

## Combining scientific survey and commercial catch data to map fish distribution

Baptiste Alglave, Etienne Rivot, Marie-Pierre Etienne, Mathieu Woillez,

James Thorson, Youen Vermard

#### ► To cite this version:

Baptiste Alglave, Etienne Rivot, Marie-Pierre Etienne, Mathieu Woillez, James Thorson, et al.. Combining scientific survey and commercial catch data to map fish distribution. ICES Journal of Marine Science, 2022, 79 (4), pp.1133-1149. 10.1093/icesjms/fsac032 . hal-03614713

### HAL Id: hal-03614713 https://hal.science/hal-03614713v1

Submitted on 4 Mar 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

## Combining scientific survey and commercial catch data to map fish distribution

Alglave Baptiste <sup>1, 2, \*</sup>, Rivot Etienne <sup>2</sup>, Etienne Marie-Pierre <sup>3</sup>, Woillez Mathieu <sup>4</sup>, Thorson James T <sup>5</sup>, Vermard Youen <sup>1</sup>

<sup>1</sup> DECOD (Ecosystem Dynamics and Sustainability), IFREMER, Institut Agro, INRAE, Nantes 44980, France

<sup>2</sup> DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, IFREMER, INRAE, Rennes 35042, France

<sup>3</sup> Mathematical Research Institute of Rennes IRMAR, Rennes University, Rennes 35042, France <sup>4</sup> DECOD (Ecosystem Dynamics and Sustainability), IFREMER, Institut Agro, INRAE, Brest 29280, France

<sup>5</sup> Habitat and Ecological Processes Research Program, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112, USA

\* Corresponding author : Baptiste Alglave, email address : <u>baptiste.alglave@agrocampus-ouest.fr</u>

#### Abstract :

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

#### 33 **1** INTRODUCTION

Developing species distribution models (SDM) is critical in marine and fisheries ecology 34 for assessing the relationship between species and their habitat (Guisan and 35 36 Zimmermann, 2000), identifying essential habitats (Paradinas et al., 2015), forecasting 37 population and ecosystems response to environmental changes (Cheung et al., 2009). 38 The development of statistical models to predict fishery resources distribution has 39 received considerable attention (Planque et al., 2011; Thorson et al., 2015a, 2015b; 40 Martínez-Minaya et al., 2018; Moriarty et al., 2020). Recent developments have 41 generalized SDM to analyze biological data representing condition, stomach contents, 42 size structure, and other demography and population dynamics features (Thorson, 2015; 43 Grüss et al., 2020). Ongoing research also seek to integrate individual movement, growth, 44 species interactions into SDM (Kristensen et al., 2014; Thorson et al., 2017a, 2019), 45 although these approaches are "data hungry" and therefore require integrating different sources of data within a single model. 46

47 Scientific survey and commercial catch data consist in two potentially complementary data sources to estimate harvested fish spatial distribution (Pennino et al., 2016). Scientific 48 49 surveys are key data sources in fisheries ecology. They most often benefit from a 50 standardized sampling plan and a constant catchability (Hilborn and Walters, 1992; Ocean 51 Studies Board and National Research Council, 2000; ICES, 2005; Nielsen, 2015). They 52 are generally designed to cover the full geographical extent of specific populations 53 including areas of low or null abundance, and are thus adapted to develop unbiased 54 abundance indices and spatial predictions of species distribution (Rivoirard et al., 2008; 55 ICES, 2012). In addition, they often seek to minimize selectivity in order to sample as 56 many species, size groups and life stages as possible. However, the related expansive 57 charges generally comes at the cost of a relatively low sampling density in space and/or 58 time. For instance, trawl survey can sample a limited number of spatial locations, and 59 most often occur once or twice a year. Thus, they may provide poor information regarding 60 intra-annual variability (Pennino *et al.*, 2016; Rufener *et al.*, 2021) and imprecise estimates 61 of species abundance and distribution (ICES, 2005).

