Article: Spatial integrated models foster complementarity between monitoring programs in producing large-scale ecological indicators

Abstract (< 300 words)

Over the last decades, large-scale conservation projects have emerged that require collecting ecological data over broad spatial and temporal coverage. Yet, obtaining relevant information about large-scale population dynamics from a single monitoring program is challenging, and often several sources of data, possibly heterogeneous, need to be integrated.

In this context, spatial integrated models combine multiple data types into a single analysis to quantify population dynamics of a targeted population. Using available information at different spatial or temporal scales, spatial integrated models have the potential to produce detailed ecological estimates that would be difficult to obtain if data were analyzed separately. So far, these models are available for open populations to estimate demographic parameters (survival, recruitment), therefore requiring data collected in long-term monitoring programs. In conservation biology however, we often need to quantify population abundance and density in closed populations.

In this paper, we showcase the implementation of spatial integrated models to closed populations in a conservation context. We analyzed spatial capture-recapture data together with distance-sampling data to estimate abundance and density. Focusing on the Mediterranean bottlenose dolphins (*Tursiops truncatus*) as a case study, we combined 21,464 km of photo-identification boat surveys collecting spatial capture-recapture data with 24,624 km of aerial line-transect following a distance-sampling protocol. We compared the performances of the spatial integrated model, with that of the distance sampling model, and the spatial capture-recapture model separated. We discussed the benefits of using a spatial integrated model in the context of the assessment of French Mediterranean bottlenose dolphin conservation status to inform continental scale public policies.

Overall, we emphasize the usefulness of spatial integrated model to make the most of available datasets in a conservation context. Spatial integrated models are widely applicable and relevant to conservation research and biodiversity assessment at large spatial scales.

Introduction

Macro-institutions get increasingly involved in large-scale programs for biodiversity conservation over regional and continental areas. Whether these policies aim at assisting governments (e.g., the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services), or at implementing environmental management such as the European Union directives (Habitat Directive, 92/43/EEC, or Marine Strategy Framework Directive, MSFD, 2008/56/EC), conducting large-scale ecological monitoring is required to establish conservation status of targeted species and ecosystems, and to inform decision-making.

At large spatial scales, logistical and financial constraints often prevent a detailed coverage of the targeted population using a single collection effort, and different monitoring programs often coexist (Lindenmayer & Likens 2010; Zipkin & Saunders 2018; Isaac et al. 2019). The multiplication of monitoring programs over the same conservation context has fostered the development of statistical models that can estimate ecological indicators while accommodating several, possibly heterogeneous, datasets (Besbeas et al. 2002; Miller et al. 2019; Zipkin et al. 2019; Isaac et al. 2019; Farr et al. 2020). Integrating data from several monitoring protocols can give complementary insights on population structure and dynamics (Schaub & Abadi 2011), increase space and time coverage of the population (Schaub & Abadi 2011; Zipkin et al. 2019), and produce more precise estimate of ecological indicators (Isaac et al. 2019; Farr et al. 2020; Lauret et al. 2021).

An important objective of ecological monitoring programs is to estimate population abundance and density (Williams et al. 2002), for which distance sampling (DS, Buckland et al., 2005), and capture-recapture (CR, Williams et al. 2002) methods are widely used. DS and CR methods allows accounting for spatial variation in abundance and density (Camp et al., 2020; Miller et al., 2013; Royle et al., 2014), possibly at large scales (Bischof et al. 2020). Recent modelling tools have emerged to integrate both DS and CR methods into integrated population models (Kéry & Royle 2020). The extension to spatial integrated models (SIMs) has been proposed to account for spatial variation in abundance and demographic parameters while analyzing jointly DS data and SCR data (Chandler et al. 2018). To date however, SIM have never been applied at large spatial scales nor in a conservation context, although we suspect that using SIMs can be promising in these situations. Besides, SIM were developed and used on open populations to estimate temporal variation in population dynamics and vital rates such as survival and recruitment (Chandler & Clark 2014; Chandler et al. 2018; Sun et al. 2019). These applications rely on long-term datasets that are not always compatible with conservation objectives. Conservation biology being a crisis discipline (Soulé 1985), the agenda of biologists and managers is time constrained (Nichols & Williams 2006). In many cases, ecological information is needed, and needed quick (Nichols & Williams 2006; Lindenmayer & Likens 2010). Consequently, ecological inference is often restricted to closed-population indicators (e.g. abundance, density, distribution). When the temporal resolution of monitoring programs does not allow to quantify population dynamics, we argue that closed-population SIM can be an asset in numerous conservation contexts to deal jointly with existing monitoring programs and assess abundance and density.

