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Combining scientific survey and commercial catch data to map fish distribution

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Developing Species Distribution Models (SDM) for marine exploited species is a major challenge in fisheries ecology. Classical modelling approaches typically rely on fish research survey data. They benefit from a standardized sampling design and a controlled catchability, but they usually occur once or twice a year and they may sample a relatively small number of spatial locations. Spatial monitoring of commercial data (based on logbooks crossed with Vessel Monitoring Systems) can provide an additional extensive data source to inform fish spatial distribution. We propose a spatial hierarchical framework integrating both data sources while accounting for preferential sampling (PS) of commercial data. From simulations, we demonstrate that PS should be accounted for in estimation when PS is actually strong. When commercial data far exceed scientific data, the later bring little information to spatial predictions in the areas sampled by commercial data, but bring information in areas with low fishing intensity and provide a validation dataset to assess the integrated model consistency. We applied the framework to three demersal species (hake, sole, and squids) in the Bay of Biscay that emphasize contrasted PS intensity and we demonstrate that the framework can account for several fleets with varying catchabilities and PS behaviours.

Keywords: hierarchical model, integrated modelling, species distribution model, survey data, Template Model Builder (TMB), VMS and logbook data.

Introduction

Developing species distribution models (SDM) is critical in marine and fisheries ecology for assessing the relationship between species and their habitat (Guisan and Zimmermann, 2000), identifying essential habitats (Paradinas *et al.*, 2015), and forecasting population and ecosystems response to environmental changes (Cheung *et al.*, 2009). The development of statistical models to predict fishery resources distribution has received considerable attention (Planque *et al.*, 2011; Thorson *et al.*, 2015a, b; Martínez-Minaya *et al.*, 2018; Moriarty *et al.*, 2020). Recent developments have generalized SDM to analyze biological data representing condition, stomach contents, size structure, and other demography and population dynamics features (Thorson, 2015; Grüss *et al.*, 2020). Ongoing research also seek to integrate individual movement, growth, and species interactions into SDM (Kristensen *et al.*, 2014; Thorson *et al.*, 2017a, 2019), although these approaches are "data hungry" and, therefore, require integrating different sources of data within a single model.

Scientific survey and commercial catch data consist in two potentially complementary data sources to estimate harvested fish spatial distribution (Pennino *et al.*, 2016). Scientific surveys are key data sources in fisheries ecology. They most often benefit from a standardized sampling plan and a constant catchability (Hilborn and Walters, 1992; Ocean Studies Board and National Research Council, 2000; ICES, 2005; Nielsen, 2015). They are generally designed to cover the full geographical extent of specific populations including areas of low or null abundance, and are thus suitable for developing unbiased abundance indices and spatial predictions of species distribution (Rivoirard *et al.*, 2008; ICES, 2012). In addition, they often seek to minimize selectivity in order to sample as many species, size groups, and life stages as possible. However, the related expansive charges generally come at the cost of a relatively low sampling density in space and/or time. For instance, trawl surveys can sample a limited number of spatial locations, and most often occur once or twice a year. Thus, they may provide poor information regarding intra-annual variability (Pennino *et al.*, 2016; Rufener *et al.*, 2021) and imprecise estimates of species abundance and spatial distribution (ICES, 2005).

Commercial catch declarations (logbooks) data constitute a complementary data source that may benefit of a higher sampling effort than scientific survey. In Europe, catch declarations must be reported in logbooks data for all fishing vessels; besides, geolocation through Vessel Monitoring System (VMS) is mandatory for all fishing boats above 12 m long (Hintzen, 2021). Hence, logbook data combined with VMS data can provide high resolution maps of Catch Per Unit Effort (CPUE—Gerritsen and Lordan, 2010; Murray *et al.*, 2013) with a relatively dense spatio-temporal sampling within the range of the commercial fleets. However, inferring SDM with commercial data can be challenging as they generally arise from a preferential sampling (PS) behaviour, i.e. a

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sampling that directly or indirectly depends upon the biomass of the target species. Indeed, fishermen tend to target areas with high biomass and may also favour fishing zones based on other criteria (like bottom substrate or distance to the coast for instance—Hintzen *et al.*, 2021) that are indirectly related to the target species abundance. When not properly considered in statistical models, PS associated with commercial data may lead to biased estimates of fish distribution and biomass (Trenkel *et al.*, 2013; Pennino *et al.*, 2019). In particular, when the biomass is spatially heterogeneous, ignoring PS may overestimate the spatial predictions and the overall biomass estimates.

Recent research has tackled this challenge and developed methods to account for PS in statistical inferences. Model based PS was first introduced by Diggle *et al.* (2010) who proposed a base framework for estimating PS and applied it to led pollution data in Galicia. The authors extended a standard geostatistical approach where the variable of interest is jointly modelled with the spatial intensity of the sampling effort which also contributes to the inference and accounts for PS towards the variable of interest. This approach was extended by Pati *et al.* (2011) who introduced covariates and random effects in the model. Conn *et al.* (2017) followed the same ideas and developed a more generic model for ecological applications, which they applied to aerial seal count data. Pennino *et al.* (2019) applied similar ideas to infer the distribution of shrimps from onboard fishery data.

Provided PS is accounted for, integrated models (IM) appear as an attractive tool to combine fishery-independent and fishery-dependent data to infer the spatial distribution of harvested fish. IM have received considerable attention in the ecological literature (Schaub and Abadi, 2011; Parent and Rivot, 2012; Gimenez *et al.*, 2014). By sharing the information between different data types, IM may provide more accurate estimates and predictions compared with separate analysis of different data types. Recently, Rufener *et al.* (2021) demonstrated the potential of IM to integrate scientific data and onboard observer count data to improve SDM of fishery resources. However, although onboard observer data provide useful complementary information to scientific survey, they generally only represent a small proportion of all sea trips (1% in average for the French observer programs—Cornou *et al.*, 2021). In contrast, the combination of commercial catch declarations in logbooks with VMS data provides a more extensive data source to map fish spatial distribution. Furthermore, the potential of embedding PS within a hierarchical SDM to integrate catch declaration data and scientific survey is still an open challenge and new methodology are required to handle PS behaviours of commercial fleets while accounting for all the complexity related to fishing locational choice (Salas and Gaertner, 2004; Haynie *et al.*, 2009; Girardin *et al.*, 2017).

In this paper, we develop an IM model to infer fish spatial distribution by combining both scientific and commercial catch declaration data while taking into account the PS induced by fishing targeting behaviour.

To assess the challenges, the benefits and also the limits of the approach, we evaluate the performance of our IM based on simulated data. Simulations are primarily designed to assess the respective contribution of each data source to inference for different model configurations. We first evaluate how the balance between the commercial and scientific sample sizes affect the model outputs. Because the commercial data may often only partially cover the distribution area of a targeted species, we assess how this issue may affect the quality of estimation and how scientific data may contribute to reduce the effect of this gap in the commercial data. Introducing PS within an IM framework involves adding new parameters, complexifying the model structure, and then increasing the computational cost. We, therefore, assess how perform a more parsimonious model that would ignore PS. Last, in addition to the PS, the fishing locations can be controlled by other factors independent from the species distribution (e.g. logistical constraints and management regulations—see Girardin *et al.*, 2017; Ducharme-Barth *et al.*, 2022). We, therefore, assess how such process blurring strict PS may affect the quality of inferences.

We demonstrate the flexibility of the approach by fitting the model to three different important European demersal fishery resources in the Bay of Biscay: common sole (*Solea solea*, Linnaeus, 1758), hake (*Merluccius merluccius*, Linnaeus, 1758), and squids (*Loliginidae* family). With these contrasted examples, we illustrate the capacity of the framework to handle multiple commercial fleets with potentially distinct PS intensities and different fishing behaviours.

Material and methods

Spatial IM

Below we provide the core elements of the modelling approach. Additional details are provided in the Supplementary material (SM 1). The model is structured in four layers: observations (here commercial and scientific CPUE in weight per unit of effort), the sampling process, the latent field (here fish biomass relative density), and the parameters (Figure 1—all notations are available in SM 1.1, Supplementary Table S1). Sampling process is usually ignored in hierarchical models as it is mostly considered independent of the quantity of interest, and then has no consequence on inference (Diggle *et al.*, 2010). Here, the spatial distribution of commercial fishing is explicitly modelled as a inhomogenous Poisson point process whose intensity may depend on the biomass field and contributes to the likelihood. The observation processes of scientific and commercial data are conditional upon the biomass latent field and the sampled locations.

All processes are considered to occur in a discrete fine grid (see for instance SM 2.1, Supplementary Figure S2.1 or SM 3.1, Supplementary Figure S3.1). We assume the density of the point process is piecewise constant in each cell grid, which brings simplification in the expression of the likelihood of the point process (Diggle, 2013—see SM 1.2). The time component is omitted and both commercial and scientific data are assumed to occur at the same time step.

The IM is designed to assimilate the scientific data of several surveys and/or the commercial data of several fleets. In the following, the subscript j refers to the different data sources either scientific or commercial. For instance, in a model with one scientific survey and two commercial fleets, j will take the values $j = 1, 2, 3$, with $j = 1$ for the scientific data and $j = 2, 3$ for the two commercial fleets.

Latent field of relative biomass

The fish biomass relative density S [Equations (1) and (2)] is modelled through a latent log Gaussian spatial field defined on the same discrete spatial domain as the point process.