62 Commercial catch declarations (logbooks) data constitute a complementary data source 63 that may benefit of a higher sampling effort than scientific survey. In Europe, catch 64 declarations must be reported in logbooks data for all fishing vessels; besides, geolocation through Vessel Monitoring System (VMS) is mandatory for all fishing boat above 12m long 65 (Hintzen, 2021). Hence, logbook data combined with VMS data can provide high 66 67 resolution maps of Catch Per Unit Effort (CPUE - Gerritsen and Lordan, 2010; Murray et 68 al., 2013) with a relatively dense spatio-temporal sampling within the range of the 69 commercial fleets. However, inferring SDM with commercial data can be challenging as 70 they generally arise from a preferential sampling (PS) behavior, i.e. a sampling that 71 directly or indirectly depends upon the biomass of the target species. Indeed, fishermen 72 tend to target areas with high biomass or may also favor fishing zones based on other 73 criteria (like bottom substrate or distance to the coast for instance - Hintzen et al., 2021) 74 that are indirectly related to the target species abundance. When not properly considered 75 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, 76 77 when the biomass is spatially heterogeneous, ignoring PS may overestimate the spatial 78 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

81 proposed a base framework for estimating PS and applied it to led pollution data in Galicia. 82 The authors extended a standard geostatistical approach within a hierarchical framework 83 where the variable of interest is jointly modelled with the spatial intensity of the sampling 84 effort which also contributes to the inference and accounts for PS towards the variable of 85 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 86 87 a more generic model for ecological applications, which they applied to aerial seal count 88 data. Pennino et al. (2019) applied similar ideas to infer the distribution of shrimps from 89 onboard fishery data.

Provided PS is accounted for, integrated models (IM) appear as an attractive tool to 90 91 combine fishery-independent and fishery-dependent data to infer harvested fish spatial 92 distribution. IM have received considerable attention in the ecological literature (Schaub 93 and Abadi, 2011; Parent and Rivot, 2012; Gimenez et al., 2014). By sharing the 94 information between different data types, IM may provide more accurate estimates and predictions compared with separate analysis of different data types. Recently, Rufener et 95 96 al. (2021) demonstrated the potential of IM to integrate scientific data and onboard 97 observer count data to improve SDM of fishery resources. However, although onboard 98 observer data provide useful complementary information to scientific survey, they 99 generally only represent a small proportion of all sea trips (1% in average for the French 100 observer programs - Cornou et al., 2021). By contrast, the combination of commercial 101 catch declarations in logbooks with VMS data provides a more extensive data source to 102 map fish spatial distribution. Furthermore, the potential of embedding PS within a 103 hierarchical SDM to integrate catch declaration data and scientific survey is still an open 104 challenge and new methodology are required to handle PS behaviors 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 behavior.

110 To assess the challenges, the benefits and also the limits of the approach, we evaluate 111 the performance of our IM based on simulated data. Simulations are primarily designed 112 to assess the respective contribution of each data source to inference for different model 113 configurations. We first evaluate how the balance between the commercial and scientific 114 sample sizes affect the model outputs. Because the commercial data may often only 115 partially cover the distribution area of a targeted species, we assess how this issue may 116 affect the quality of estimation and how scientific data may contribute to reduce the effect 117 of this gap in the commercial data. Introducing PS within an IM framework involves adding 118 new parameters, complexifying the model structure and then increasing the computational 119 cost. We therefore assess how perform a more parsimonious model that would ignore PS. 120 Last, in addition to the PS, the fishing locations can be controlled by other factors 121 independent from the species distribution (e.g. logistical constraints, management 122 regulations – see Girardin et al., 2017; Ducharme-Barth et al., 2022). We therefore assess 123 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

- 128 framework to handle multiple commercial fleets with potentially distinct PS intensities and
- 129 different fishing behaviors.

#### 130 **2 MATERIAL AND METHODS**

#### 131 **2.1 Spatial integrated model**

Below we provide the core elements of the modelling approach. Additional details are 132 provided in supplementary material (SM 1). The model is structured in four layers: 133 134 observations (here commercial and scientific CPUE in weight per unit of effort), sampling 135 process, latent field (here fish biomass relative density) and parameters (Figure 1 - all 136 notations are available in SM 1.1, Table S1). Sampling process is usually ignored in 137 hierarchical models as it is mostly considered independent of the quantity of interest, and 138 then has no consequence on the estimation procedure (Diggle et al., 2010). Here, the 139 spatial distribution of commercial fishing is explicitly modelled as a inhomogenous Poisson 140 point process whose intensity may depend on the biomass field and contributes to the 141 likelihood. The observation processes of scientific and commercial data are conditional 142 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, Figure S2.1 or SM 3.1, 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.