In this paper, we showcase the use of SIM in a closed-population context demonstrating the benefit of combining DS and SCR to inform conservation policies. We consider a case study on Bottlenose dolphins (*Tursiops truncatus*) that is considered as “vulnerable” by the IUCN

Red List in the North-Western Mediterranean Sea (IUCN 2009). The protected status of Bottlenose dolphins within the French seas (listed on Annex II of the European Habitats Directive) led to the development of specific programs to monitor Mediterranean bottlenose dolphins within the implementation of the European marine strategy framework directive, which requires assessing the conservation status of this species every 6 years (Authier et al. 2017). We analyzed DS data collected by aerial line-transect surveys over a large area covering coastal and pelagic seas (Laran et al. 2017). We also analyzed SCR data collected by a photo-identification monitoring program restricted to coastal waters (Labach et al. 2019). We compared the abundance and density of bottlenose dolphins estimated from DS model, SCR model, and SIM to highlight the benefits of the integrated approach in a conservation context. We discussed the promising opportunities and the conservation implications of using closed-population SIM to make the best of available datasets.

Methods

Spatial integrated models for closed populations

To integrate DS and SCR data, we used the hierarchical model approach proposed by Chandler et al. (2018). However, while initially developed for open populations, we built a model for closed populations to estimate abundance and density (Fig 1). Our SIM is structured around two layers with i) an ecological model that describes the latent density and spatial variation in abundance based on an inhomogeneous point process (*Spatial abundance* section below), and ii) two observation models that describe how the DS and SCR data arise from the latent ecological model (*Capture-recapture data* and *Distance-sampling data* sections below).

Spatial abundance

For the ecological state model, we use a latent spatial point process modelling the density of individuals and the overall abundance. Over the study area *S*, an intensity function returns the expected number of individuals at location *s* in *S*. To account for spatial variation, we model the latent density surface as an inhomogeneous point process. For every location *s* in the study area *S*, the expected abundance λ is written as a log-linear function of an environmental covariate, say habitat:

$$log\big(\lambda(s)\big) = \mu_0 + \mu_1 \text{habitat}(s) \tag{1}$$

where parameters to be estimated are μ_0 and μ_1 respectively the density asymptote and the regression coefficient of the environmental covariate. Then, the expected abundance is derived by integrating the intensity function over the study area:

$$E(N) = \int_S \lambda(s) ds. \tag{2}$$

The latent state process defined by Eq. 1 is an inhomogeneous point process that is common to both the SCR and DS models, hence allowing integration and sharing SCR and DS data for estimating density λ. To account for unseen individuals, we used the data augmentation technique and augmented the observed datasets to reach M individuals (Royle & Dorazio 2012). Each individual *i* is considered being (z_i = 1) or not (z_i = 0) a member of the population according to a draw in a Bernoulli distribution of probability ψ, with $z_i \sim \text{Bernoulli}(\psi)$ where ψ is the probability for individual *i* to be a member of the population, with $\psi = E(N)/M$ and $N = \sum_{i=1}^{M} z_i$.

