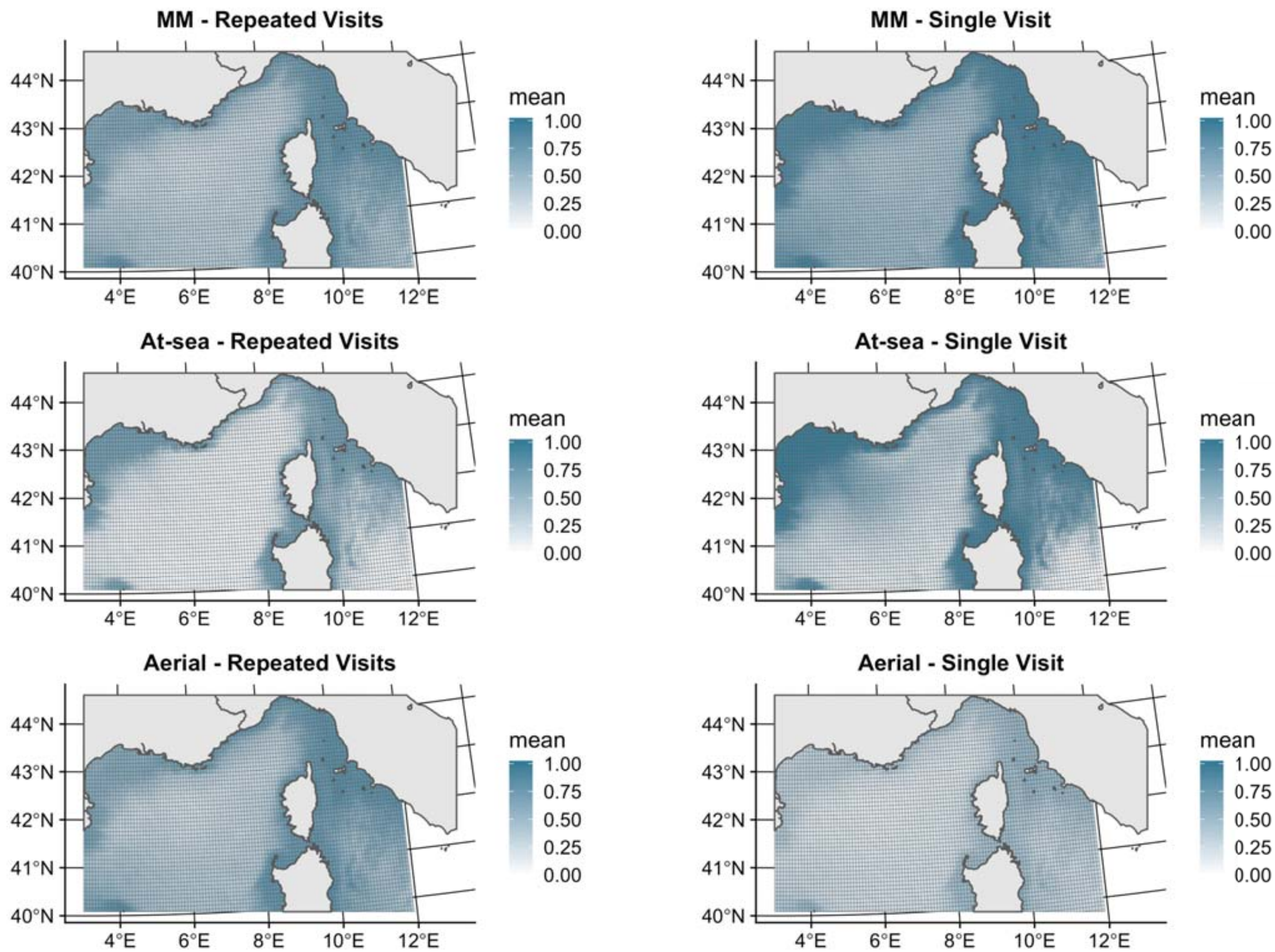

Figure 3: Probability of space use by Bottlenose dolphins (*Tursiops truncatus*) over the NW Mediterranean Sea. "MM" stands for *multi-method* occupancy models, in which aerial surveys and at-sea surveys are combined. Repeated-visit occupancy maps refer to occupancy models with 4 sampling occasions. Single-visit maps refer to occupancy models considering 1 sampling occasion. Using the posterior mean of regression parameters, we estimated the probability that site *i* was used by bottlenose dolphins.

Authors' contribution

VL, MA and OG conceived the ideas and designed methodology; HL and MA collected the data; VL analysed the data; VL and OG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supporting information

R codes are available on Github.

https://github.com/valentinlauret/SuppInfo_Lauret_et_al

Supporting Information is provided under HTML format

SuppInfo_Lauret_et_al.html