#### 153 2.1.1 Latent field of relative biomass

The fish biomass relative density S (eq. (1) – (2)) is modeled through a latent log Gaussian 154 155 spatial field defined on the same discrete spatial domain as the point process. The mean 156 of the Gaussian field depends on environmental covariates through a log link where the 157 linear predictor combines an intercept  $\alpha_s$ , the linear effect of environmental covariates 158  $\Gamma_{S}(x)$  (effects captured by the corresponding fixed parameters  $\beta_{S}$  representing the species-habitat relationship). The remaining spatial variation is accounted for through a 159 160 zero-mean Gaussian random field (GRF) denoted  $\delta(x)$  parameterized with a Matérn correlation function  $M(x, x'; \kappa, \phi)$ , characterized by the shape  $\kappa$  and the scale  $\phi$  (Cressie, 161 162 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  $\rho$  is the distance for which the correlation 163 164 between points is near 0.1.

165 
$$\log(S(x)) = \alpha_S + \Gamma_S(x)^T \cdot \beta_S + \delta(x)$$
(1)

$$\delta(x) \sim GRF(0, M(x, x'; \kappa, \phi))$$
(2)

#### 167 2.1.2 Sampling process

Recent literature has emphasized the complexity of the targeting behavior processes (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, 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.

174 Let us denote  $X_{com j}$  the spatial point process where commercial vessels of fleet *j* are 175 identified as fishing. In the following, all vessels in the same commercial fleet are assumed to have homogeneous behaviors. Following Diggle *et al.* (2010), the set of fishing locations are modeled conditionally on *S*, as a inhomogeneous Poisson point process with piecewise constant intensity  $\lambda_i(x)$  (eq. (3) - (4)).

179 
$$X_{com\,j} \sim \mathcal{IPP}(\lambda_j(x)) \qquad (3)$$

180 
$$\log(\lambda_j(x)) = \alpha_{Xj} + b_j \cdot \log(S(x)) + \eta_j(x)$$
(4)

For any fleet *j*, intensity  $\lambda_j(.)$  of the Poisson point process is modeled as a log-linear combination of the intercept  $\alpha_{Xj}$ , 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  $\kappa$  and  $\phi$ . All parameters  $\alpha_{Xj}$ ,  $b_j$  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 harbor, logistical constraints, management regulations - spatial closures, 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(.).

193 In that sense, a zero value for  $b_j$  indicates that the choice of the sampling locations does 194 not depend on the fish biomass relative density but only on the spatial random effect.

195 In addition to  $b_j$ , a dimensionless spatial metric was developed to quantify the strength of 196 PS (SM 1.3).

#### 197 2.1.3 Observation process

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

203 Observations are modelled through a zero-inflated lognormal model conditionally on 204 biomass S(x) in cell x (eq. (5-6)). The model is derived from Thorson *et al.* (2016) or 205 Thorson (2018). We assume that the expected catch  $\mu_i(x)$  for any fleet/data source *j* in the cell x depends on the latent field value S(x) and a catchability coefficient  $q_i$  (eq. (5)). 206 207 A zero catch (y = 0) is modeled as a Bernoulli random variable with parameter  $exp(-e^{\xi_j} \cdot$  $\mu_j(x)$ ), where  $\xi_j$  is the parameter controlling the intensity of zeros relatively to the 208 209 expected catch (eq. (6)). Then,  $\mu_i(x)$  being fixed, the higher (resp., the lower)  $\xi_i$ , the lower (resp. the higher) the probability of obtaining a zero-catch. 210

The distribution of a positive catch y > 0 at a given x is defined as the combination of the probability of obtaining a non-zero 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  $\sigma_j$ . This formulation allows to represent the zero

215 catch while assuring that the expected catch still equals  $\mu_j(x)$ .