Capture-recapture data

To accommodate capture-recapture data, we built a SCR model (Royle et al. 2014). Detection history of individuals were collected over T sampling occasions and captures were recorded at detectors. We stored observations in a three-dimensional array *y* with y_{ijt} indicating whether individual *i* was captured at detector *j* during sampling occasion *t*. We assume that observation y_{ijt} is an outcome from a Bernoulli distribution with capture probability p_{ijt}, $y_{ijt} \sim \text{Bernoulli}(p_{ijt})$. We model capture probability with a half-normal detection function $p_{ijt} = p_0 exp(-\frac{d_{ij}^2}{2\sigma^2})$ where d_{ij} is the Euclidian distance between the activity center of individual *i* and the detector location *j*, σ is the scale parameter of the half-normal function, and p_0 is the baseline encounter rate (Royle et al. 2014).

Distance-sampling data

To accommodate distance data, we built a hierarchical DS model (Kéry & Royle 2016). We model the DS data conditional on the underlying density surface defined by Eqs (1) and (2). We assume that the probability of detecting individual *i* in transect *l* is a decreasing function of d_{il} the perpendicular distance between transect *l* and individual *i*, with $r_{il} = r_0 exp(-\frac{d_{il}^2}{2\eta^2})$, where η is the scale parameter of the half-normal function, and r_0 is the probability of detection on the transect, which we will set to 1. Because distance may not be estimated with perfection by observers, we discretized the distance of observation in B distance bins. We assume that density within each transect is uniform and that the number of individuals in each transect is Poisson distributed. This leads to a Poisson model for the DS data in which the expected number of detections at transect *l* in distance bin *b* is given by the expected number of individuals in bin *b* multiplied by the average detection probability within each bin *b*.

Bottlenose dolphins case study

To illustrate the SIM, we focused on an area of 255,000 km^2 covering the North-Western Mediterranean Sea within which we considered two monitoring programs about bottlenose dolphins. We used SCR data from at-sea boat surveys over 21,464 km of the French continental shelf. Observers performed monitoring aboard small boats to locate and photo-identify bottlenose dolphins all year long between 2013 and 2015. Taking pictures of the dorsal fin of each individual in the group makes possible the construction of detection history and hence the analysis of the population through capture-recapture methods (Labach et al. 2019). Boat surveys were restricted to the coastal waters of France, and is homogeneous in space and time. We divided the duration of the monitoring programs into 8 equal sampling occasions as in Labach et al. (2019). We also used DS data that were collected during winter and summer aerial line-transect surveys covering 24,624 km of both coastal and pelagic NW Mediterranean Sea between November 2011 to February 2012 and May to August 2012 (Laran et al. 2017). Two trained observers collected cetacean data following a DS protocol (i.e. recording species identification, group size, declination angle). Aerial surveys were conditional on a good weather forecast and aerial sampling effort was homogeneous over the studied area. Although the SCR and DS datasets were collected during separated time frames, we assumed that the bottlenose dolphin abundance did not change much between 2011 and 2015 considering a long-lived species such as bottlenose dolphins (Bearzi et al. 2009).

We divided the study area in 4356 contiguous pixel/sites creating a 5’x5’ Mardsen grid (WGS 84). To model spatial variation in the inhomogeneous point process, we used bathymetry as an environmental covariate, which is expected to have a positive effect on bottlenose dolphins’ occurrence (Bearzi et al. 2009; Labach et al. 2019). To estimate the sampling effort of aerial and boat surveys, we calculated the transect length (in km) prospected by each monitoring protocol within each site during a time period. Sampling effort was therefore site and occasion-specific in the case of the SCR model, and site specific for the DS model. For the SCR model, we accounted for spatial and temporal variation in detection probability modeling the scale parameter σ as a log-linear function of sampling effort E_{jt} at detector *j* during sampling occasion *t*: $\log(\sigma_{jt}) = \beta_0 + \beta_1 E_{jt}$. We also modeled p_0 as a logit-linear function of E_{jt}:

$\text{logit}(p0_{ijt}) = \delta_0 + \delta_1 E_{jt}$. For the DS model, we accounted for spatial variation in the scale parameter of the detection function modeling η as a log-linear function of sampling effort S_j and of weather condition W_j in transect j: $log(\eta_j) = \alpha_0 + \alpha_1 S_j + \alpha_2 W_j$.