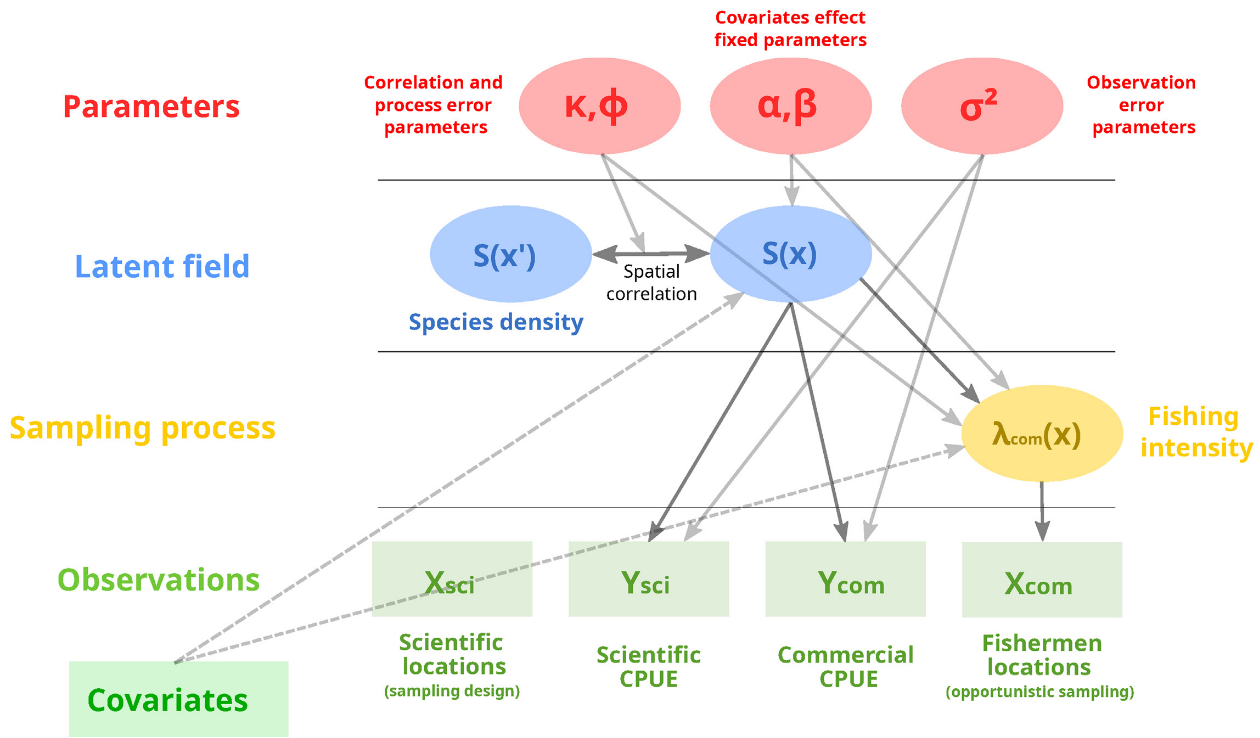

Figure 1. Diagram of the spatial IM including PS for commercial data. Locations of scientific trawls do not contribute directly to the likelihood.

The mean of the Gaussian field depends on environmental covariates through a log link where the linear predictor combines an intercept α_S, the linear effect of environmental covariates $\Gamma_S(x)$ (effects captured by the corresponding fixed parameters β_S representing the species-habitat relationship). The remaining spatial variation is accounted for through a zero-mean Gaussian random field (GRF) denoted $\delta(x)$ [Equations (2)] parameterized with a Matérn correlation function $M(x, x'; \kappa, \phi)$, characterized by the shape κ and the scale ϕ [Cressie, 1993; Gelfand *et al.*, 2010; Lindgren *et al.*, 2011 and Banerjee *et al.*, (2014)]. The shape can be expressed in term of range $\rho = \frac{\sqrt{8}}{\kappa}$ where ρ is the distance for which the correlation between points is near 0.1.

$$\log\left(S\left(x\right)\right) = \alpha_S + \Gamma_S(x)^T \cdot \beta_S + \delta\left(x\right). \tag{1}$$

$$\delta\left(x\right) \sim GRF\left(0, M\left(x, x'; \kappa, \phi\right)\right). \tag{2}$$

Sampling process

Recent literature has emphasized the complexity of fishers targeting behaviour (Salas and Gaertner, 2004; Haynie *et al.*, 2009; Abbott *et al.*, 2015; Girardin *et al.*, 2017; Hintzen, 2021). In this paper, we did not attempt to model explicitly all those processes (e.g. resource distribution, logistical constraints, tradition, and management regulations) and opted for a simplified representation where the spatial targeting directly depends on the biomass field S and on an additional spatially structured random term.

Let us denote $X_{com\ j}$, the spatial point process, where commercial vessels of fleet j are identified as fishing. In the following, all vessels in the same commercial fleet are assumed to have homogeneous behaviours. Following Diggle *et al.* (2010), the set of fishing locations are modelled conditionally on S, as a inhomogeneous Poisson point process with piecewise constant intensity $\lambda_j(x)$ [Equations (3) and (4)].

$$X_{com\ j} \sim \mathcal{IPP}\left(\lambda_j\left(x\right)\right). \tag{3}$$

$$\log\left(\lambda_j\left(x\right)\right) = \alpha_{X\ j} + b_j \cdot \log\left(S\left(x\right)\right) + \eta_j\left(x\right). \tag{4}$$

For any fleet j, intensity $\lambda_j(.)$ of the Poisson point process [Equations (3)] is modelled as a log-linear combination of the intercept $\alpha_{X\ j}$, the logarithm of the relative biomass $S(.)$ scaled by a parameter b_j, and a residual spatial effect $\eta_j(.)$ with the same structure as $\delta(.)$ but with specific parameters κ and ϕ. All parameters $\alpha_{X\ j}$, b_j, and the spatial random effect $\eta_j(x)$ are specific to each fleet.

The parameter b_j quantifies the strength of PS by scaling the relationship between the local value of the resource field and the local fishing intensity.

Fishing locations potentially depend on many other factors than fish distribution such as distance to harbour, logistical constraints, management regulations—spatial closures, and quotas—or fishing habits/tradition (Salas and Gaertner, 2004; Haynie *et al.*, 2009; Girardin *et al.*, 2017). The spatial random effect $\eta_j(.)$ is needed to capture any remaining additional effect not captured by the dependence to $S(.)$.

In that sense, a zero value for b_j indicates that the choice of the sampling locations does not depend on the fish biomass density but only on the spatial random effect.

In addition to b_j, a dimensionless spatial metric was developed to quantify the strength of PS (SM 1.3).

Observation process

Both scientific and commercial observations are considered proportional to the underlying biomass through a zero-inflated observation process. In our applications, observations are expressed as CPUE (in weights unit effort^{-1}), with high proportion of zeros (zeros represent on average 30% of the commercial data and 10–50% of scientific data).

Observations are modelled through a zero-inflated lognormal model conditionally on biomass $S(x)$ in cell x [Equations (5) and (6)]. The model is derived from Thorson *et al.* (2016) or Thorson (2018). We assume that the expected catch $\mu_j(x)$ for any fleet/data source j in the cell x depends on the latent field value $S(x)$ and a catchability coefficient q_j [Equation (5)]. A zero catch ($y = 0$) is modelled as a Bernoulli random variable with parameter $exp(-e^{\xi_j} \cdot \mu_j(x))$, where ξ_j is the parameter controlling the intensity of zeros relatively to the expected catch [Equation (6)]. Then, $\mu_j(x)$ being fixed, the higher (resp., the lower) ξ_j, the lower (resp. the higher) the probability of obtaining a zero-catch.

The distribution of a positive catch $y > 0$ at a given x is defined as the combination of the probability of obtaining a nonzero catch $(1 - exp(-e^{\xi_j} \cdot \mu_j(x)))$ times a positive continuous distribution L (here a lognormal distribution) with expected value $\frac{\mu_j(x)}{(1-exp(-e^{\xi_j} \cdot \mu_j(x)))}$ and standard deviation σ_j. This formulation allows to represent the zero catch while assuring that the expected catch still equals $\mu_j(x)$.

$$\mu_j(x) = q_j \cdot S(x). \tag{5}$$

$$P(Y = y|x, S(x)) = \begin{cases} \exp\left(-e^{\xi_j} \cdot \mu_j(x)\right) & \text{if } y = 0 \\ \left(1 - \exp\left(-e^{\xi_j} \cdot \mu_j(x)\right)\right) \cdot L\left(y, \frac{\mu_j(x)}{\left(1-\exp\left(-e^{\xi_j} \cdot \mu_j(x)\right)\right)}, \sigma_j^2\right) & \text{if } y > 0 \end{cases} \tag{6}$$

Per se, catchability q_j are not identifiable as there is no information in the model to estimate the absolute scale of S. Commercial catches and/or scientific surveys will be only informative about fish biomass relative density and additional information must be provided to ensure statistical identifiability. If only one data type feeds the model (only scientific or commercial data), relative catchability is fixed to 1 and the spatial random field values is in the same scale as the data. If two data types (or more) are used to feed the model, one of the relative catchability (denoted q_{ref}) has to be fixed, the other ones being estimated relatively to the first one through a scaling factor k_j [Equation (7)].

$$q_j = k_j * q_{ref}. \tag{7}$$

As it is illustrated further in the simulation-estimation study (see the first section of the results), the choice of the reference level can have important consequences on the precision of estimation.

