Using integrated multispecies occupancy models to map co-occurrence between bottlenose dolphins and fisheries in the Gulf of Lion, French Mediterranean Sea

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Abstract: In the Mediterranean Sea, interactions between marine species and human activities are prevalent. The coastal distribution of bottlenose dolphins (*Tursiops truncatus*) and the predation pressure they put on fishing stocks lead to regular interactions with fisheries. Multispecies occupancy models are a relevant framework to estimate co-occurrence between two (or more) species while accounting for false negatives and potential interspecific dependance although requiring substantial quantity of data to fit. Here, we extended multispecies occupancy model to integrate multiple datasets to map spatial co-occurrence between trawlers and bottlenose dolphins in the Gulf of Lion, French Mediterranean Sea combining data from aerial surveys and boat surveys at a large spatial scale. The integrated multispecies occupancy model produced more precise estimate than single-dataset multispecies occupancy models. Our results support that both integrated and multispecies frameworks are relevant to map distribution and understand species interactions in our case study. Besides, our application of multispecies occupancy models to bottlenose dolphins and fishing trawlers enabled to map co-occurrence probability, which open promising avenues in the understanding of interactions between human activities and marine mammals that occur at large spatial scales.

Keywords: cetaceans, human-animal interaction, integrated models, NIMBLE, odontocetes, occupancy models, trawlers

Introduction

The Mediterranean Sea, being on the busiest sea on Earth, is especially affected by anthropogenic pressures (Coll et al. 2012, Giakoumi et al. 2017). In particular, there are significant interactions between marine species and human activities (Avila et al. 2018). Among marine mammals, odontocetes frequently forage in the proximity of fishing vessels (Bonizzoni et al. 2022). Despite facilitating access to prey, foraging behind trawlers leads to depredation or by-catch interactions that pose conservation concerns (Lewison et al. 2004, Snape et al. 2018, Santana-Garcon et al. 2018, Bonizzoni et al. 2020, 2022). The coastal ecology of common bottlenose dolphins (*Tursiops truncatus*, hereafter bottlenose dolphins) and the depredation pressure they put on fishing stocks lead to regular interactions with human recreational activities and fisheries (Bearzi et al. 2009, Queiros et al. 2018, Leone et al. 2019). Bottlenose dolphins are often reported in close proximity to fishing activities, and are known to forage behind trawlers worldwide, including the Mediterranean Sea (Allen et al. 2017, Bonizzoni et al. 2022). Following documented bottlenose dolphins mortality events (Manlik et al. 2022), interactions have raised conservation concerns and mitigation measures tested to date have not proven effective (Snape et al. 2018, Bonizzoni et al. 2020). Interactions between bottlenose dolphins and fisheries have been studied via *in-situ* observations (Santana-Garcon et al. 2018) and passive acoustic monitoring (Bonizzoni et al. 2022) to describe the behavioral drivers of interaction, which constitute a major asset despite such being restricted to a limited spatial scale. At a larger extent, one can use trawlers data as covariate on dolphin distribution models (Pirotta et al. 2015). While a useful point, such modelling approach do not take into account biotic interactions that can lead to bias estimation of interaction risks.

Mapping human-wildlife interactions is a preliminary step to better understand and manage conservation conflicts and is, therefore, particularly strategic in the case of the mammal by-catch issue. This is usually achieved by calculating and mapping the overlap between the distribution of a species and human pressure(s). This overlapping approach raises two issues. First, when modelling species distributions, failure to account for interspecific interactions between co-occurring species may lead to biased inference, which arises when modelling only abiotic and habitat associations (Rota et al. 2016b). In particular, one needs to account for biotic effects when mapping potential interactions between marine mammals and fisheries as we know that cetaceans can forage in association to trawling vessels (Jourdain & Vongraven 2017, Allen et al. 2017). Second, another challenge when quantifying species interactions is to account for imperfect detection, e.g. when species do co-occur but one or several of the species involved go undetected by sampling (Rota et al. 2016a, Fidino et al. 2019). Ignoring imperfect detection leads to the underestimation of species distribution and imprecise or even inaccurate quantification of species interactions (MacKenzie 2006).

To account for these issues, multispecies occupancy models have been developed to estimate occupancy probabilities of two or more interacting species while accounting for imperfect detection (Rota et al. 2016b, Fidino et al. 2019, Devarajan et al. 2020). One caveat of multispecies models is that they require substantial data for robust ecological inference (Clipp et al. 2021). To overcome data scarcity, several authors have suggested combining multiple datasets within an integrated modelling framework (see Kéry & Royle (2020), Chapter 10, for a review). In that spirit, we previously developed a single-species integrated occupancy model to map the distribution of bottlenose dolphins over the Northwestern Mediterranean Sea (Lauret et al. 2021).

Here, our first objective was to showcase the extension of multispecies occupancy models to integrate multiple datasets and to assess its performances. Our second objective was to illustrate a statistical tool that enable to map co-occurrence probabilities of fishing trawlers and bottlenose dolphins while integrating multiple datasets. We built an integrated multispecies occupancy model to quantify interactions between bottlenose dolphins and fisheries using data collected from aerial surveys and boat surveys in the Gulf of Lion (French Mediterranean Sea). We assessed whether the multispecies occupancy model benefit from data integration compared to models using dataset in isolation (hereafter single-dataset models), and whether the multispecies framework helped to estimate dolphins and trawlers occupancy compared to single-species occupancy models. Finally, we discussed the opportunity of multispecies occupancy models to study interactions between marine mammals and fisheries.