216 
$$\mu_j(x) = q_j \cdot S(x) \tag{5}$$

217 
$$P(Y = y | x, S(x)) = \begin{cases} \exp(-e^{\xi_j} \cdot \mu_j(x)) & \text{if } y = 0\\ \left(1 - \exp(-e^{\xi_j} \cdot \mu_j(x))\right) \cdot L\left(y, \frac{\mu_j(x)}{\left(1 - \exp(-e^{\xi_j} \cdot \mu_j(x))\right)}, \sigma_j^2\right) & \text{if } y > 0 \end{cases}$$
(6)

219 Per se, catchability  $q_i$  are not identifiable as there is no information in the model to 220 estimate the absolute scale of S. Commercial catches and/or scientific surveys will be only 221 informative about fish biomass relative density and additional information must be 222 provided to ensure statistical identifiability. If only one data type feeds the model (only 223 scientific or commercial data), relative catchability is fixed to 1 and the spatial random field 224 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 225 226 estimated relatively to the first one through a scaling factor  $k_i$  (eq. (7)).

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

As it is illustrated further in the simulation-estimation study (see section 3.1.1), the choice of the reference level can have important consequences on the precision of estimation.

230 2.1.4 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).

# 235 2.1.5 Integrated model validation 236 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

238 framework, the key question is whether integrating commercial data in addition to scientific 239 data will complement or will disrupt the inferences obtained from the scientific data, 240 considered as a reference source of information. To address this issue, we propose a 241 validation procedure based on the consistency check initially developed by Rufener et al. 242 (2021) and designed to check whether estimates obtained from the IM are consistent with 243 those obtained from the model fitted to scientific data only. The procedure would reject 244 consistency if the parameters estimates from the IM fall outside the 95% confidence region 245 of parameters estimates from scientific data only (see SM 1.5 for more details on the 246 procedure). This validation step is applied to both simulations and case studies.

#### 247 **2.2 Simulation-estimation experiments**

248 We conducted simulation-estimation experiments to assess the performance of the 249 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 250 parameterized to tailor the case studies described hereafter. All scenarios and 251 252 configurations are repeated 100 times so as to capture the variability between replicates. 253 Simulation-estimation experiments were specifically designed to address four questions 254 detailed below. In all cases, commercial data were simulated with various levels of PS 255 (b = 0 for uniform sampling, b = 1 for moderate PS, b = 3 for strong PS) to assess the 256 effect of PS on model's performance (Figure 2).

257

#### (**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, 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. eq. (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?

276 While scientific surveys are supposed to cover the full population distribution area, partial 277 coverage of the area by commercial fishing boats may arise from different sources like 278 spatial management closures (e.g. box closure) or too expensive travels from the coast. 279 To assess how a partial coverage by commercial data can affect estimates, we simulated 280 data with the commercial sampling intensity arbitrarily fixed to 0 in a fixed 9x9 box (15% 281 of the domain) while some biomass and some scientific samples are still simulated in this 282 area. We compared estimates of the biomass in the entire area with those obtained with 283 commercial data available on the whole domain.

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

293 Fishing locations potentially depend on many other factors independent from the species 294 distribution (Salas and Gaertner, 2004; Haynie et al., 2009; Girardin et al., 2017). To 295 assess how such process blurring strict PS may affect the quality of inferences, we 296 simulate data with a sampling intensity that depends on both the biomass distribution (PS) 297 and an additional spatial random terms  $\eta_f(.)$  independent from the biomass distribution 298 (eq. (4); see Table 1 for more details on  $\eta_f(.)$  parameterization), and compare the 299 inferences obtained from a data set simulated with strict PS ( $\eta_f(.) = 0$  on the full domain). 300 Note that for questions Q1, Q2 and Q3, the random effect  $\eta$  was fixed to 0 in simulations 301 (but it is still estimated in the estimation model), so that the sampling process only 302 depends on the distribution of biomass.

303 2.2.1 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  $\rho$  as these parameters are meaningful for understanding species distribution. The precision of the spatial predictions was studied with the mean squared prediction error

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).

#### 317 **2.3 Case studies**

We applied the approach on three case studies of demersal fisheries in the Bay of Biscay: the common sole (*Solea solea*, Linnaeus, 1758), the hake (*Merluccius merluccius*, Linnaeus, 1758) and the squids (Loliginidae family). These case studies were selected because they emphasize different intensities of preferential sampling. 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, 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 contrastedlevel of PS.