To highlight to benefit of data integration in estimating spatial density, we compared i) the output of the spatial DS model, ii) the SCR model, and iii) the SIM.

Bayesian implementation

We ran all models with three Markov Chain Monte Carlo chains with 100,000 iterations each in the NIMBLE R package (de Valpine et al. 2017). We checked for convergence calculating the *R-hat* parameter (Gelman et al. 2013) and reported posterior mean and 80% credible intervals (CI) for each parameter. We considered as important the effect of a regression parameter whenever the 80% CI of its posterior distribution did not include 0. We also calculated the predicted density of bottlenose dolphins (i.e. λ). Data and codes are available on GitHub (*Link to be added after the double-blind peer review process*).

RESULTS

We detected 536 dolphins through aerial surveys clustered in 129 groups. We identified 927 dolphins over 1707 detections in photo-identification surveys, out of which 638 dolphins were captured only once (68%), 144 were captured twice (15.5%), 149 were captured 3 times and up to 8 times for one individual. The maximum distance between two sightings of the same individual was 302 km and 115 km during the same sampling occasion.

We estimated 2450 dolphins (2276; 2631) with SIM over the study area (Table 1), 8470 dolphins (7620; 9329) with the DS model and 1756 dolphins (1645; 1872) with the SCR model (Table 1). Density asymptotes of SIM (μ_0= -0.67 (-0.75; -0.60)) and SCR model (μ_0= -1.01 (-1.37; -0.89)) were lower than asymptote of DS model (μ_0= 0.6 (0.50; 0.71)).

In SIM, estimated abundance increased when bathymetry increased (μ_1= 0.43 (0.37;0.48), Table 1), suggesting a preference for low-depth seafloors (Fig. 2). DS model also estimated a positive effect of bathymetry (μ_1= 0.34 (0.28; 0.39), Table 1), while the SCR model did not detect any effect of bathymetry on density (μ_1= 0.02 (-0.73; 0.83), Table 1). Then, SIM and DS models predicted higher densities of bottlenose dolphins in the coastal seas than in the pelagic seas, whereas the SCR model did not predict any variation in density between coastal and pelagic waters (Fig. 2).

We detected a positive effect of aerial sampling effort on detection probability in both DS model (α_1= 0.61 (0.54; 0.67)) and SIM (α_1= 0.47 (0.36; 0.57)). Boat sampling effort exhibited a positive effect on detection probability for both the SCR model (β_1= 0.84 (0.73; 0.96), $□_1$= 0.76 (0.71; 0.81)) and the SIM (β_1= -0.22 (-1.34; 0.76), $□_1$= 0.70 (0.65; 0.75), Table 1). For the SIM and the DS model, the detection probability increased when the weather condition improved (SIM: α_2= 0.30 (0.18; 0.42), DS: α_2= 0.14 (0.08; 0.20), Table 1).

DISCUSSION

Integrated models make the most of distance sampling and capture-recapture data

With our SIM, we estimated bottlenose dolphin abundance within the range of what was found in previous studies in nearby areas (Gnone et al. 2011; Lauriano et al. 2014), and found that densities were more likely to be higher in coastal areas (Bearzi et al. 2009).

A striking result was the large differences in abundance estimates between DS and SCR models, which were also found in previous studies analyzing the same datasets in isolation. Using capture-recapture data only, Labach et al. (2019) estimated 2647 dolphins (95% confidence interval: 2059; 3528) inhabiting the French continental coast where our model predicted 2450 dolphins (2276; 2631). Analyzing distance sampling data, Laran et al., (2017) estimated 2946 individuals (95% confidence interval: 796; 11,462) during summer, and 10,233

(95% confidence interval: 4217; 24,861) during winter where our DS model estimated 8470 (7413; 9595) all year long.