Material and Methods

Data

We combined bottlenose dolphin and fisheries data extracted from two large-scale monitoring programs. First, we used Aerial Surveys of Marine Megafauna (SAMM in French) conducted in 2011 and 2012 in the French Mediterranean sea and Italian waters of the Pelagos Sanctuary (Laran et al. 2017). These aerial surveys aimed to collect data on marine mammals, seabirds, fish, and human activities (Baudrier et al. 2018, Lambert et al. 2020). We used detection / no-detection data of bottlenose dolphins and of fishing trawlers collected during 4 sampling occasions, 1 per season (winter, spring, summer, and autumn). The second monitoring program targeted bottlenose dolphin habitats in the French Mediterranean Sea using a boat photo-identification protocol between 2013 and 2015 collecting data all year long (Labach et al. 2021). We focused our attention on the Gulf of Lion and we used data collected by EcoOcean Institut. We extracted data of bottlenose dolphins and trawlers. We considered a trawler every commercial fishing boat that we observed actively dragging. We only used data on trawlers seen fishing as we focused on fishing areas and not traveling routes between harbours and fishing areas.

We divided the Gulf of Lion study area into 397 5’ × 5’ contiguous Marsden grid-cells (WGS 84) for statistical analysis (Figure 1). We calculated the sampling effort as the total length (in km) of transects conducted in each grid-cell by each monitoring program per time unit. We used seabed depth as an environmental covariate affecting spatial variation in occupancy of bottlenose dolphins and trawlers (Bearzi et al. 2009, Labach et al. 2021). Depth values in meters was scaled before its use in models. At the date of our modelling developments, the resolution of the grid and our ability to explore multiple environmental descriptors of co-occurrence patterns was impaired by the limited size of our datasets. As new monitoring programs are implemented on this case study, we believe that our integrated bottlenose dolphins - fisheries occupancy model would benefit from further ecological investigation when more data would be collected and available to test for competing ecological hypotheses and models (Broms et al. 2016).

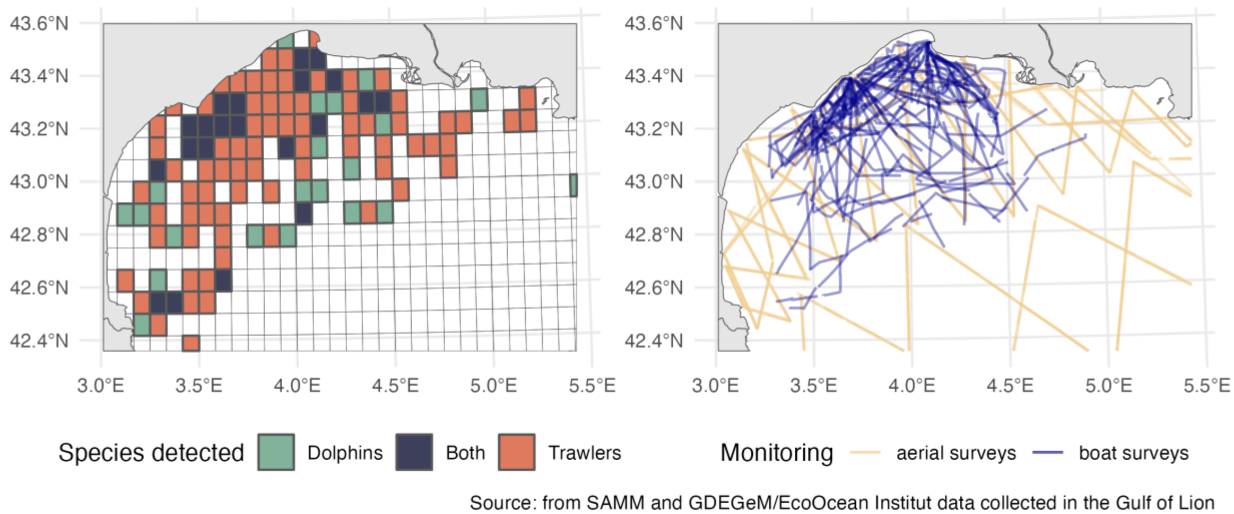

Figure 1: Gulf of Lion detections of bottlenose dolphins and trawlers by aerial surveys (SAMM) and boat surveys (GDEGeM and EcoOcean Institut) along with the sampling effort for each monitoring program. We plotted data on 397 5' × 5' contiguous Marsden grid-cells (WGS 84)

Integrated multispecies occupancy model

Several assumptions need to be met to safely apply multispecies occupancy models: i) geographic and demographic closure of grid-cells and of the study area (i.e. individuals do not move in and out the grid-cell, and no birth or death event occur during the sampling period), ii) independence of the detection / no-detection data over space and time, iii) accurate identification (i.e. no misidentification) (Rota et al. 2016b). In our case study, dolphins and trawlers moved in and out grid-cells during the sampling period making the geographic closure unlikely to be respected. Thus, we interpreted occupancy as "space-use", that is the probability that the species uses the grid-cell given it is present in the study area. In this article, we presented an extension of multispecies occupancy models to integrate multiple datasets. Then, to ensure clarity of the integrated multispecies occupancy model we did not perform a deep investigation of ecological predictors.

Latent ecological process

We followed Rota et al. (2016a) to formulate the ecological model describing the occupancy process. In grid-cell i, the latent occupancy state can take 4 values: $z = [1,0,0,0]$ if neither dolphins nor trawlers use the grid-cell, $z = [0,1,0,0]$ if dolphins use the grid-cell but trawlers do not, $z = [0,0,1,0]$ if trawlers use the grid-cell but dolphins do not, and $z = [0,0,0,1]$ if both dolphins and trawlers use the grid-cell. Then, ignoring the grid-cell index, our multispecies occupancy model estimated 4 occupancy probabilities.