#### 331 2.3.1 Survey data

332 Scientific data (CPUE, in kg/hour - Figure 3) were derived from the Orhago survey for common sole and EVHOE survey for hake and squids (ICES, 2020a). The sampling 333 334 density (number of data points / km<sup>2</sup>) of those two surveys revealed representative of the 335 sampling density of the main European trawl surveys from the DATRAS database (see 336 SM 3.2). In comparison, commercial data used in the case studies are denser by 2 orders 337 of magnitude. Scientific data was aligned on commercial data by filtering only individuals 338 above the minimum landing size when available (24 cm for sole, 27 cm for hake - ICES, 339 2020). The Orhago survey provides 49 samples for 2017 and 2018 and the EVHOE survey 340 provides 86 samples for 2014 and 2015.

#### 341 **2.3.2 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/hour). 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.

#### 352 2.3.3 Habitat covariates

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).

#### 357 2.3.4 Model configurations

358 As for the simulation-estimation experiments, the models of the case studies were fitted 359 under different configurations. To assess the information brought by each dataset, we 360 compared the model fitted to scientific data only, to commercial data only and to both 361 scientific and commercial data. To assess the effect of PS on model outputs, we compared 362 the IM accounting for PS (b is estimated) with the IM where PS is ignored (b is fixed to 0). 363 For the sole case study, we compared results obtained from the IM by considering one 364 homogeneous or two distinct fleets with specific catchability and targeting parameters. 365 Note that splitting one fleet in 2 distinct fleets is performed through a PCA coupled with a 366 HCPC analysis on vessels characteristics data derived from both logbooks and VMS data. 367 All the clustering analysis is described in SM 3.9.

#### 368 2.3.5 Model evaluation

Uncertainty of the predictions are quantified through the coefficient of variation and all estimates (e.g. fixed parameters, total biomass) are represented with related 95 % confidence intervals. We assess the consistency of the IM through the statistical tests described in section 2.1.5 and in SM 1.5. Finally, the different IM are compared through a 5-fold cross validation, and model performance was quantified based on two metrics: the  $MSPE_{fit}$  that measures goodness of fit (MSPE – mean squared prediction error), and the PCV that measures predictive capacity (see SM 3.10 for more details on the metrics and 376 guidelines for interpretation). For both metrics, the lower the values, the better the model377 fits/predicts the data.

#### 378 **3 Results**

#### 379 3.1 Simulations

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

#### 382 **3.1.1 Contribution of each data source in the integrated model**

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, 1<sup>st</sup> row), and the variance of estimations decreases with scientific sample size. Note that the specieshabitat 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,  $2^{nd}$  row).

399 As expected, the contribution of each data sources in the IM directly depends on the 400 balance in the sample size. When sample size is balanced between the data sources, 401 then integrating the two data sources in the model systematically improves the inferences 402 with regards to situations where only one data source is analyzed. For instance, for large 403 commercial and scientific sample size (com.L sci.L) and no PS, the precision is 1.5 higher 404 (i.e. the MSPE is 1.5 lower) for the IM compared to single-data models (either scientific or commercial - Figure 4, 3<sup>rd</sup> row, 1<sup>st</sup> column). However, when the sample sizes are 405 406 unbalanced, the data source with the larger sample size (here commercial data) 407 dominates inference and integrating another data source with a smaller sample size (here 408 scientific data) contributes to a much lesser extent to inference. See for instance the 409 situation where commercial sample size is large and scientific sample size is small (com.L sci.S - Figure 4, 3<sup>rd</sup> row, 1<sup>st</sup> column). In this case, the performances of the model 410 411 fitted to commercial data alone - with reference level fixed to commercial data - are very 412 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,  $3^{rd}$  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; 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). 422 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, 1<sup>st</sup> row). When the 423 424 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 425 426 to scientific data. When defining scientific data as reference level, the intercept of the 427 latent field of relative biomass is estimated from the few scientific samples and resulting 428 estimates are less precise than when defining the reference level with a more numerous 429 data source (here commercial data). This is also true - to a lesser extent - for spatial predictions (Figure 4,  $3^{rd}$  row). 430

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).