We see several reasons that might explain these differences. First, the seasonal difference in Laran et al. (2017) DS abundance estimates suggests an issue with the geographic closure assumption that might explain the discrepancy in estimates obtained from SCR and DS models. Although the Mediterranean bottlenose dolphins population is clustered in coastal sub-units (Carnabuci et al. 2016), groups can be encountered offshore (Bearzi et al. 2009). In the DS dataset, large dolphin groups were detected in the pelagic seas at the extreme south of sampling design (Supporting information). These groups could either be i) occasional pelagic individuals that belong to coastal populations and that are mainly resident outside our study area (e.g. Balearic, South-Western Sardinia), or ii) resident pelagic populations that are not sampled by coastal boat surveys (Louis et al. 2014). Second, DS and SCR models do not estimate the same quantities. While DS models take a snapshot of abundance and density in the study area at the moment of the sampling, SCR models estimate abundance and density of the sampled population, whether or not the individuals are present in the study area during the sampling period (Calambokidis & Barlow 2004). In our case study, SCR data were restricted to the French continental coast and did not sample dolphin populations that exist elsewhere in the study area, e.g. in Corsica, Liguria, and Tuscany (Carnabuci et al. 2016). Despite this geographic sampling bias in the capture-recapture data, SCR models should predict the existence of Corsican and Italian populations if the relationship between density and habitat in Eq (1) was correct and consistent throughout the study area. As the capture-recapture survey did not sample the lower range of bathymetry, our model underestimated abundance.

Overall, because groups of the Sardinian and Balearic populations and offshore groups can be sampled in the distance-sampling surveys, the DS model drives upward abundance compared to the SCR model that is unlikely to account for animals that are members of the

Southern neither the Eastern populations. To perform detailed analysis of the NW Mediterranean bottlenose dolphin populations, one should consider additional environmental covariates to better capture spatial variation in density (e.g., sea surface temperature, distance to coast, or 200m contour, Lambert et al. 2017).

SIM overcomes the limitations of DS and SCR models, and makes the best of each monitoring program. Using the DS data that were collected in both coastal and pelagic seas, we informed the slope of the inhomogeneous point process (μ_1), and detected the effect of bathymetry on density with SIM by correcting for the geographic sampling bias in the SCR data. On the other hand, the SCR data were more informative (more detections, more individuals) that the DS data to inform the asymptote of density (μ_0), making the SIM abundance estimate closer to the SCR model estimate (Table 1).

Conservation implications

To date, the assessment of French Mediterranean bottlenose dolphin population required by the EU are established using the DS data (Laran et al. 2017). Aerial surveys provide crucial information on marine megafauna taxa, and on human pressures to fill several criteria of the Marine Strategy Framework Directive (Laran et al. 2017; Pettex et al. 2017; Lambert et al. 2020). However, in the Mediterranean context, several monitoring programs are available and SIM makes it possible to include existing datasets that have been discarded so far to inform public policies (Cheney et al. 2013; Isaac et al. 2019). For bottlenose dolphins, at-sea photo-identification programs collecting detailed data are an important asset to inform abundance. Ecological indicators required by the EU directive for bottlenose dolphins would benefit from integrating aerial line-transect with more data when available (Lauret et al. 2021).

We argue that the bottlenose dolphin is a relevant candidate for a real-life implementation of the SIM. Between the aerial line-transects repeated every 6 years, many stakeholders routinely collected detailed data about bottlenose dolphins in the French Mediterranean Sea. The Marine Protected Areas network is currently developing long-term monitoring programs to perform bottlenose dolphin photo-identifications, and the French Research Institute for Exploitation of the Sea (i.e. IFREMER) collected yearly bottlenose dolphins' data during line transects surveys for pelagic fisheries (Baudrier et al. 2018). Adding complementary long-term datasets to the aerial-surveys would make possible to access the demographic parameters (*e.g.* recruitments, survival (Chandler et al. (2018)), which would represent a major opportunity for the knowledge about French Mediterranean bottlenose dolphin populations and to produce a reliable EU ecological indicator. The use of SIM for the French Mediterranean bottlenose dolphin population also opens perspectives to extend the modelling approach exploring seasonality in density, and to measure immigration and dispersal between bottlenose dolphins populations (Zipkin & Saunders 2018).