- ψ^4 is the probability that both dolphins and trawlers use the grid-cell;
- ψ^3 is the probability that trawlers use the grid-cell and dolphins do not;
- ψ^2 is the probability that dolphins use the grid-cell and trawlers do not;
- ψ^1 is the probability that neither dolphins nor trawlers use the grid-cell, which corresponds to the probability that none of the previous events occurs, with $\psi^1 = 1 - \psi^2 - \psi^3 - \psi^4$.

We modeled the occupancy state of each grid-cell z as a multinomial logistic regression, z being draw in vector $\pi = [(1 - \psi^2 - \psi^3 - \psi^4), \psi^2, \psi^3, \psi^4]$:

$$z \sim Multinomial(1, \pi)$$

with π adjusted to sum to 1 using a generalized logit link function. We modeled occupancy probabilities ψ^2, ψ^3, and ψ^4 as a function of depth and non-parametric functions geographical coordinates of the grid-cell center X and Y with Generalized Additive Models (GAMs) (Wood 2006) using a multinomial-logit link. For grid-cell i:

$$\psi_i^1 = \frac{1}{1 + \exp(\delta_i^2) + \exp(\delta_i^3) + \exp(\delta_i^2 + \delta_i^3 + \delta_i^4)}$$

$$\psi_i^2 = \frac{\exp(\delta_i^2)}{1 + \exp(\delta_i^2) + \exp(\delta_i^3) + \exp(\delta_i^2 + \delta_i^3 + \delta_i^4)}$$

$$\psi_i^3 = \frac{\exp(\delta_i^3)}{1 + \exp(\delta_i^2) + \exp(\delta_i^3) + \exp(\delta_i^2 + \delta_i^3 + \delta_i^4)}$$

$$\psi_i^4 = \frac{\exp(\delta_i^2 + \delta_i^3 + \delta_i^4)}{1 + \exp(\delta_i^2) + \exp(\delta_i^3) + \exp(\delta_i^2 + \delta_i^3 + \delta_i^4)}$$

where, for $k \in \{2,3,4\}$, δ_i^k in grid-cell i is:

$$\delta_i^k = \alpha_0^k + \alpha_1^k \text{depth}_i + s^k(X_i, Y_i)$$

where $s^k(.)$ is a smooth function (see Supplementary Information). Quantities $s^k(.)$, α_0^k and α_1^k were to be estimated. δ^2, δ^3 are called first-order parameters estimating log odds of species occurrence, conditional on absence of the other species, while δ^4 is a second-order parameter estimating change in log odds when both species are co-occurring. For additional detail about the modelling formulation, one can refer to Fidino et al. (2019), and Rota et al. (2016a).

Observation process

We considered 4 sampling occasions j with similar sampling effort for each monitoring program (winter, spring, summer, and autumn). We extended the observation process of the multispecies occupancy model of Rota et al. (2016a) to integrate two datasets in the spirit of Lauret et al. (2021). We considered dataset A (i.e. aerial line transects), and dataset B (i.e. boat photo-id surveys). In both monitoring programs, detection and non-detection data on bottlenose dolphins and trawlers were collected. Each "species" had a different detection probability depending on the monitoring program considered, which led to four different detection probabilities:

- p_d^B that is the probability of detecting dolphins by boat photo-id surveys;
- p_d^A that is the probability of detecting dolphins by aerial surveys;
- p_t^B that is the probability of detecting trawlers by boat photo-id surveys;
- p_t^A that is the probability of detecting trawlers by aerial surveys.

For each grid-cell i and each sampling occasion j, we modeled the detection probability $p_{i,j}$ as a logit-linear function of sampling effort. For example, regarding the probability of detecting bottlenose dolphins by boat photo-id surveys, we estimated:

$$\text{logit}\left(p_d^B(i,j)\right) = \beta_{0d}^B + \beta_{1d}^B \text{sampling effort}_{i,j}^B$$

where β_{0d}^B, and β_{1d}^B were to be estimated. One can argue that trawlers trawlers detection is perfect as they are not an elusive animal species. However, due to the large grid-cell size considered (i.e. 55 km2), trawlers can remain undetected during sampling, e.g. sparse sampling of the edge of the grid-cell can limit trawlers detection. Then, we accounted for possible imperfect detection of trawlers and we modeled trawlers detection probability as the logit-linear function of sampling effort.

The four detection probabilities could then be used to explain the simultaneous detection / no-detection of each species by each survey, resulting in 16 observation "events" (i.e. (2 species)^(2 detections status)^(2 surveys)) (See Supplementary materials for details about the observation process).

Then, with 4 ecological states (in columns) and 16 observation events (in rows), we described the observation process with the following (transposed) 4x16 matrix.