#### 434 **3.1.2** 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 435 436 provide valuable information to predict biomass spatial distribution whatever the PS intensity is (Figure 5, 2<sup>nd</sup> column). When sampling is not preferential (data simulated with 437 438 b = 0), a partial coverage of the distribution area produces on average 1.5 less precise spatial predictions but estimates remain unbiased (Figure 5, 3<sup>rd</sup> row, comparing 1<sup>st</sup> and 439 440  $2^{nd}$  column). When sampling is preferential (either moderate or high), biomass estimates 441 are slightly underestimated. Integrating scientific data in the analysis does not correct this 442 bias.

Finally, all model configurations allow for unbiased and precise estimation of the specieshabitat parameters  $\hat{\beta}_s$  whether or not there is a partial coverage of the domain (see SM 445 4.1) and overall almost all IM are consistent with scientific-based model (SM 4.2.2).

446 **3.1.3 How does ignoring PS impact inferences?** 

447 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 448 increases in the truth (Figure 5,  $3^{rd}$  column). With no surprise, when data are generated 449 450 with no PS (b = 0), ignoring PS in the estimation procedure has no effect on the estimation 451 performance. When PS is moderate, total biomass estimates are 5 % overestimated (b =452 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, 1<sup>st</sup> row, 3<sup>rd</sup> column). 453 454 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 455 when accounting for PS (Figure 5, 3<sup>rd</sup> row, 1<sup>st</sup> column). SM 4.4 (Figure S4.4.1) presents 456 457 maps comparing a simulated biomass field and model predictions obtained by considering 458 or ignoring PS when b = 3. The areas with high biomass values (i.e. where commercial 459 sampling is dense) are well predicted by the models accounting for PS or not. The main 460 differences are localized in poorly sampled areas where biomass is low. Accounting for 461 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, Figure S4.4.2). 462 463 Finally, from a computational point of view, accounting for PS on average multiplies by 4

463 Finally, from a computational point of view, accounting for PS on average multiplies by 4 464 the computational time (see SM 4.5).

#### 465 **3.1.4 Effect of other spatially structured processes affecting fishing locations**

466 As expected, precision of estimates are deteriorated when fishing locations actually depend upon a combination of biomass distribution (PS) and other mechanisms (here 467 captured by a spatially structured random term - Figure 5, 4<sup>th</sup> column). In this case, the 468 469 IM still provides valuable inferences on fish distribution, fish total biomass and estimates 470 of b, although estimations are less accurate than the base case. For instance, MSPE are 5 times lower when nothing else than PS affects sampling locations compared with a case 471 472 where sampling locations depend on both PS and other independent spatial processes (Figure 5, 3<sup>rd</sup> row, 1<sup>st</sup> and 4<sup>th</sup> column). But interestingly, the weight of scientific data 473 increases when the sampling distribution of commercial data is blurred by spatial 474 475 processes independent from biomass spatial distribution. MSPE and relative bias 476 provided by the IM are both 1.4 smaller compared to those obtained when the model is 477 fitted to commercial data only.

#### 478 **3.2 Case studies**

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

#### 481 **3.2.1** Contribution of each dataset to the inferences

482 Almost all the case studies successfully passed the consistency test between the IM and483 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 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 provide 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).

#### 498 **3.2.2** *Preferential sampling and other processes affecting fishing locations*

499 In this section and related SM (SM 5.7 to SM 5.10), we focus on results from the IM only. 500 For the three case studies, estimates of b are positive, suggesting sampling by fishermen 501 is preferential towards high biomass density areas. The hake case study has the lowest 502 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 503 504 how it varies in space, refer to SM 5.7. In all case studies, the spatial random term  $\eta$  in 505 the sampling process turned out to be spatially structured (SM 5.8) and captures 25% to 506 97% of the spatial variability of fishing locations (SM 5.9). This highlights the importance 507 of other spatial mechanisms in the choice of fishing locations compared to strict PS 508 towards biomass distribution.

509 Consistently with simulations, the higher the PS intensity, the higher the differences 510 between inferences obtained with and without considering PS. When comparing biomass 511 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).

518 When the estimated PS intensity is high (i.e. in the case of squids) accounting for PS can 519 improve model goodness-of-fit and predictive capacity (SM 5.10).

#### 520 **3.2.3** Benefits of considering different fleets in the estimation model

521 Based on the sole case study, we demonstrate the capacity of the model to integrate 522 multiple commercial fishing fleets, each with specific parameters (catchability and 523 targeting). In the sole case studies, considering two different fleets in the IM (instead of 524 one homogeneous) improves goodness-of-fit towards scientific data (SM 5.11, y-axis) and 525 modifies spatial predictions (SM 5.12).