Maximum likelihood estimation

The estimation of the model is performed with TMB [Template Model Builder—Kristensen *et al.* (2016)] and the spatial random effects are estimated through the SPDE approach (Lindgren *et al.*, 2011) within the R software (R Core Team, 2020). More details on estimation are available in the Supplementary material (SM 1.4).

IM validation

A key issue with IM is whether the different data sources provide consistent or conflicting information (Saunders *et al.*, 2019; Zipkin *et al.*, 2019; Peterson *et al.*, 2021). In our framework, the key question is whether integrating commercial data in addition to scientific data will complement or will disrupt the inferences obtained from the scientific data, considered as a reference source of information. To address this issue, we propose a validation procedure based on the consistency check initially developed by Rufener *et al.* (2021) and designed to check whether estimates obtained from the IM are consistent with those obtained from the model fitted to scientific data only. The procedure would reject consistency if the parameters estimates from the IM fall outside the 95% confidence region of parameters estimates from scientific data only (see SM 1.5 for more details on the procedure). This validation step is applied to both simulations and case studies.

Simulation–estimation experiments

We conducted simulation–estimation experiments to assess the performance of the method for different data/model configurations (Table 1, see also SM 2 for extended details on simulations). For all scenarios, simulations of data, covariates, and GRF were parameterized to tailor the case studies described hereafter. All scenarios and configurations are repeated 100 times so as to capture the variability between replicates.

Simulation–estimation experiments were specifically designed to address four questions detailed below. In all cases, commercial data were simulated with various levels of PS ($b = 0$ for uniform sampling, $b = 1$ for moderate PS, and $b = 3$ for strong PS) to assess the effect of PS on model's performance (Figure 2).

(Q1) How does each data source contribute to inferences?

In real case study, commercial data sample size may be far superior to scientific data (specifically when using landings data), which might result in commercial data that dominate inferences. To assess how the balance between the scientific and commercial sample sizes drives the relative contribution of each data source, simulations were conducted with few scientific samples (50 each) with increasing commercial samples (50 = small, 400 = medium, and 3000 = large), and with a large commercial sample size (3000) with increasing scientific sample size (50 = small, 400 = medium, and 3000 = large). No scenario with more scientific samples than commercial samples is presented here as it is a very unlikely configuration when using logbook catch data.

For each combination of commercial and scientific sample size, we fitted four different models: a model fitted to scientific data only, a model fitted to commercial data only, and two IM fitted to both commercial and scientific data, one with the scientific data used as reference level and another one using the commercial data as reference level (Cf. Equation (7)).

For questions Q2, Q3, and Q4, all simulations were conducted using $n_{scientific} = 50$ and $n_{commercial} = 3000$ to tailor the case studies. Commercial data are used as the reference for catchability in the IM.

(Q2) How does a partial coverage of the study area by the commercial data affect the quality of the estimation?

While scientific surveys are supposed to cover the full population distribution area, partial coverage of the area by commercial fishing boats may arise from different sources like spatial management closures (e.g. box closure) or too expensive travels from the coast. To assess how a partial coverage by commercial data can affect estimates, we simulated data with

Table 1. Simulations description.

General simulations description	
Biomass field	Depends on one continuous covariate (Γ_S) and one random spatial effect (δ). Simulated within a 25 × 25 grid. Both are simulated independently through a GRF with Matérn covariance function. Their range (ρ) and marginal variance are fixed respectively to 10 and 1. n.b. the marginal variance quantifies the variability of the spatial process. For more details on marginal variance parameterization, see Lindgren *et al.* (2011).
Scientific data	Random stratified plan within four strata (see Supplementary Figure S2.1) Catchability fixed to 1 Simulated with 10% of zeroes ($\xi_j = 0$).
Commercial data	Simulated according to three PS levels (i.e. three values for b – see Figure 2). – $b = 0$: commercial sampling is not preferential; – $b = 1$: PS is moderate, commercial vessels mainly target areas where fish biomass is high; – $b = 3$: commercial sampling is highly preferential and vessels strongly target zones where biomass is high. η is set to 0 for Q1, Q2, and Q3. For Q4, η is set to tailor the sole case study. The range of η is set to 40 (four times the range of δ), the marginal variance is set to 5 (five times the marginal variance of δ). Catchability fixed to 1 Simulated with 30% of zero when PS is null ($\xi_j = -1$).

	Simulation scenarios					Model configurations		
	b	Scientific sample size	Commercial samples size	Coverage of the study area	Additional random effect in sampling intensity (η)	Data sources considered in the model	PS estimated	Fixed catchability
Question 1: How does each data source contribute to inferences?	0,1,3	50	50, 400, 3 000	Full	No	Scientific only, commercial only, both	Yes	Scientific or commercial
	0,1,3	50, 400, 3 000	3 000	Full	No	Scientific only, commercial only, both	Yes	Scientific or commercial
Question 2: How does a partial coverage of the study area by the commercial data affect the quality of the estimation?	0,1,3	50	3 000	No fishing in a 9 × 9 cells box	No	Scientific only, commercial only, both	Yes	Commercial
Question 3: What is the cost of ignoring PS in estimation when sampling is preferential?	0,1,3	50	3 000	Full	No	Scientific only, commercial only, both	No (b fixed to 0)	Commercial
Question 4: How does the estimation perform when additional processes other than PS drive the fishing locations?	0,1,3	50	3 000	Full	Yes	Scientific only, commercial only, both	Yes	Commercial

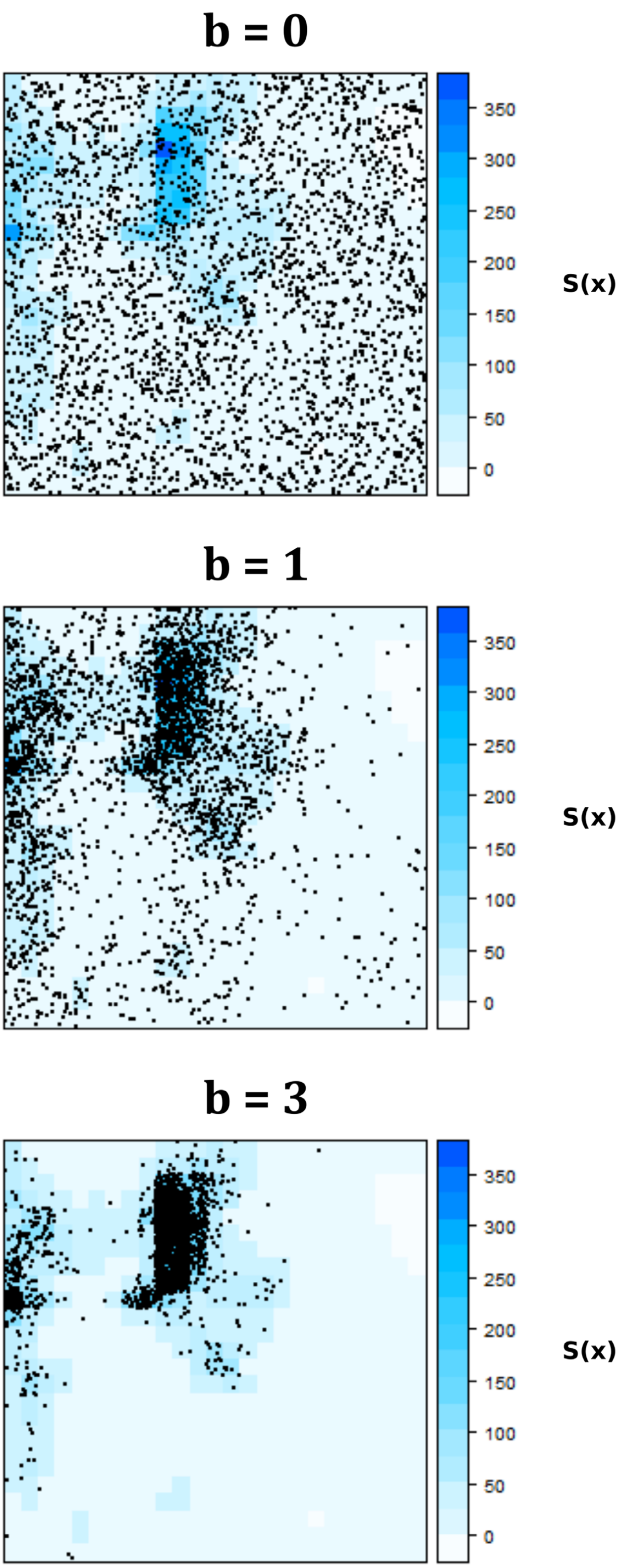

Figure 2. Maps of simulated commercial sampling points obtained for three values of PS (b = 0, b = 1, and b = 3). Blue scale: values of the simulated biomass field. Dots: fishing points. For b = 0, the targeting metric $T_j(x) = 1$. For b = 1, arg $\max(T_j(x)) = 12$, $q_{50\%}(T_j(x)) = 0.4$. For b = 3, arg $\max(T_j(x)) = 80$, $q_{50\%}(T_j(x)) = 0.002$ (SM 1.3).

the commercial sampling intensity arbitrarily fixed to 0 in a fixed 9 × 9 box (15% of the domain) while some biomass and some scientific samples are still simulated in this area. We compared the outputs obtained form the models fitted to commercial data that partially cover the entire area with those obtained with commercial data available on the whole domain.