$$t(\theta) = \begin{bmatrix} 1 & (1-p_D^B)(1-p_D^A) & (1-p_T^B)(1-p_T^A) & (1-p_T^B)(1-p_T^A)(1-p_D^A)(1-p_D^B) \\ 0 & p_D^B(1-p_D^A) & 0 & (1-p_T^A)(1-p_D^A)p_D^B(1-p_T^B) \\ 0 & 0 & p_T^B(1-p_T^A) & (1-p_T^A)(1-p_D^A)p_T^B(1-p_D^B) \\ 0 & 0 & 0 & (1-p_T^A)(1-p_D^A)p_D^B p_T^B \\ 0 & p_D^A(1-p_D^B) & 0 & p_D^A(1-p_T^A)(1-p_D^B)(1-p_T^B) \\ 0 & p_D^B p_D^A & 0 & p_D^A(1-p_T^A)p_D^B(1-p_T^B) \\ 0 & 0 & 0 & p_D^A(1-p_T^A)p_T^B(1-p_D^B) \\ 0 & 0 & 0 & p_D^A(1-p_T^A)p_D^B p_T^B \\ 0 & 0 & 0 & p_T^A(1-p_D^A)(1-p_D^B)(1-p_T^B) \\ 0 & 0 & p_T^B p_T^A & p_T^A(1-p_D^A)p_D^B(1-p_T^B) \\ 0 & 0 & 0 & p_T^A(1-p_D^A)p_T^B(1-p_D^B) \\ 0 & 0 & 0 & p_T^A(1-p_D^A)p_T^B p_D^B \\ 0 & 0 & 0 & p_D^A p_T^A(1-p_T^B)(1-p_D^B) \\ 0 & 0 & 0 & p_D^A p_T^A p_D^B(1-p_T^B) \\ 0 & 0 & 0 & p_D^A p_T^A p_T^B(1-p_D^B) \\ 0 & 0 & 0 & p_T^B p_T^A p_D^B p_D^A \end{bmatrix}$$

Each observation y was linked to the ecological state z via a Categorical distribution. To do so, let $\theta_z = \big(Pr(y=1), Pr(y=2), \ldots, Pr(y=16)\big)$ represents a column of $t(\theta)$ that lines up with the latent state of a given grid-cell. In other words, each column of $t(\theta)$ represents all observation probabilities conditional on the latent state of a given grid-cell and hence sum to 1.

$$y|z \sim \text{Categorical}(\theta_z)$$

Assessing the benefit of data integration

To assess the benefit of the integrated model, we ran multispecies occupancy models with aerial surveys dataset and with boat photo-identification dataset separately. We compared the precision between each single-dataset multispecies occupancy models and precision of the integrated multispecies occupancy model (See for more details about this study, we refer to supplementary materials.

Assessing the benefit of the multispecies framework

To assess the benefit of the multispecies framework, we ran two single-species occupancy models: i) an integrated occupancy model using bottlenose dolphins data, and ii) an integrated occupancy model using trawlers data. We compared the precision of ecological estimation of the two single-species integrated occupancy models to the estimations of the multispecies integrated occupancy model. As we compared models with limited amount of data, note that in this case we modeled the occupancy probabilities with a linear effect of bathymetry (i.e. without the GAM on geographical coordinates as described above). For more details about the model comparison, we refer to supplementary materials.

Implementation in NIMBLE

We used the `jagam()` function in the `mgcv` R package to implement our GAM (Wood 2019). We ran all models using three Markov Chain Monte Carlo chains with 200,000 iterations and 20,000 burnin each in the NIMBLE R package (Valpine et al. 2017). We reported posterior mean and 80% credible intervals (CI) for each parameter. We considered a significant effect of covariate when its 80% CI does not overlap 0. Data and codes are available on a Zenodo repository. For another Bayesian pipeline to fit integrated multispecies occupancy model, one can refer to {spOccupancy} R-package (Doser et al. 2022).

Results

We detected 60 trawlers, and 18 groups of bottlenose dolphins by aerial surveys, while we detected 71 trawlers and 30 groups of bottlenose dolphins by boat photo-id surveys.