Spatial integrated models as a promising tool for conservation

When establishing species conservation status for large-scale environmental policies, discarding some datasets from the analysis can reduce the reliability of the ecological estimation (Bischof et al. 2016). Using multiple datasets into SIM help to overcome some limitations present when using separated datasets (e.g. limited spatial or temporal survey coverage, Zipkin & Saunders 2018; Isaac et al. 2019). However, caution should be taken as integrating data requires additional modelling assumptions (Dupont et al., 2019; Farr et al., 2020; Fletcher et al., 2019; Simmonds et al., 2020). Overall, SIM are flexible tools that can include more than 2 datasets (Zipkin & Saunders 2018), and various type of data that enlarge the scope of usable information (presence-absence (Santika et al. 2017), count data (Chandler et al. 2018), citizen science data (Sun et al. 2019)). Recent and current developments of SCR models open perspectives to extend the SIM to account for unidentified individuals, or to better describe animal movement (Milleret et al. 2019; Turek et al. 2020; Jiménez et al. 2020). Over the last decades, the spatial scope of conservation efforts has greatly increased, and the analytical methods have had to adapt accordingly (Zipkin & Saunders 2018). Spatial integrated models are a promising tool that can make the most of available data to inform conservation policies, especially for wide-range management decisions.

SUPPORTING INFORMATION

Supplementary information about study area, transects, and data is available online (Appendix S1). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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TABLES

Table 1: Parameter estimates for the spatial integrated model (SIM), spatial capture-recapture (SCR) model, and distance-sampling (DS) model. For each parameter, we display the posterior mean and its 80% credible interval (CI).