(Q3) What is the cost of ignoring PS in estimation when sampling is preferential?

Modelling PS involves conditioning results upon a specified structural assumption about sampling as well as increased computational cost. Here, we assess how ignoring PS would affect the quality of inferences when sampling is actually preferential. We voluntary introduce misspecification between the model used for simulating the data (with various levels of PS intensity) and the one used in the estimation procedure (b is alternatively estimated or arbitrarily fixed at 0).

(Q4) How does the estimation perform when additional processes other than PS drive the fishing locations?

Fishing locations potentially depend on many other factors independent from the species distribution (Salas and Gaertner, 2004; Haynie *et al.*, 2009; Girardin *et al.*, 2017). To assess how such process blurring strict PS may affect the quality of inferences, we simulate data with a sampling intensity that depends on both the biomass distribution (PS) and an additional spatial random terms $\eta_f(.)$ independent from the biomass distribution (Equation (4); see Table 1 for more details on $\eta_f(.)$ parameterization), and compare the inferences obtained from a data set simulated with strict PS ($\eta_f\ (.) =\ 0$ on the full domain).

Note that for questions Q1, Q2, and Q3, the random effect η was fixed to 0 in simulations (but it is still estimated in the estimation model), so that the sampling process only depends on the distribution of biomass.

Performance metrics

The performance of the estimation method was assessed using different metrics on key model outputs such as the total biomass, the PS parameter b and the spatial biomass predictions.

The quality of the total biomass estimation (the sum over all grid cells, $B\ = \sum_x S\ (x)$) was explored through the relative bias $\frac{(B-\hat{B})}{B}$, that quantifies how much the total biomass is over or under-estimated.

The quality of the estimation of the parameter b is assessed through the relative bias defined as $\frac{b-\hat{b}}{b}$ (except for $b\ =\ 0$, where only the absolute bias is considered). We also assessed the relative bias of the species–habitat relationship estimate $\hat{\beta}_S$ and range parameter ρ as these parameters are meaningful for understanding species distribution.

The precision of the spatial predictions was studied with the mean squared prediction error (MSPE) between the simulated and the estimated latent field values $\frac{1}{n}\sum_x (S(x) - \widehat{S(x)})^2$ (MSPE—n stands for the number of grid cells).

Case studies

We applied the approach on three case studies of demersal fisheries in the Bay of Biscay: the common sole (*S. solea*, Linnaeus, 1758), the hake (*M. merluccius*, Linnaeus, 1758), and the squids (Loliginidae family). These case studies were se-

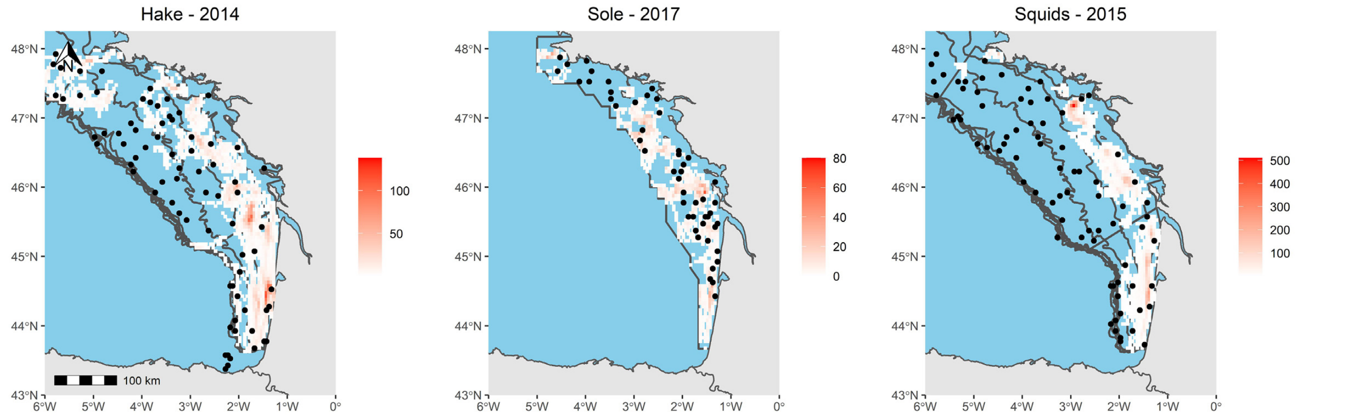

Figure 3. Map of scientific samples (black dot) and commercial sampling distribution (red colour scale—unit: fishing hours). Note that all scientific hauls last around 30 min. Black lines—limits of the spatial domains covered by the scientific survey (Orhago and EVHOE) that delineate the study area. Left—hake, November 2014 (EVHOE; commercial data from otter bottom trawls targeting demersal species OTB_DEF). Middle—sole, November 2017 (Orhago; commercial data from otter bottom trawls targeting demersal species OTB_DEF). Right—squids, year 2015 (EVHOE; commercial data from otter bottom trawls targeting cephalopods OTB_CEP).

lected because they emphasize different intensities of PS. Further details on case studies and data are provided in SM 3.

To compare models on the same spatial domain for the three species, we limited the analysis to scientific and commercial data available on the Bay of Biscay only (SM 3.1, Supplementary Figure S3.1 for the spatial grids). Besides, to get some replicates of the analysis, we applied the approach on 2 years for each case study (2017 and 2018 for common sole—2014 and 2015 for hake and squid). To keep it synthetic, only the data and the results of the models for hake in 2014, sole in 2017 and squids in 2015 are presented in this manuscript as the related IM pass the consistency check and they emphasize contrasted level of PS.

Survey data

Scientific data (CPUE, in kg h^{-1} - Figure 3) were derived from the Orhago survey for common sole and EVHOE survey for hake and squids (ICES, 2020a; ICES, 2020b). The sampling density (number of data points km^{-2}) of those two surveys revealed representative of the sampling density of the main European trawl surveys from the DATRAS database (see SM 3.2). In comparison, commercial data used in the case studies are denser by 2 orders of magnitude. Scientific data was aligned on commercial data by filtering only individuals above the minimum landing size when available (24 cm for sole and 27 cm for hake—ICES, 2020). The Orhago survey provides 49 samples for 2017 and 2018 and the EVHOE survey provides 86 samples for 2014 and 2015.

Commercial data

For each species, we filtered commercial data for 'bottom trawlers' as they cover a wide part of the study area (Figure 3) and provide easy to compute and reliable CPUE. Commercial data were standardized by the fishing effort in (kg h^{-1}). For hake and sole, we filtered the métier targeting demersal fish (called OTB_DEF) and for squids, the métier targeting cephalopods (called OTB_CEP).

In comparison with scientific data, the orders of magnitude of commercial sample size is much larger. For hake (i.e. OTB_DEF), there are 6852 commercial samples in 2014 and 5000 in 2015. For squids (i.e. OTB_CEP), there are 7486 commercial samples in 2014 and 9611 in 2015. For sole (i.e. OTB_DEF), there are 2401 samples in 2017 and 3325 in 2018.

Habitat covariates

A total of two covariates classically used to describe benthic species distribution were selected: depth and sediment type (Le Pape *et al.*, 2003; Witman and Roy, 2009; Rochette *et al.*, 2010). Depth was separated into several categories and was considered (as sediment) as a categorical variable (SM 3.7, 3.8).

Model configurations

As for the simulation–estimation experiments, the models of the case studies were fitted under different configurations. To assess the information brought by each dataset, we compared the model fitted to scientific data only, to commercial data only and to both scientific and commercial data. To assess the effect of PS on model outputs, we compared the IM accounting for PS (b is estimated) with the IM where PS is ignored (b is fixed to 0).

For the sole case study, we compared results obtained from the IM by considering one homogeneous or two distinct fleets with specific catchability and targeting parameters. Note that splitting one fleet in two distinct fleets is performed through a PCA coupled with a HCPC analysis on vessels characteristics data derived from both logbooks and VMS data. All the clustering analysis is described in SM 3.9.

Model evaluation

Uncertainty of the predictions are quantified through the coefficient of variation and all estimates (e.g. fixed parameters and total biomass) are represented with related 95% *CI*s. We assess the consistency of the IM through the statistical tests described in the section 'IM validation' and in SM 1.5. Finally, the different IM are compared through a fivefold cross-validation, and model performance was quantified based on two metrics: the $MSPE_{fit}$ that measures goodness of fit and the *PCV* that measures predictive capacity (see SM 3.10 for more details on the metrics and guidelines for interpretation). For both metrics, the lower the values, the better the model fits/predicts the data.

Results

Simulations

We summarize the main results of the simulation–estimation experiments below. Additional results are provided in SM 4.

Contribution of each data source in the IM

Models fitted on scientific data only provide systematically unbiased estimates of total biomass (the mean bias is close to 0 for all sample size—Figure 4, 1st row), and the variance of estimations decreases with scientific sample size. Note that the species-habitat relationship estimates $\hat{\beta}_S$ are also unbiased (see SM 4.1).

Overall, inferences from the IM revealed consistent with those obtained from scientific data only (SM 4.2.1). Even when the commercial sample size is large and the scientific sample size is small, only 3% of the *p*-values fall below the 0.05 threshold for the fixed effect test (the test wrongly rejects consistency). For the random effect test, the results are more contrasted as 10% of the *p*-values fall below the 0.05 threshold when data size are very unbalanced (low scientific sample—high commercial sample).