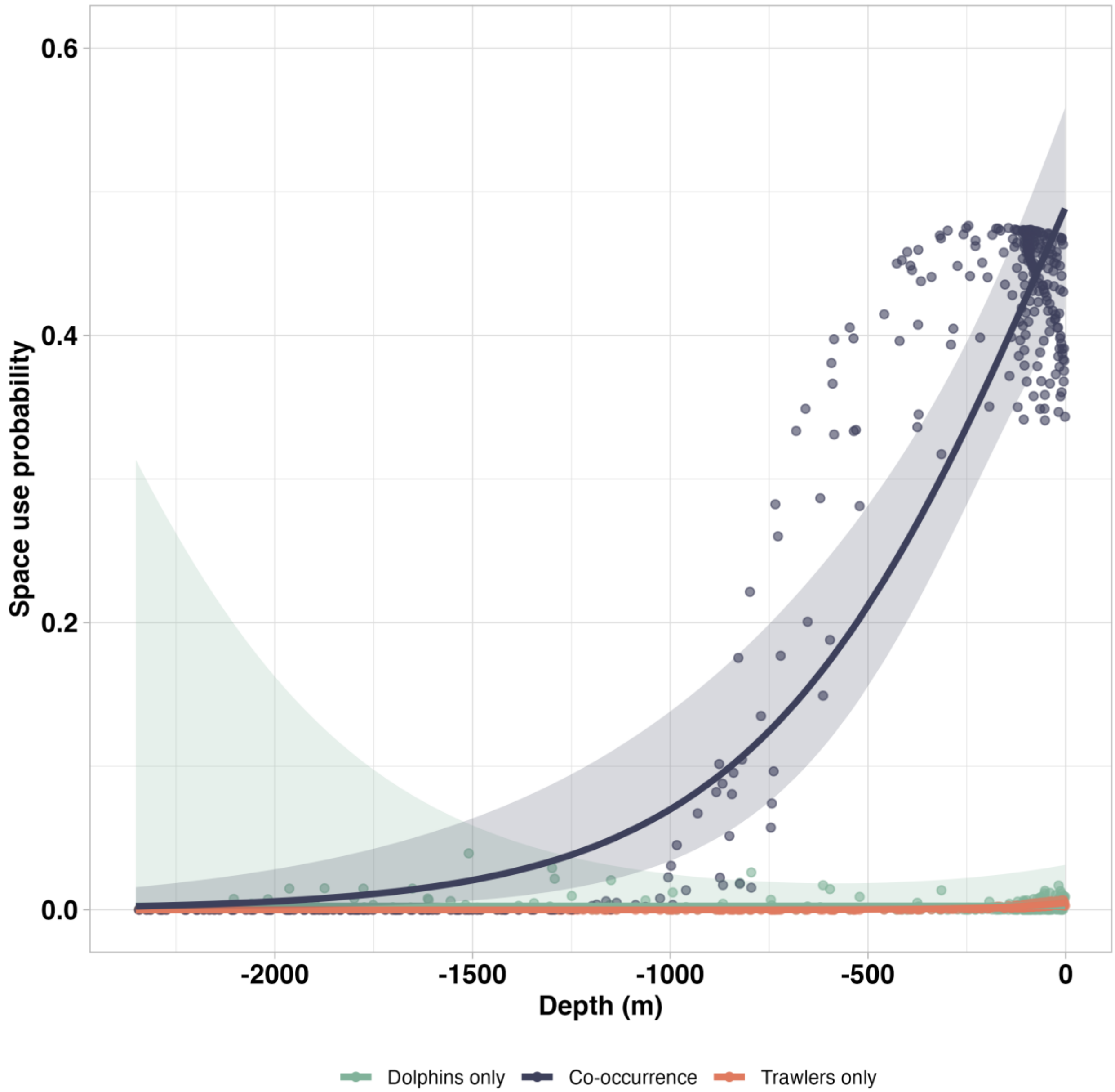

Figure 2: Occupancy probabilities estimated from the integrated multispecies model as function of depth (in meters). Green points and lines represent Psi2, the probability that only bottlenose dolphins used the space. Orange points and lines represent Psi3, the probability that only fishing trawlers used the space. Blue points and lines represent Psi4, the probability that both bottlenose dolphins and fishing trawlers used the space, i.e. co-occurrence. We represented 80% credible interval in shaded areas

Overall, the probability that dolphins only ψ_2 or that trawlers only ψ_3 use a grid-cell was lower than the co-occurrence probability ψ_4 (Figure 2). Comparing average co-occurrence probability ($\psi_4 = 0.29$) to marginal dolphins space-use ($\psi_2 + \psi_4 = 0.30$) or trawlers space-use ($\psi_3 + \psi_4 =$

0.30), we conclude that most of the study area displays either a high probability that both species use the grid-cell, or a low probability for any species to use the grid-cell, *i.e.* space-use of both species overlap. Co-occurrence probability increased with decreasing depth (Figure 2 & 3). Both trawlers space-use ($\psi_3 + \psi_4$) and dolphins space-use($\psi_2 + \psi_4$) were higher in the coastal waters than the pelagic seas (Figure 3, and Supplementary Information). Although, dolphins space-use probability in pelagic seas appeared to be higher than trawlers space-use probability in Figure 2, the difference is not significant.