#### 527 4 DISCUSSION

#### 528 Main findings

529 Combining multiple sources of data to build more informative spatio-temporal models for 530 fish distribution is a major challenge in fishery ecology. Commercial catch per unit effort 531 data have long been recognized as a valuable source of information eventually highly 532 complementary to scientific survey data. But the complexity of the mechanisms driving 533 the way fishermen sample in space and time make the combination of scientific and 534 commercial data challenging.

535 In this paper, we provide a hierarchical framework to integrate scientific surveys and 536 commercial catch declaration data to infer species distribution while considering the effect 537 of PS on fishing points distribution. The new model allows for exploring and questioning 538 the challenges raised by such integration. The benefit but also the limits of the new 539 approach were evaluated using simulations and through the application of the model to three contrasted demersal case studies (sole, hake and squids) of the Biscay Bay fishery. 540 541 Both simulations and case studies demonstrate that ignoring PS in the inference may be 542 highly detrimental when the intensity of PS is strong. The present framework can serve 543 as a tool to assess the benefit of including PS in analysis, depending on the intensity of 544 PS but also on the modelling objectives. As already shown in previous studies (Conn et 545 al., 2017; Pennino et al., 2019), when PS actually occurs in commercial catches, ignoring 546 this process may bias inferences on total biomass estimates. Even if ignoring PS may not 547 hamper the capacity to detect areas of high biomass, the biomass in low-density areas 548 may be overestimated. Therefore, if the objective is to compute biomass indices integrated 549 over a large area, then it might be worth accounting for PS to avoid biased results. By

550 contrast, if the objective is to identify hotspots, the benefits of considering PS may be 551 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 552 553 behavior among species and fleets. Low PS was revealed for hake, while a moderate and 554 strong PS was revealed for sole and squids, respectively, which is consistent with the 555 expert knowledge on the behavior of those bottom trawls fleets (Y. Vermard, com. pers.). 556 Results also demonstrate the capacity of the framework to integrate commercial catch 557 data from multiple fleets, and the benefits for the quality of inferences when those fleets 558 have different features such as distinct catchabilities or targeting behaviors. For the sole case study, this approach proves useful to distinguish two segments in the bottom trawl 559 560 fleet, which improved model outputs. This framework could be extended to more than two 561 fleets and combined with other studies analyzing fleets structure (Pelletier and Ferraris, 562 2000; Ferraris, 2002; Stephens and MacCall, 2004; Deporte et al., 2012; Winker et al., 563 2013; Okamura et al., 2018).

#### 564 Challenges in modelling PS

565 Still, modelling the spatial distribution of commercial fishing locations remains highly 566 challenging (Hintzen, 2021; Hintzen et al., 2021). Our framework is shaped to integrate 567 data from homogeneous fishing fleets supposed to share the same fishing behavior, which 568 simplifies the modelling of the non-uniform spatial intensity of fishing for each fleet. We 569 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 570 571 departure from this hypothesis may obviously exist in the truth. For instance, the intensity 572 of PS could vary in space such as in Conn et al. (2017) who considered that the degree

573 of PS could change across the landscape. On the other hand, however, the log-log linear 574 assumption is easy to implement in other software including the VAST R package used 575 for operational assessments in some management regions (Thorson *et al.*, 2019).

576 Of course, many other factors may drive the spatial intensity of fishing, and those were 577 simply captured in our model through an additional spatial random term. For instance, 578 fishers' behavior may depend on prior knowledge of fish spatial distribution, on information 579 sharing within fishing cooperatives, on expected distribution of bycatch species, or 580 logistical constraints (e.g., transit costs) (Salas and Gaertner, 2004; Haynie *et al.*, 2009; 581 Girardin *et al.*, 2017). Targeting behavior may also be directed toward an assemblage of 582 species rather than toward a single species (Bourdaud *et al.*, 2019).

583 The random effect should be able to capture additional variations whenever the departure 584 from a continuous Gaussian random field is not too high. If not, for instance in the case of 585 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 586 587 misspecification. We did not detect such misspecification in our case study, but we 588 recommend that future analyses based on fishery-dependent data present a log-log plot 589 between sampling intensity and predicted biomass density to diagnose strong departure 590 from model hypothesis.