In almost all configurations, the IM provide unbiased and more precise estimates for total biomass and spatial biomass predictions compared to the model fitted to scientific data only (Figure 4). As expected, the larger the commercial and the scientific sample size, the more accurate the spatial predictions, the PS parameter b, and total biomass estimates. Estimates of b are unbiased in most cases except when commercial sample size is small and PS is strong (Figure 4, 2nd row).

As expected, the contribution of each data sources in the IM directly depends on the balance in the sample size. When sample size is balanced between the data sources, then integrating the two data sources in the model systematically improves the inferences with regards to situations where only one data source is analyzed. For instance, for large commercial and scientific sample size (com.L_sci.L) and no PS, the precision is 1.5 higher (i.e. the MSPE is 1.5 lower) for the IM compared to single-data models (either scientific or commercial—Figure 4, 3rd row, 1st column). However, when the sample sizes are unbalanced, the data source with the larger sample size (here commercial data) dominates inference and integrating another data source with a smaller sample size (here scientific data) contributes to a much lesser extent to inference. See, for instance, the situation where commercial sample size is large and scientific sample size is small (com.L_sci.S—Figure 4, 3rd row, 1st column). In this case, the performances of the model fitted to commercial data alone—with reference level fixed to commercial data—are very close to those of the IM whatever the intensity of PS.

Interestingly, the higher the intensity of PS, the higher the benefits of fitting commercial data in the model (Figure 4, 3rd row); for instance, when both datasets have large sample sizes (com.L_sci.L), increasing PS reduces error predictions (i.e. increases accuracy) by 2 each time (i.e. for $b = 0$, $E\ (MSPE) = 20$; for $b = 1$, $E\ (MSPE) = 10$; and for $b = 3$, $E\ (MSPE) = 5$).

Still, the simulations also reveal some limits in the inferences. First, the range parameter might be poorly estimated and slightly biased when the sample size is small while being better estimated when increasing the sample size or integrating additional data in the analysis (see SM 4.3).

Also, in unbalanced cases the accuracy of total biomass estimates from the IM revealed highly sensitive to the choice of the reference level (Figure 4, 1st row). When the commercial sample size far exceeds the scientific sample size, setting the reference level to the commercial data produces more precise estimates than setting the reference level to scientific data. When defining scientific data as reference level, the intercept of the latent field of relative biomass is estimated from the few scientific samples and resulting estimates are less precise than when defining the reference level with a more numerous data source (here commercial data). This is also true—to a lesser extent—for spatial predictions (Figure 4, 3rd row).

In the following, only the case where commercial samples exceed scientific samples and the reference level is fixed with commercial data is explored further as it is the closest to the case studies configuration (Table 1).

Impact of a partial coverage of the study area by the commercial data

When commercial data only partially cover the distribution area, commercial data still provide valuable information to predict biomass spatial distribution whatever the PS intensity is (Figure 5, 2nd column). When sampling is not preferential (data simulated with $b = 0$), a partial coverage of the distribution area produces on average 1.5 less precise spatial predictions but estimates remain unbiased (Figure 5, 3rd row, comparing 1st and 2nd column). When sampling is preferential (either moderate or high), biomass estimates are slightly underestimated. Integrating scientific data in the analysis does not correct this bias.

Finally, all model configurations allow for unbiased and precise estimation of the species–habitat parameters $\hat{\beta}_S$, whether or not there is a partial coverage of the domain (see SM 4.1) and overall almost all IM are consistent with scientific-based model (SM 4.2.2).

How does ignoring PS impact inferences?

As expected, the impact of ignoring PS in the estimation model is negligible when data is simulated with no PS, and becomes more and more detrimental when the intensity of PS increases in the truth (Figure 5, 3rd column). With no surprise, when data are generated with no PS ($b = 0$), ignoring PS in the estimation procedure has no effect on the estimation performance. When PS is moderate, total biomass estimates are 5% overestimated ($b = 1$). In the case of strong PS ($b = 3$), ignoring PS in the estimation strongly deteriorates the quality of inferences regarding total biomass estimates (Figure 5, 1st row, 3rd column). Total biomass estimates are overestimated by 50% on average. However, the main spatial patterns are well identified with or without consideration of PS, even though more precise when accounting for PS (Figure 5, 3rd row, 1st column). SM 4.4 (Supplementary Figure S4.4.1) presents maps comparing a simulated biomass field and model predictions obtained by considering or ignoring PS when $b = 3$. The areas with high biomass values (i.e. where commercial sampling is dense) are well-predicted by the models accounting for PS or not. The main differences are localized in poorly sampled areas where biomass is low. Accounting for PS in estimation allows to interpret the low sampling intensity areas as low-density areas, and therefore, to reduce the bias in those areas (SM 4.4, Supplementary Figure S4.4.2).

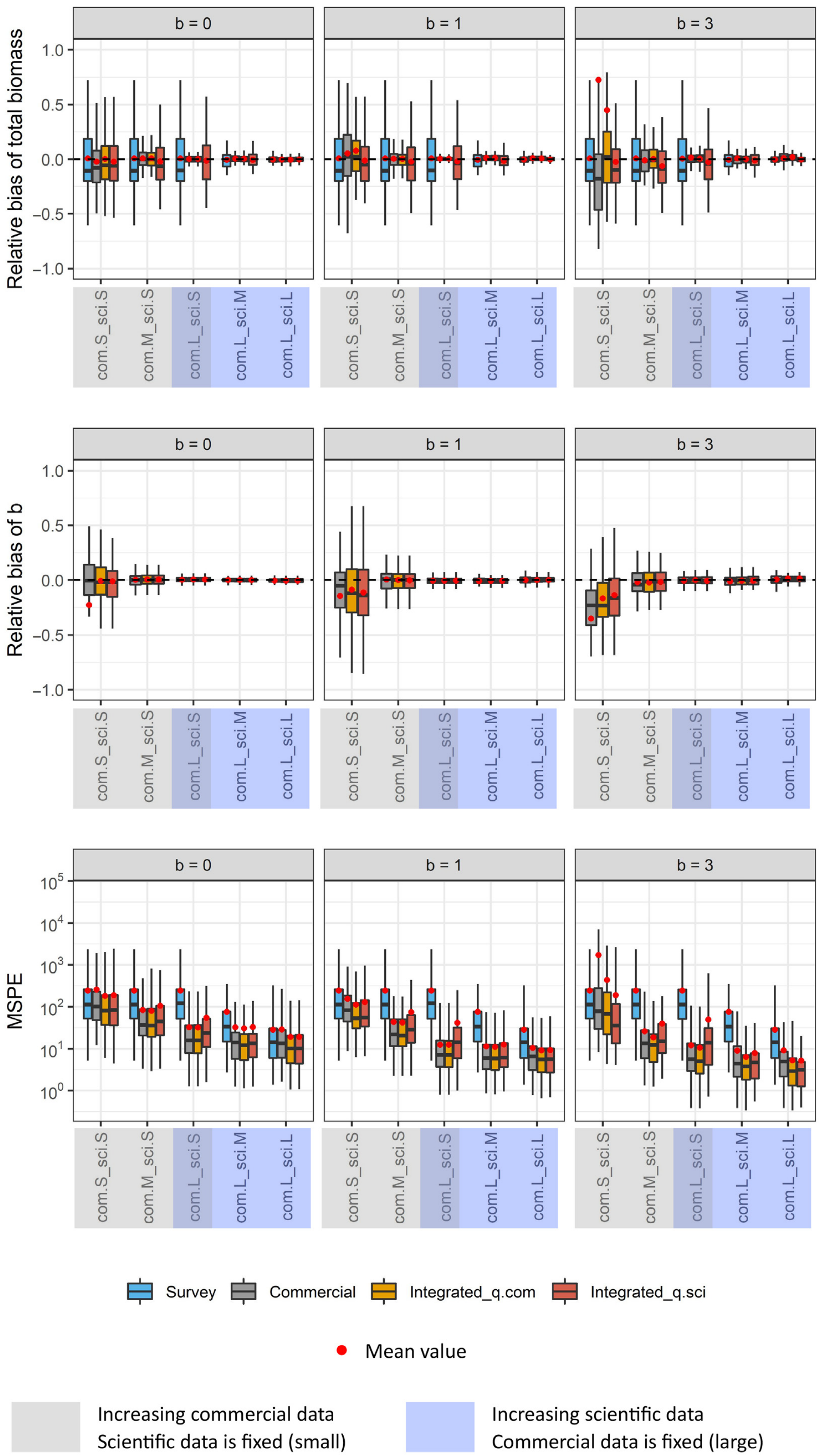

Figure 4. Performance metrics obtained for various commercial and scientific data sample size. Column: intensity of the PS in simulated data. *x*-axis: five combinations of commercial and scientific sample size. 'com' stands for commercial, 'sci' stands for scientific, S stands for small sample size (50), M stands for medium sample size (400), and L stands for large sample size (3000). Colours: model configurations. Integrated_q.com: IM with catchability fixed to 1 for commercial data; Integrated_q.sci: IM with catchability fixed to 1 for scientific data. Boxplots represent the variability among the 100 replicates.