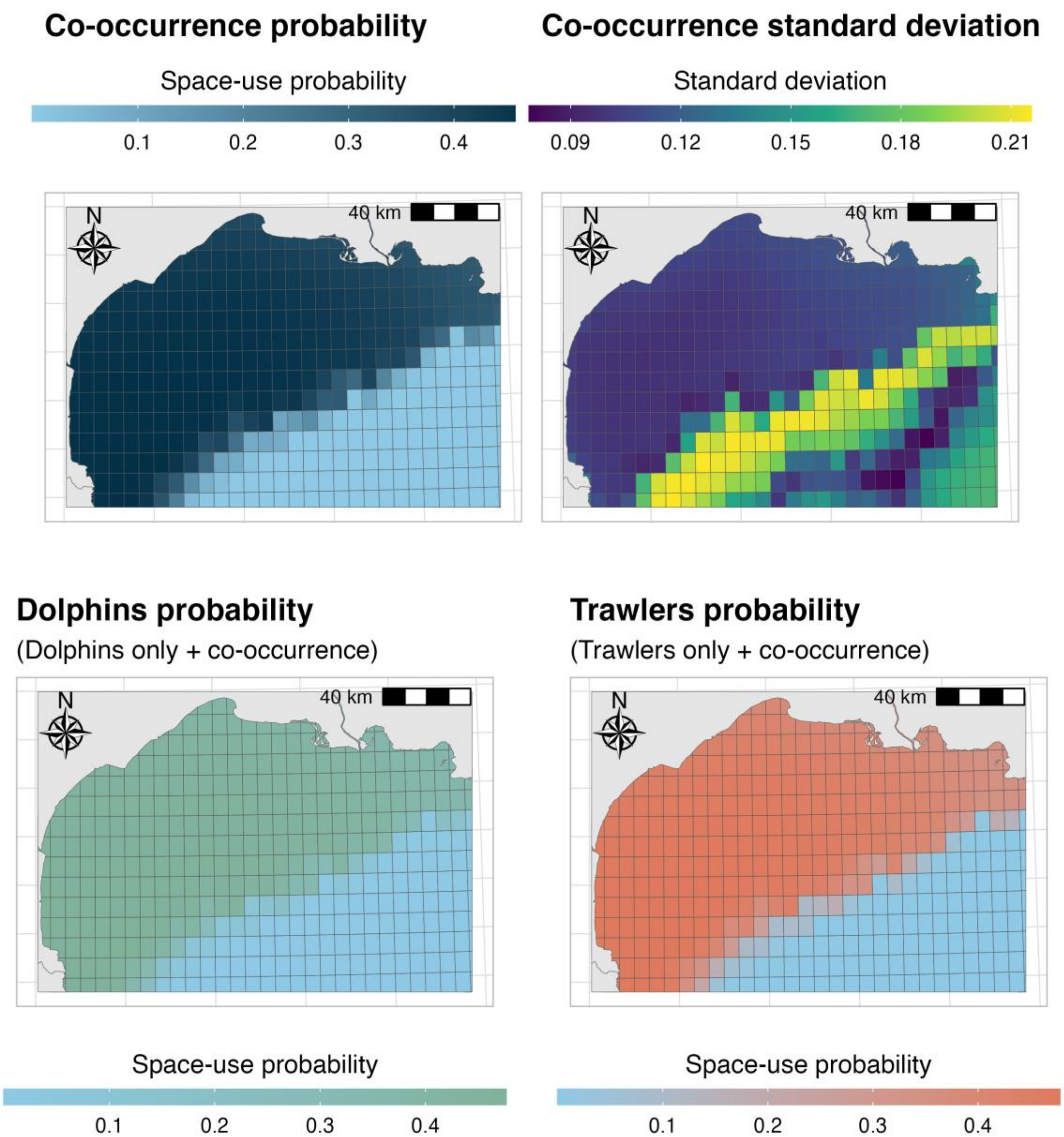

Figure 3: Co-occurrence probability of dolphins and trawlers in the Gulf of Lion (Northwestern Mediterranean Sea) and associated standard deviation (upper panel). Lower panel shows dolphins and trawlers space-use probabilities.

Both dolphins and trawlers detection probabilities increased with increasing sampling effort. Boat photo-id monitoring had higher detection probabilities than aerial surveys (Figure 4). Trawlers were more easily detected than bottlenose dolphins for both monitoring programs.

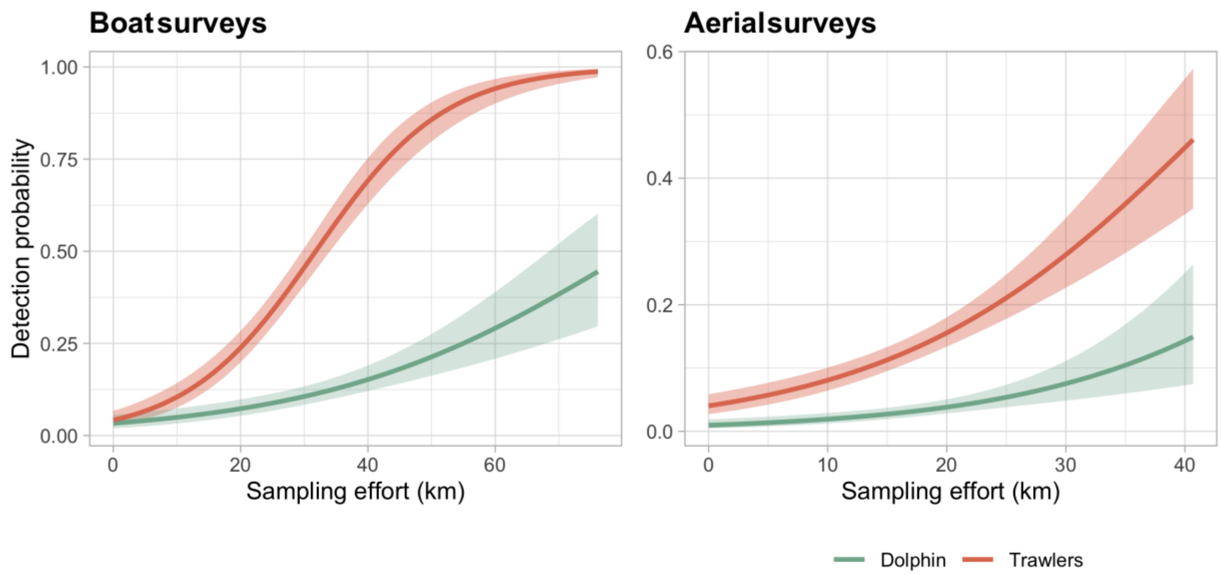

Figure 4: Estimated detection probability of dolphins and trawlers as a function of sampling effort for each monitoring program. We provide posterior medians (solid line) and 80% credible intervals (shaded area).

Increased precision of integrated and multispecies frameworks

Integrated multispecies occupancy model estimated more precise co-occurrence probability (i.e. lower standard deviation) than multispecies occupancy models using datasets in isolation (Figure 5).