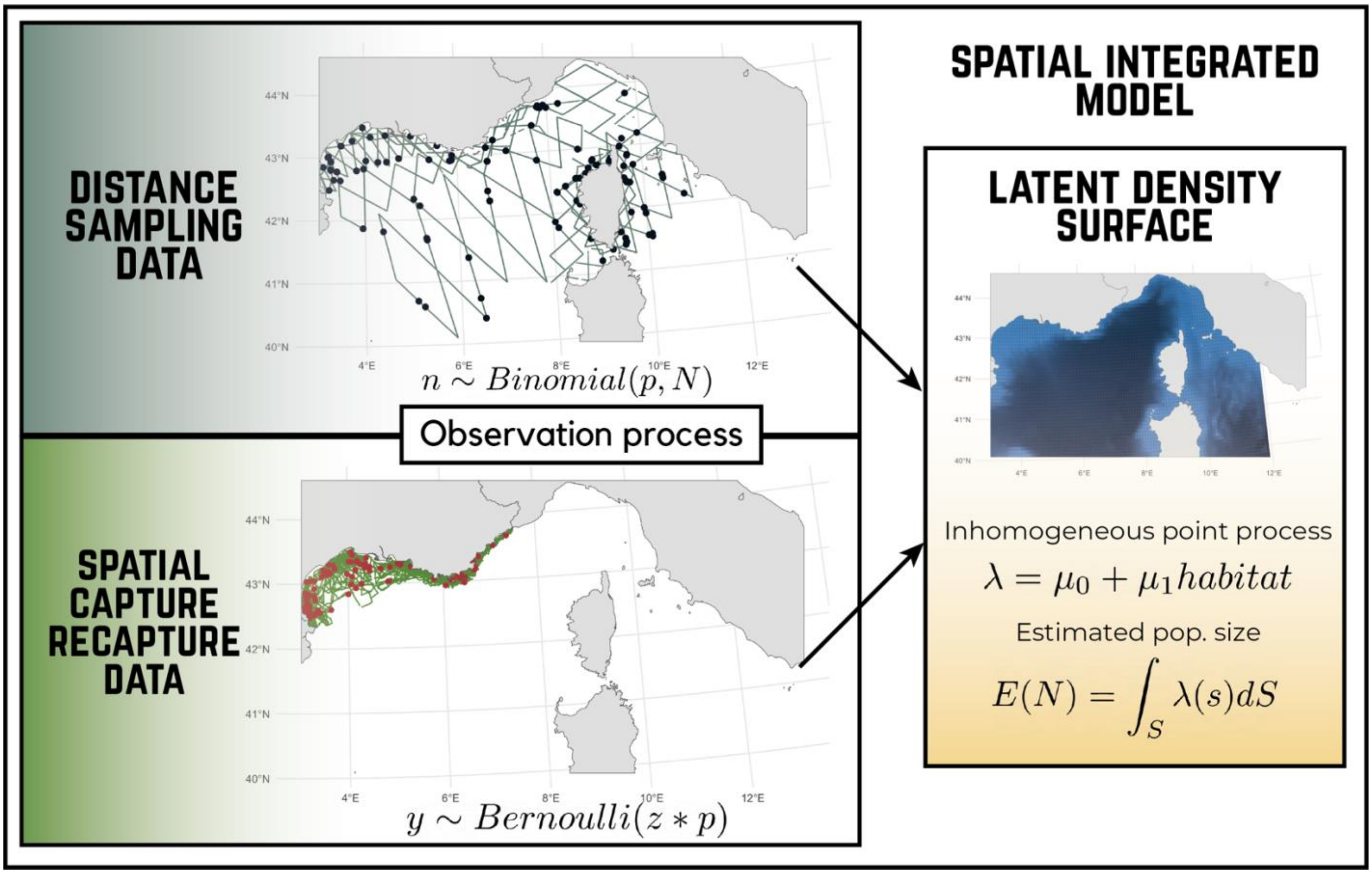
	SIM		SCR model		DS model	
Parameter	**Mean**	**80% CI**	**Mean**	**80% CI**	**Mean**	**80% CI**
Estimated population size N	2450	2276, 2631	1756	1645, 1872	8470	7620, 9329
Asymptote of density μ_0	-0.67	-0.75, -0.60	-1.01	-1.37, -0.89	0.60	0.50, 0.71
Effect of bathymetry on density μ_1	0.43	0.37, 0.48	0.02	-0.73, 0.83	0.34	0.28, 0.39
SCR scale parameter: Intercept β_0	0.23	-0.82, 1.45	0.04	-1.01, 1.12		
SCR scale parameter: Effect of at-sea sampling-effort β_1	0.84	0.71, 0.95	0.84	0.73, 0.96		
SCR p_0 parameter: Intercept d_0	-6.65	-7.05, -6.27	-6.51	-6.93, -6.11		
SCR p_0 parameter: Effect of at-sea sampling-effort d_1	0.70	0.65, 0.75	0.76	0.71, 0.81		
DS scale parameter: Intercept α_0	-5.52	-6.50, -4.34			-7.91	-8.52, -7.24
DS scale parameter: Effect of aerial sampling-effort α_1	0.47	0.36, 0.57			0.61	0.54, 0.67
DS scale parameter: Effect of weather condition α_2	0.30	0.18, 0.42			0.14	0.08, 0.20

FIGURE-LEGEND PAGE

Figure 1: Graphical description of the Spatial Integrated Model (SIM) that combines Spatial Capture Recapture (SCR), and Distance Sampling (DS). The SIM is a hierarchical model with three processes: i) latent population size N and density informed by an inhomogeneous point process, ii) DS observation process that link the line-transect dataset to the latent density surface, iii) SCR observation process that links the detection histories to the latent density. The observation process is stochastic according to detection probability. For DS model, the observed group size is a Binomial draw in the latent abundance N at the sampling location. For SCR model, observing an individual is a Bernoulli draw with a detection probability p. See text for notation and more details.

Figure 2: Estimated density surface of bottlenose dolphins (*Tursiops truncatus*) for the 3 models. Lighter color indicates number of individuals per area unit. Both spatial integrated model (SIM) and distance sampling (DS) predicted higher density in coastal seas, while spatial capture-recapture (SCR) predicted homogeneous density across the study area. Note that density scales are different between maps, indicating a higher overall population size for DS model than for SIM, and SCR model.