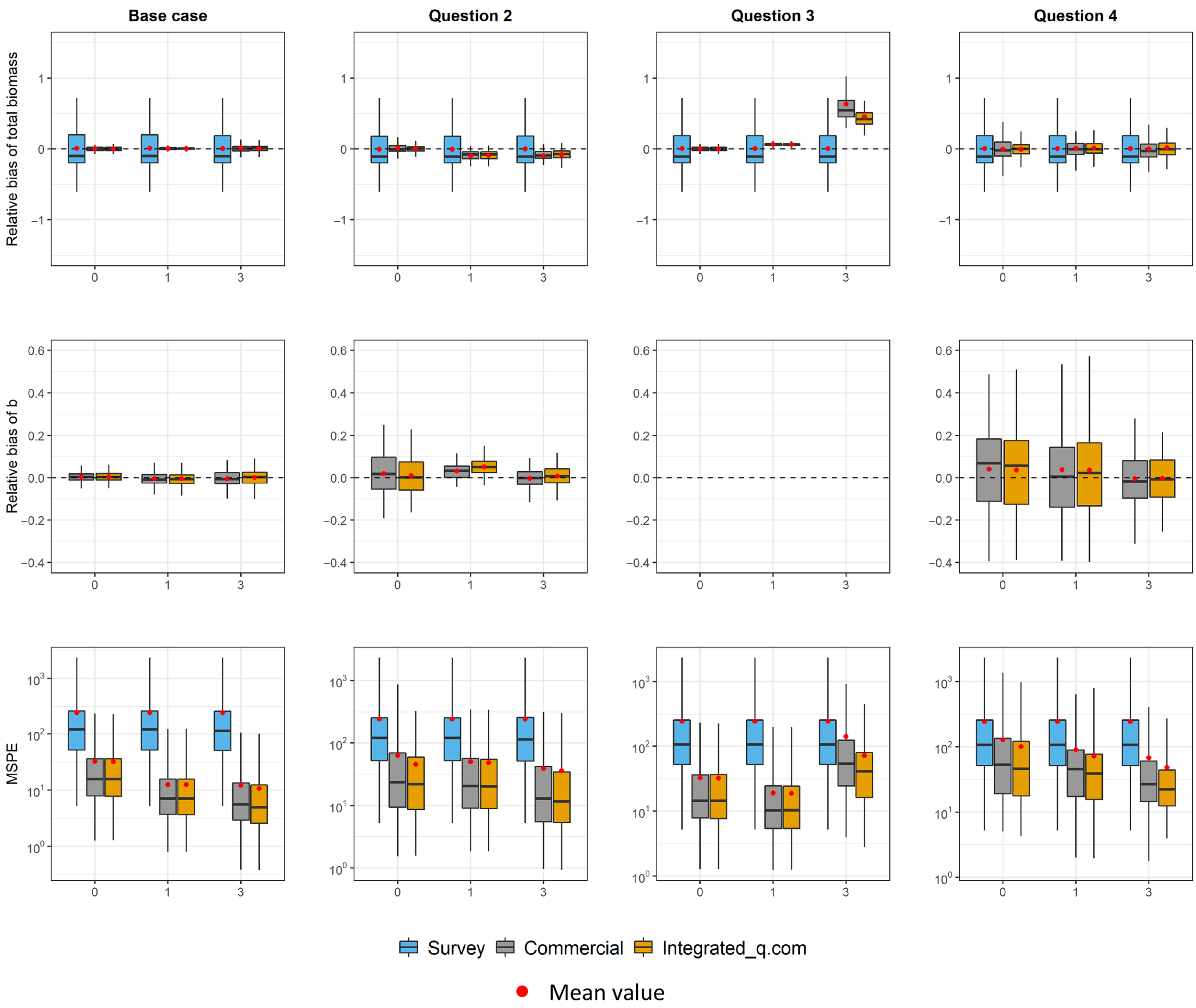

Figure 5. Performance metrics obtained in different data and model configurations. Red points: mean value. 1st column: no discrepancy between simulation and estimation. 2nd column: commercial data do not cover a 9 × 9 zone of the grid. 3rd column: b is arbitrarily fixed to 0 in the estimation models. 4th column: data simulated with a random effect η in the sampling intensity process. In all configurations, simulations are conducted for three levels of PS (*x*-axis: b = 0, b = 1, and b = 3). Colours: data sources used in the IM for inferences. Integrated_q.com: IM with catchability fixed with commercial data. Boxplots represent the variability among the 100 replicates.

Finally, from a computational point of view, accounting for PS on average multiplies by 4 the computational time (see SM 4.5).

Effect of other spatially structured processes affecting fishing locations

As expected, precision of estimates are deteriorated when fishing locations actually depend upon a combination of biomass distribution (PS) and other mechanisms (here captured by a spatially structured random term—Figure 5, 4th column). In this case, the IM still provides valuable inferences on fish distribution, fish total biomass and estimates of *b*, although estimations are less accurate than the base case. For instance, MSPE are five times lower when nothing else than PS affects sampling locations compared with a case where sampling locations depend on both PS and other independent spatial processes (Figure 5, 3rd row, 1st and 4th column). But interestingly, the weight of scientific data increases when the sampling distribution of commercial data is blurred by spatial processes independent from biomass spatial distribution. MSPE and relative bias provided by the IM are both 1.4 smaller compared to those obtained when the model is fitted to commercial data only.

Case studies

Below we summarize the main results obtained from the application of the framework to the three case studies. Additional results and maps are provided in SM 5.

Contribution of each dataset to the inferences

Almost all the case studies successfully passed the consistency test between the IM and the model fitted to scientific data only (see SM 5.1).

Models based on scientific data provide different spatial predictions compared with the IM. Predictions for sole and squids from the scientific-based model are mainly shaped by the covariate effects (Figure 6; for further analysis see SM 5.2, SM 5.3, and SM 5.4). On the other hand, predictions from the

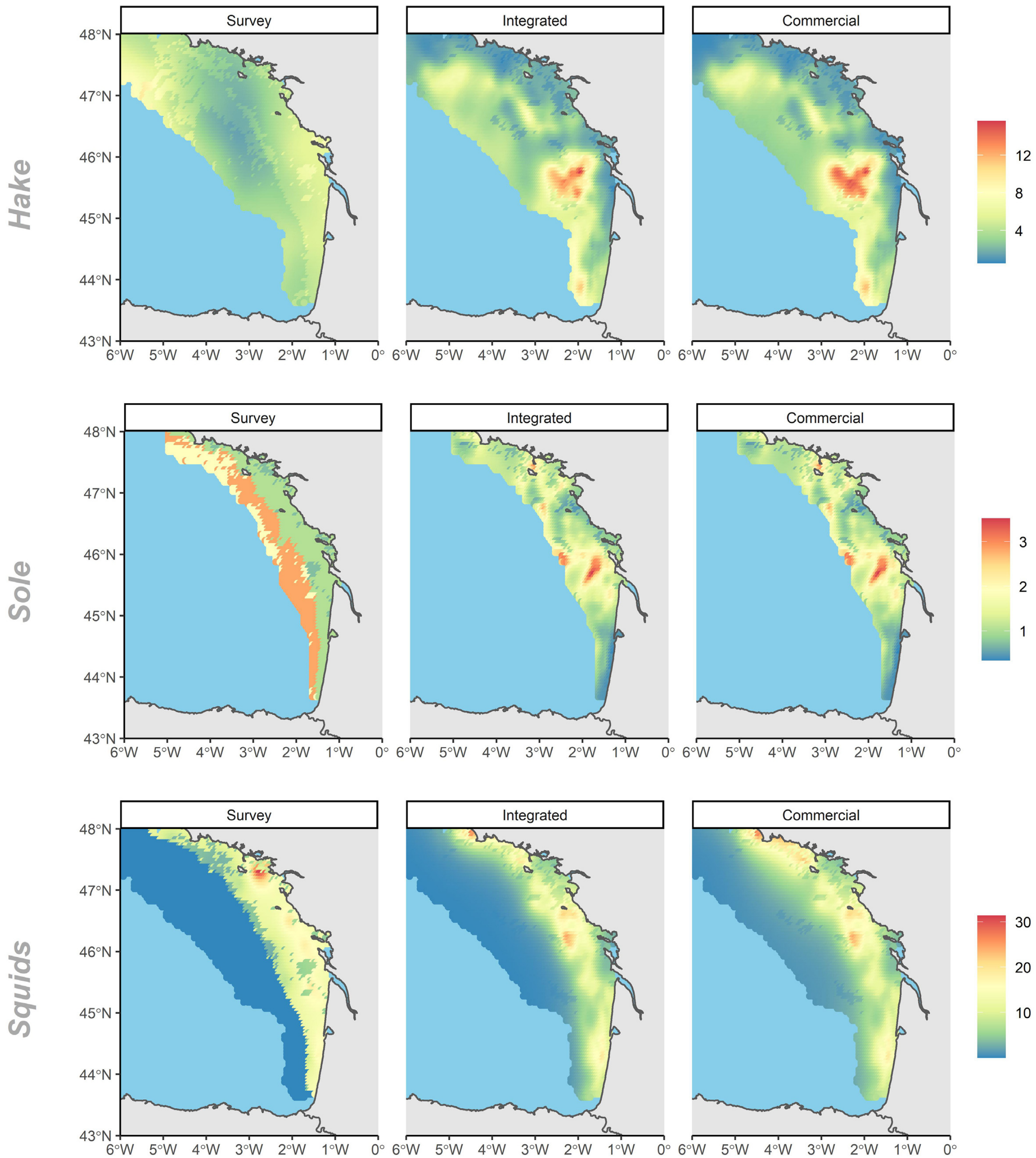

Figure 6. Prediction of the relative biomass for each case study. 1st column: model fitted to scientific data only; 2nd column: IM accounting for PS; and 3rd column: commercial-based model accounting for PS. When the model is fitted to scientific data only, relative biomass is rescaled with the relative catchability parameter estimated within the IM so that all maps are in the same scale.