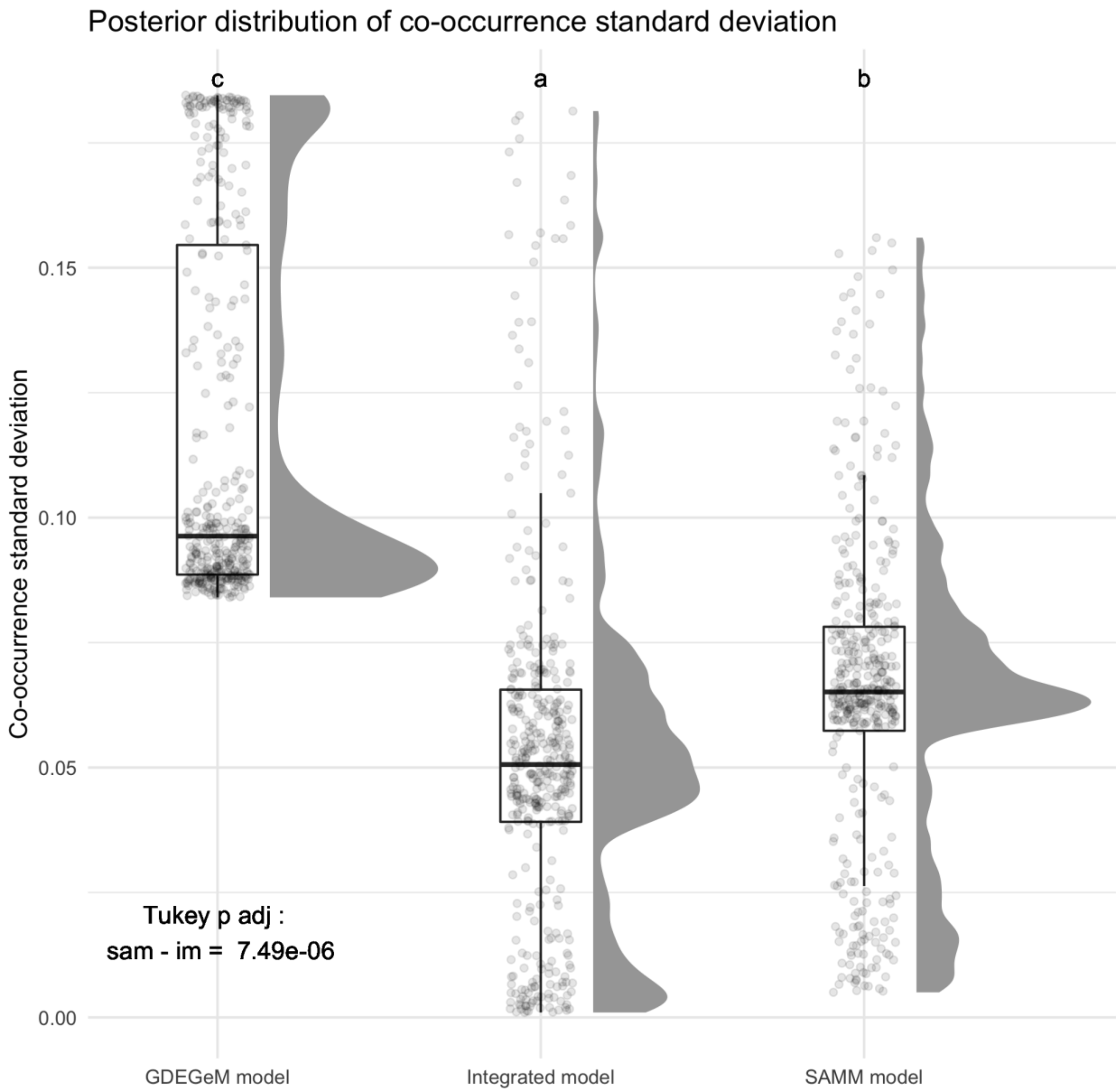

Figure 5: Standard deviation associated with co-occurrence probability. SAMM model uses only aerial surveys data, GDEGeM model uses only boat surveys data. We tested for statistical differences between posterior distribution. 'sam' and 'im' respectively refer to SAMM and integrated model

Similarly, multispecies integrated occupancy model exhibits a higher precision of marginal space-use probabilities of dolphins and trawlers (i.e. lower standard deviation) that single-species occupancy models that estimate dolphins or trawlers occupancy in isolation (Figure 6). Trawlers data being more abundant than bottlenose dolphins data, standard deviation of space-use probability are lower for trawlers than for dolphins (Figure 6).