FIGURES WITH LEGEND



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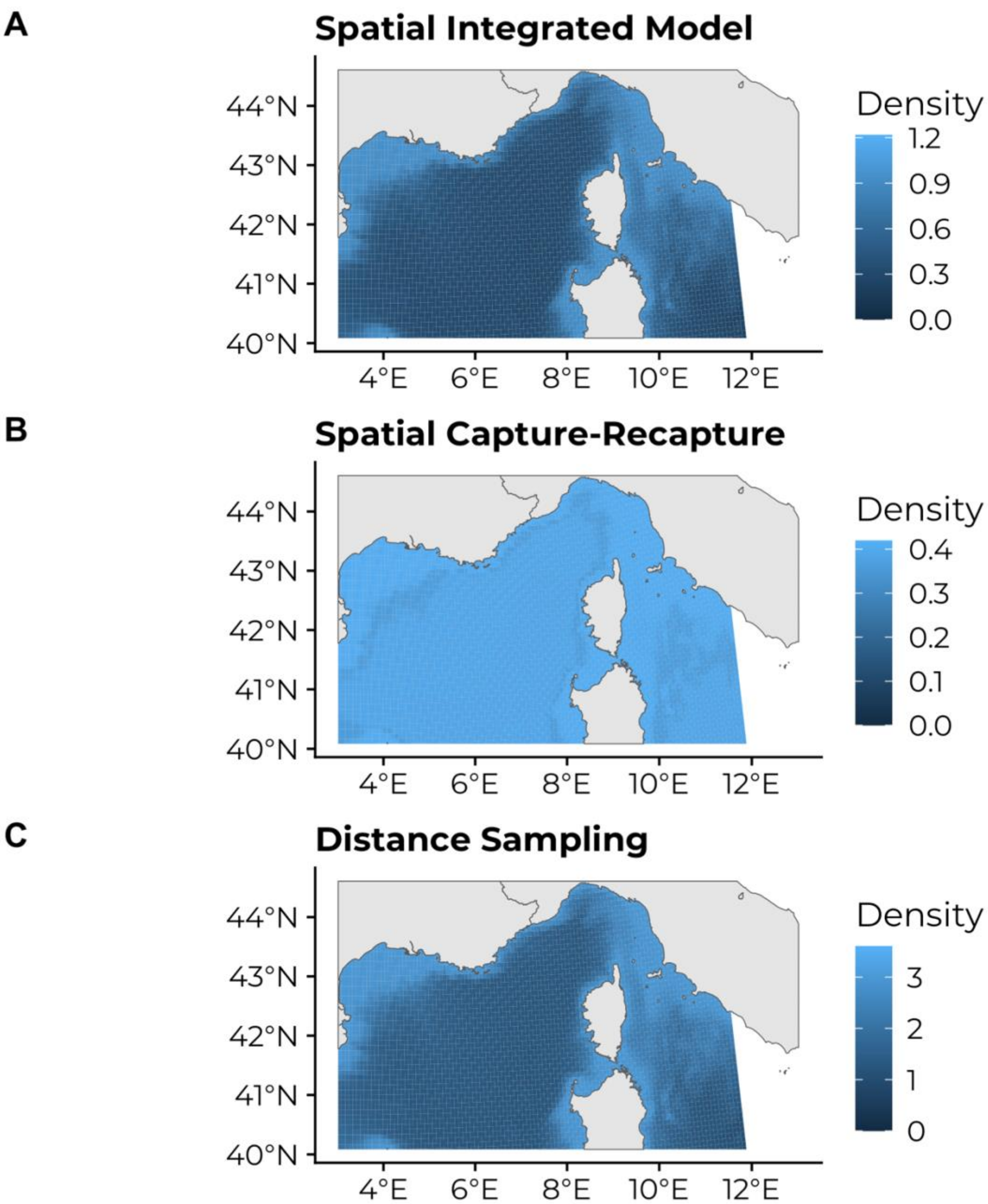

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