IM are mainly shaped by the spatial random effect as commercial data allow to better capture the local spatial correlation structures.

Consistently with simulations, inferences from the IM are mainly driven by the commercial data (Figure 6). This logically arise from the much larger sample size of commercial data compared with scientific data, combined with the good coverage of commercial data in high-density areas (Figure 3). As commercial data is denser than scientific data, they will better capture local spatial correlation structures than scientific data. SM 5.5 provides some additional analysis of the information brought by commercial data in the IM.

In this configuration, scientific data bring information to model predictions in areas poorly covered by the commercial data (SM 5.6—e.g. for squids, the offshore predictions are downscaled by scientific data).

PS and other processes affecting fishing locations

In this section and related SM (SM 5.7 to SM 5.10), we focus on results from the IM only.

For the three case studies, estimates of b are positive, suggesting the sampling of fishermen is preferential towards high biomass density areas. The hake case study has the lowest PS parameter ($\hat{b} = 0.88,\ sd(\hat{b}) = 0.107$), followed by sole ($\hat{b} = 2.4,\ sd(\hat{b}) = 0.046$), and squids ($\hat{b} = 3.5,\ sd(\hat{b}) = 0.025$). For more intuition concerning the strength of PS and how it varies in space, refer to SM 5.7. In all case studies, the spatial random term η in the sampling process turned out to be spatially structured (SM 5.8) and captures 25–97% of the spatial variability of fishing locations (SM 5.9). This highlights the importance of other spatial mechanisms in the choice of fishing locations compared to strict PS towards biomass distribution.

Consistently with simulations, the higher the PS intensity, the higher the differences between inferences obtained with and without considering PS. When comparing biomass field values (Figure 7, left column), ignoring PS increases predictions in poorly sampled areas (all red areas—compare with Figure 3). This effect is particularly marked for the squid case study where the relative difference is the strongest in the offshore areas. However, considering PS or not has relatively little effect in areas where sampling is spatially denser (all white areas). Ignoring PS affects total biomass indices estimates and the relative difference between biomass estimates with or without PS increases with the value of b estimates (Figure 7, right column).

When the estimated PS intensity is high (i.e. in the case of squids) accounting for PS can improve model goodness-of-fit and predictive capacity (SM 5.10).

Benefits of considering different fleets in the estimation model

Based on the sole case study, we demonstrate the capacity of the model to integrate multiple commercial fishing fleets, each with specific parameters (catchability and PS behaviour). In the sole case studies, considering two different fleets in the IM (instead of one homogeneous) improves goodness-of-fit towards scientific data (SM 5.11, y-axis) and modifies spatial predictions (SM 5.12).

Discussion

Main findings

Combining multiple sources of data to build more informative spatio-temporal models for fish distribution is a major challenge in fishery ecology. Commercial CPUE data have long been recognized as a valuable source of information eventually highly complementary to scientific survey data. But the complexity of the mechanisms driving the way fishermen sample in space and time make the combination of scientific and commercial data challenging.

In this paper, we provide a hierarchical framework to integrate scientific surveys and commercial catch declaration data to infer species distribution while considering the effect of PS on fishing points distribution. The new model allows for exploring and questioning the challenges raised by such integration. The benefit but also the limits of the new approach were evaluated using simulations and through the application of the model to three contrasted demersal case studies (sole, hake, and squids) of the Bay of Biscay fishery.

Both simulations and case studies demonstrate that ignoring PS in the inference may be highly detrimental when the intensity of PS is strong. The present framework can serve as a tool to assess the benefit of including PS in analysis, depending on the intensity of PS but also on the modelling objectives. As already shown in previous studies (Conn *et al.*, 2017; Pennino *et al.*, 2019), when PS actually occurs in commercial catches, ignoring this process may bias inferences on total biomass estimates. Even if ignoring PS may not hamper the capacity to detect areas of high biomass, the biomass in low-density areas may be overestimated. Therefore, if the objective is to compute biomass indices integrated over a large area, then it might be worth accounting for PS to avoid biased results. In contrast, if the objective is to identify hotspots, the benefits of considering PS may be small with regard to the additional computational time it requires.

The three case studies illustrated the potential of the model to handle the variability of PS behaviour among species and fleets. Low PS was revealed for hake, while a moderate and strong PS was revealed for sole and squids, respectively, which is consistent with the expert knowledge on the behaviour of those bottom trawls fleets (YV, pers. comm.).

Results also demonstrate the capacity of the framework to integrate commercial catch data from multiple fleets, and the benefits for the quality of inferences when those fleets have different features such as distinct catchabilities or targeting behaviours. For the sole case study, this approach proves useful to distinguish two segments in the bottom trawl fleet, which improved model outputs. This framework could be extended to more than two fleets and combined with other studies analyzing fleets structure (Pelletier and Ferraris, 2000; Ferraris, 2002; Stephens and MacCall, 2004; Deporte *et al.*, 2012; Winker *et al.*, 2013; Okamura *et al.*, 2018).

Challenges in modelling PS

Still, modelling the spatial distribution of commercial fishing locations remains highly challenging (Hintzen, 2021; Hintzen *et al.*, 2021). Our framework is shaped to integrate data from homogeneous fishing fleets supposed to share the same fishing behaviour, which simplifies the modelling of the non-uniform spatial intensity of fishing for each fleet. We propose a parsimonious model where the dependence of the sampling intensity to the biomass is supposed to be linear in the log scale. This is a strong hypothesis and departure from this hypothesis may obviously exist in the truth. For instance, the intensity of PS could vary in space such as in Conn *et al.* (2017) who considered that the degree of PS could change across the landscape. On the other hand, however, the log–log linear assumption is easy to implement in other software including the VAST R package used for operational assessments in some management regions (Thorson *et al.*, 2019).

Of course, many other factors may drive the spatial intensity of fishing, and those were simply captured in our model through an additional spatial random term. For instance, fishers' behaviour may depend on prior knowledge of fish spatial distribution, on information sharing within fishing cooperatives, on expected distribution of bycatch species, or logistical constraints (e.g. transit costs) (Salas and Gaertner, 2004; Haynie *et al.*, 2009; Girardin *et al.*, 2017). Targeting behaviour