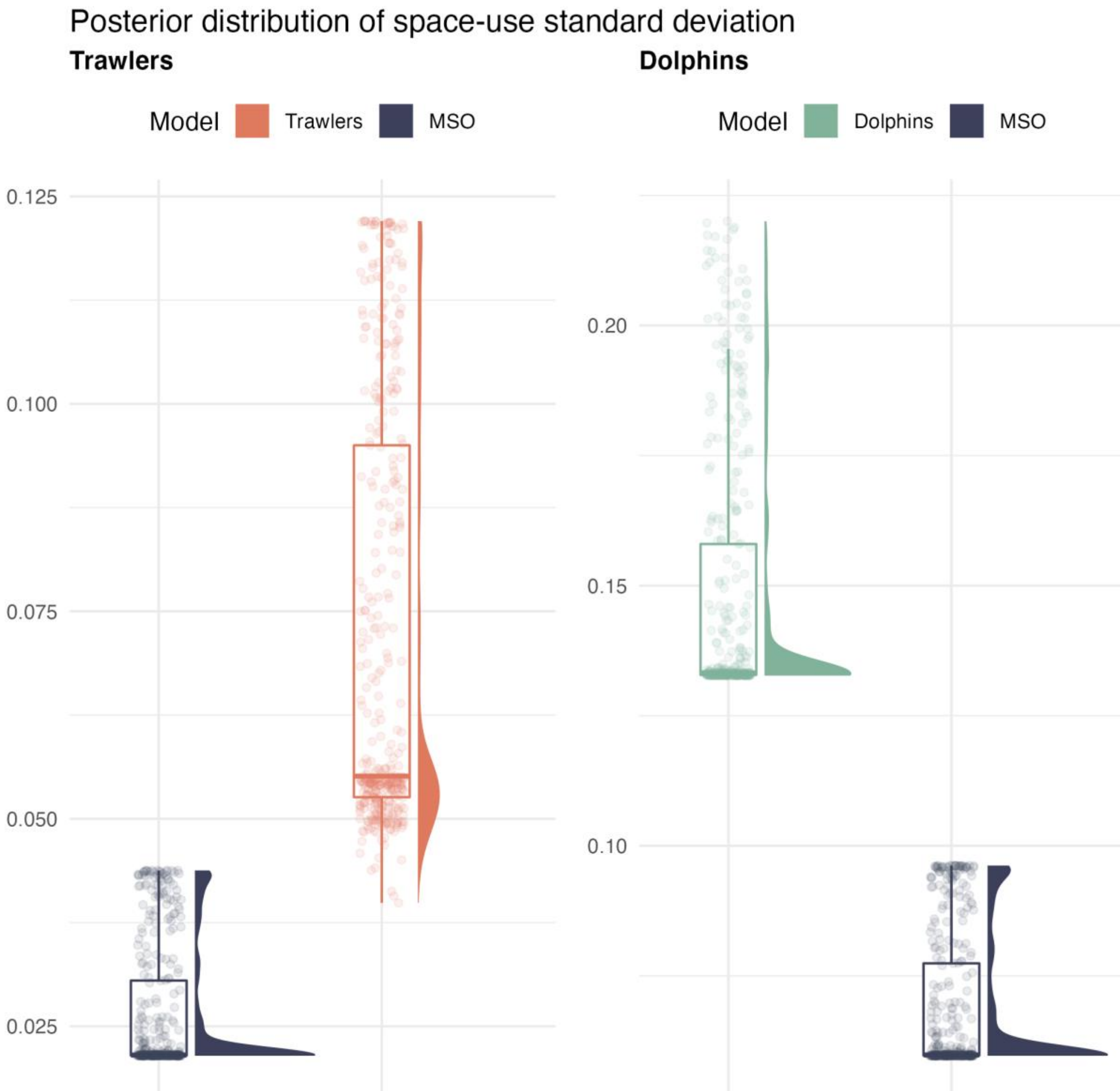

Figure 6: Standard deviation associated with space-use probability for single-species vs multispecies integrated occupancy models.

Discussion

Using integrated multispecies occupancy models, we mapped the probability of co-occurrence between French fisheries and bottlenose dolphins in the Gulf of Lion waters (Figure 3). Our integrated multispecies occupancy models estimated a 0.40 probability of co-occurrence between trawlers and bottlenose dolphins in the coastal seas of the Gulf of Lion.

While multispecies occupancy models require substantial amount of data to precisely estimate co-occurrence (Clipp et al. 2021), integrated approaches can provide stronger inferences compared to an analysis of each dataset in isolation (Zipkin et al. 2019, Lauret et al. 2021). Our integrated multispecies occupancy model helped to overcome data scarcity and produced more precise estimations of co-occurrence probabilities than multispecies models using separated datasets (Figure Figure 5 & Supplementary materials). Our integrated approach emphasized that data integration can be particularly promising for multispecies occupancy models that are impaired by data quantity. Besides, fitting multispecies occupancy models helped to precise ecological estimations of space-use probabilities that are fitted with single-species occupancy models (Figure 6 & Supplementary materials). Thus, both the multispecies and the integrated frameworks benefit to our occupancy models to study the co-occurrence of bottlenose dolphins and fishing trawlers.

However, we underlined that we inferred co-occurrence probability and not interactions between dolphins and trawlers. This means that, despite the fact that interactions can occur, dolphins and trawlers also use the same space without interacting. Mapping co-occurrence, we include potential interactions such as depredations or bycatch, and co-occurrence without interactions. However, to understand species interactions, mapping co-occurrence is definitely a first step. Beyond mapping, multispecies occupancy enables to estimate potential human-wildlife interaction as a function of covariates (*i.e.* how co-occurrence is affected by depth in our case study), which is crucial to understand mechanisms driving interaction risks and ultimately to implement management (Devarajan et al. 2020).

Our approach echoes recent work integrating human activities into multispecies occupancy models to identify and quantify threats of anthropic pressures on the environment (Marescot et al. 2020). Outside the Gulf of Lion case study, integrated multispecies occupancy models can be leveraged to provide robust maps of co-occurrence between marine megafauna and anthropogenic activities while integrating several data sources. Additional presence-absence data, e.g. from scientific fishing surveys, aerial surveys for tuna stock assessment (Bauer et al. 2015), or Automatic Identification System for fishing vessels would further allow to better delineate fishing areas and hence areas of potential interactions. Building co-occurrence maps is the first step when studying species interactions. From there, practitioners can design dedicated surveys to determine what features favor the shift from co-occurrence to interaction. The flexibility of occupancy models and the extension to integrated occupancy models enable to accommodate a large panel of sampling protocols and to include data from several monitoring programs in the same analysis, which permit to foster the complementarity of different sampling designs and protocols (Lauret et al. 2021).

The ability to predict areas of human-wildlife potential interactions is of critical importance to implement conservation measures as required under conservation legislation (e.g. the European Union Marine Strategy Framework Directive). To mitigate marine mammal depredation and/or bycatch, acoustic deterrents are implemented worldwide despite raising ethical and conservation concerns (Santana-Garcon et al. 2018, Bonizzoni et al. 2022). Using multispecies occupancy models to map potential hotspots of depredation may help to reduce the deployment of acoustic deterrents and minimize the associated negative impacts (Estabrook et al. 2016, Snape et al. 2018). Similarly, fin whales (*Balaenoptera physalus*) and sperm whales (*Physeter macrocephalus*) are at high risk of collision with ferries in the Northwestern Mediterranean Sea and in particular in the Pelagos Sanctuary Marine Protected Area (Ham et al. 2021, David et al. 2022). Mapping collision risk with multispecies occupancy models can ultimately direct the measures of speed limitation. Overall, we support that integrated multispecies occupancy models represent promising tools to understand and map human-cetacean interactions hotspots.

Data script and codes

Data and codes are available on a Zenodo repository.

Supplementary materials

Supplementary materials are available on a Zenodo repository.

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Conflict of interest disclosure

The authors declare they have no conflict of interest relating to the content of this article.

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