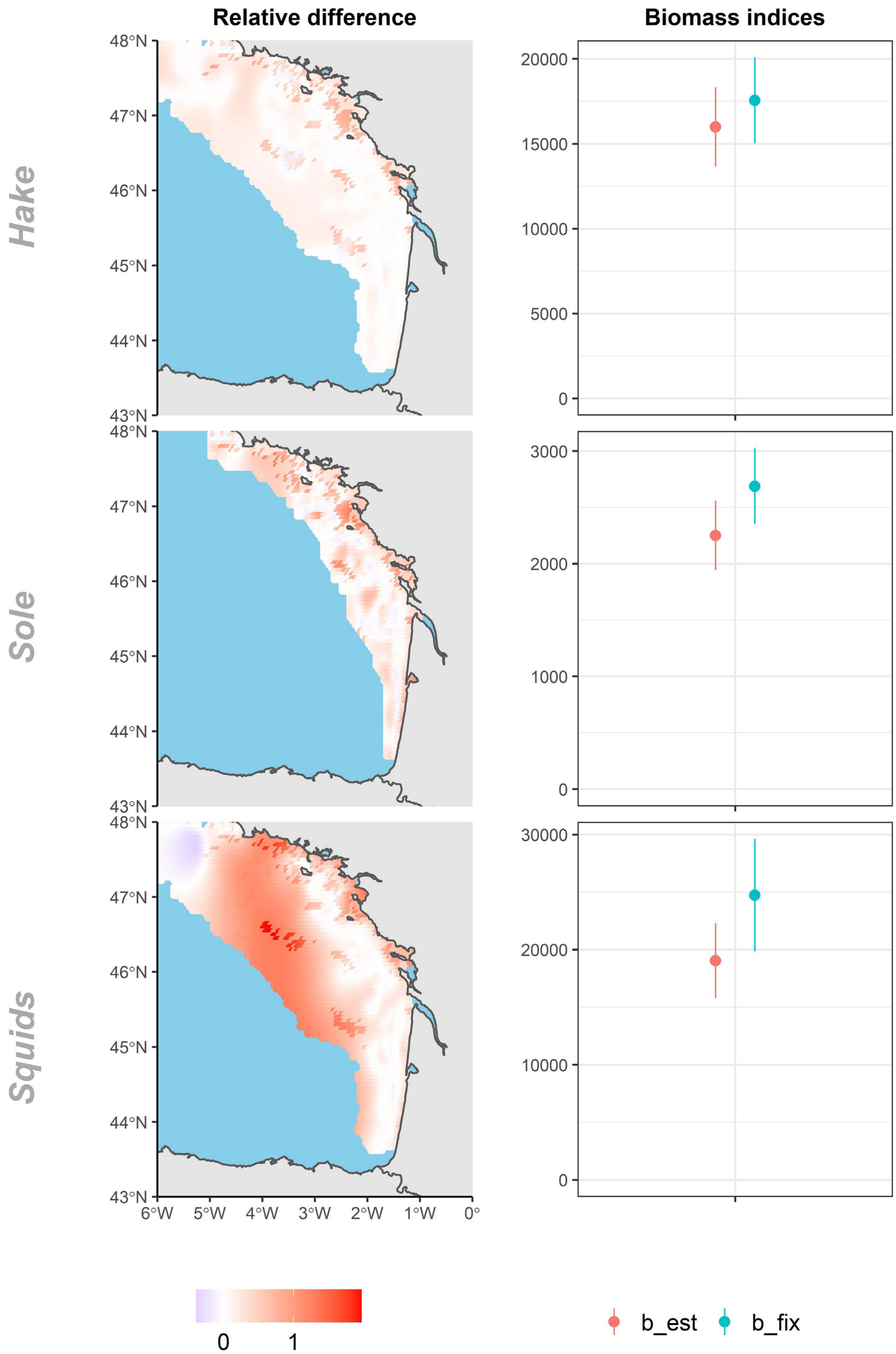

Figure 7. Relative difference in biomass spatial predictions between IM accounting or not for PS for the three case studies (left). Comparison of the total biomass estimates obtained from the IM when accounting or not for PS (right). b_est: PS is estimated. b_fix: PS is not accounted for. The relative bias is calculated as $(S_{b\_fix}(x) - S_{b\_est}(x))/S_{b\_est}(x))$. The total biomass is computed as the sum of the latent field values on the spatial domain.

may also be directed toward an assemblage of species rather than toward a single species (Bourdaud *et al.*, 2019).

The random effect should be able to capture additional variations whenever the departure from a continuous Gaussian random field is not too high. If not, for instance in the case of fishery closures where fishing activity suddenly drops to very low levels (as explored in simulation–estimation), the model may produce biased estimates due to model misspecification. We did not detect such misspecification in our case study, but we recommend that future analyses based on fishery-dependent data present a log–log plot between sampling intensity and predicted biomass density to diagnose strong departure from model hypothesis.

Still, some non-spatial targeting has been reported from multi-species catch records (Stephens and MacCall, 2004; Okamura *et al.*, 2018). Efforts to integrate these methods into spatio-temporal models are underway (Thorson *et al.*, 2016), although these methods have not previously been extended to jointly analyze multi-species fishery and survey data.

Relative contribution of scientific and commercial data

Our analysis exemplifies that a key issue in such integrated modelling exercise is to get a sensible evaluation of the relative contribution of the different sources of data in estimation. In particular, critical issues with the IM are whether the different data sources provide eventually highly unbalanced quantity of information (then the inferences are fully dominated by one of the data sources; Fletcher *et al.*, 2019), and whether they provide complementary or conflicting information to the final inferences (Saunders *et al.*, 2019; Zipkin *et al.*, 2019; Peterson *et al.*, 2021).

We implemented a likelihood ratio-test (Rufener *et al.*, 2021) to check for model consistency between the IM and the scientific-based model. In most cases, models passed the consistency check successfully, although it was rejected in some cases. Some further analysis should investigate in detail the reasons of these inconsistencies as they could probably shed light on some new research avenues for model improvement. For instance, some neglected vessel effect (e.g. difference in catchability among vessels—Thorson and Ward, 2014) or some too simplistic representation of the sampling and/or the observation process of commercial data might partly explain these inconsistencies.

Simulations revealed that when scientific data and commercial data have balanced sample size, they both contribute to inference and the IM provide better biomass predictions than models based on single-data set. As expected, when the sample size of commercial data far exceeds scientific data, inference about spatial patterns is mainly driven by the commercial data. In the three case studies, we used commercial data with sample sizes that far exceed the scientific one. In that case, scientific data have relatively limited weight in the final inference. Still, they bring valuable information in areas that are not sampled by the commercial fishery. Also, scientific data remain a critical component in the analysis as they provide some reference data through a standardized sampling plan and a controlled protocol allowing then to assess for the IM consistency. It would be worth applying our framework to other case study that may consist in more balanced data sets, such as models seeking to combine scientific with onboard observer data (Rufener *et al.*, 2021), or in pelagic fisheries where acoustic surveys can provide continuous observations over the full domain.

Our results also point out the importance of setting the reference level for the catchability coefficient with either the scientific or the commercial data. In particular, when the sample size of the commercial data far exceeds the scientific survey, fixing the reference level with scientific surveys generally results in higher imprecision, due to the smaller sample size. But still, in certain cases, the scientific data may provide absolute information on biomass and fixing the catchability factor associated with the survey data can result in an interpretable measure of index scale (Thorson *et al.*, 2021). Hence, the choice of the reference level could be a matter of trade-offs between precision of inferences and interpretation of the results in terms of scale.

The limits of reallocated catch data

Probably one of the major limits of our approach is that the actual framework ignores the uncertainty that arises from the procedure used to reallocate the catch declarations in space. Obtaining the spatialized CPUE inputs used in the model requires pre-treatment of the commercial catch declaration data to allocate declaration data to VMS positions (Hintzen *et al.*, 2012). Raw data corresponds to fishing operations that are daily aggregated and reported at coarse administrative spatial units (0.5° latitude by 1° longitude rectangles). These declarations are then reallocated uniformly on all GPS locations previously identified as fishing in the vessel path. This procedure has been demonstrated to be robust while being a fast and a pragmatic approach for reallocating landings to VMS pings (Gerritsen and Lordan, 2010; Murray *et al.*, 2013). However, it implies strong hypotheses that may artificially increase or transform the information provided by the data. Typically, the uniform reallocation of catch declarations on all GPS positions identified as fishing may smooth the spatial signal, which could potentially explain the lack of species–habitat relationship obtained from the IM. The effect of such reallocation should be explored in further study to better understand its consequences on model predictions/estimates and further model development should investigate how to mitigate its consequences.

Perspectives

Our work raises some major challenges, which all constitutes exciting tracks for future research.

Data-weighting approaches could be explored further to better control the contribution of the two sources of data and eventually assess if increasing scientific data weight could improve model predictive capacity. Data-weighting methods intend to modify the relative influence of the data sources by assigning or estimating a weight for each data source (Francis, 2017; Punt, 2017; Wang and Maunder, 2017; Punt *et al.*, 2020). Only very few studies have already explored the potential for data weighting in the SDM context (Fletcher *et al.*, 2019). Still, several questions regarding the weight specification remain open or largely debated. For instance, how to rigorously fix/estimate/interpret the weight? Also, when can we consider that a data-weighting approach is relevant or is it only a matter of model misspecification? Some theoretical and modelling development could be highly valuable to provide a generic and rigorous formalization for either data weighting or model correction in the context of SDM (but see for instance the approach provided by Thorson *et al.* (2017b) for composition data in the context of stock assessment models).

Another option would consist in developing an alternative observation model for the commercial CPUE in order to better capture the uncertainty associated with the reallocation procedure. As a general idea, an observation model could be developed to explicitly represent that CPUE are available at the scale of the daily fishing activity (the scale that corresponds to the catch declaration), rather than artificially reallocating uniformly catch declarations on related VMS pings. Doing so, the quantity of information provided by commercial data would be more representative of the information they really contain.

Future work should also seek to better integrate the discrete-choice and econometric analyses emphasizing the complexity of the processes related to the choice of fishing locations. For instance, the sampling process could account for the pluri-specific nature of fisheries (Bourdaud *et al*., 2019) and additional factors other than fish distribution could be included to explain the variability of sampling intensity in space and time (Salas and Gaertner, 2004; Haynie *et al*., 2009; Girardin *et al*., 2017).

Finally, including a temporal dimension in the model and fitting a longer time series looks a fruitful research avenue. Moving to spatio-temporal modelling that would consider temporal autocorrelation in the spatial distribution may be methodologically challenging (Cameletti *et al*., 2013), but represents an exciting step towards a better understanding of the seasonal spatial distribution of fish resources. Indeed, commercial data are often available all along the year, when scientific surveys most often occur once or twice a year. Combining scientific and catch declarations data within an integrated spatio-temporal framework built at an infra-annual time step (e.g. season or month) would allow to complement the gap of information to investigate fish spatio-temporal distribution at a finer temporal scale than what is possible using scientific data only (Bourdaud *et al*., 2017; Pinto *et al*., 2019; Rufener *et al*., 2021). It would offer new opportunities to interpret seasonal patterns of distribution (Kai *et al*., 2017), identify fish functional habitats such as spawning areas (Paradinas *et al*., 2015; Delage and Le Pape, 2016), and provide the required knowledge for protecting those habitats (Schmitten, 1999; Erisman *et al*., 2020).

Supplementary material

All the Supplementary material documents are available at the ICESJMS online version of the manuscript. They provide additional information on the modelling framework (SM1), material and methods for simulations (SM2) and case studies (SM3), results for simulations (SM4), and case studies (SM5).

Authors' contributions

All authors contributed to the conceptualization and methodology of the study. All authors contributed to analysis of findings as well as drafting and revising the manuscript.

Data availability statement

Survey data are available through the DATRAS portal (https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx) with the package 'icesDatras' (https://cran.r-project.org/web/packages/icesDatras/index.html). Logbooks and VMS data are confidential data and they are available on specific request to DPMA. Codes that support the findings of this study are on gitlab and can be given access on request at the address: baptiste.alglave@agrocampus-ouest.fr.

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