591 Still, some non-spatial targeting has been reported from multi-species catch records 592 (Stephens and MacCall, 2004; Okamura *et al.*, 2018). Efforts to integrate these methods 593 into spatio-temporal models are underway (Thorson *et al.*, 2016), although these methods 594 have not previously been extended to jointly analyzing multi-species fishery and survey 595 data.

#### 596 Relative contribution of scientific and commercial data

597 Our analysis exemplifies that a key issue in such integrated modelling exercise is to get a 598 sensible evaluation of the relative contribution of the different sources of data in 599 estimation. In particular, critical issues with the IM are whether the different data sources 600 provide eventually highly unbalanced quantity of information (then the inferences are fully 601 dominated by one of the data sources; Fletcher *et al.*, 2019) and whether they provide 602 complementary or conflicting information to the final inferences (Saunders *et al.*, 2019; 603 Zipkin *et al.*, 2019; Peterson *et al.*, 2021).

604 We implemented a likelihood ratio-test (Rufener et al., 2021) to check for model 605 consistency between the IM and the scientific-based model. In most cases, models 606 passed the consistency check successfully, although it was rejected in some cases. Some 607 further analysis should investigate in detail the reasons of these inconsistencies as they 608 could probably shed light on some new research avenues for model improvement. For 609 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 610 611 the observation process of commercial data might partly explain these inconsistencies.

612 Simulations revealed that when scientific data and commercial data have balanced 613 sample size, they both contribute to inference and the IM will provide better biomass 614 predictions than models based on single-data set. As expected, when the sample size of 615 commercial data far exceeds scientific data, inference about spatial patterns is mainly 616 driven by the commercial data. In the three case studies, we used commercial data with 617 sample sizes that far exceed the scientific one. In that case, scientific data have relatively 618 limited weight in the final inference. Still, they bring valuable information in areas that are 619 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.

626 Our results also point out the importance of setting the reference level for the catchability 627 coefficient with either the scientific or the commercial data. In particular, when the sample 628 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 629 630 size. But still, in certain cases, the scientific data may provide absolute information on 631 biomass and fixing the catchability factor associated with the survey data can result in an 632 interpretable measure of index scale (Thorson et al., 2021). Hence, the choice of the 633 reference level could be a matter of tradeoffs between precision of inferences and 634 interpretation of the results in terms of scale.

#### 635 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 643 locations previously identified as fishing in the vessel path. This procedure has been 644 demonstrated to be robust while being a fast and a pragmatic approach for reallocating 645 landings to VMS pings (Gerritsen and Lordan, 2010; Murray et al., 2013). However, it 646 implies strong hypotheses that may artificially increase or transform the information 647 provided by the data. Typically, the uniform reallocation of catch declarations on all GPS 648 positions identified as fishing may smooth the spatial signal, which could potentially 649 explain the lack of species-habitat relationship obtained from the IM. The effect of such 650 reallocation should be explored in further study to better understand its consequences on 651 model predictions/estimates and further model development should investigate how to 652 mitigate its consequences.

#### 653 **Perspectives**

654 Our work raises some major challenges which all constitutes exciting tracks for future 655 research.

656 Data-weighting approaches could be explored further to better control the contribution of 657 the two sources of data and eventually assess if increasing scientific data weight could 658 improve model predictive capacity. Data-weighting methods intend to modify the relative 659 influence of the data sources by assigning or estimating a weight for each data source 660 (Francis, 2017; Punt, 2017; Wang and Maunder 2017; Punt et al., 2020). Only very few 661 studies have already explored the potential for data weighting in the SDM context 662 (Fletcher et al., 2019). Still, several questions regarding the weight specification remain 663 open or largely debated. For instance, how to rigorously fix/estimate/interpret the weight? 664 Also, when can we consider that a data-weighting approach is relevant or is it only a matter 665 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).

669 Another option would consist in developing an alternative observation model for the 670 commercial CPUE in order to better capture the uncertainty associated with the 671 reallocation procedure. As a general idea, an observation model could be developed to 672 explicitly represent that CPUE are available at the scale of the daily fishing activity (the 673 scale that corresponds to the catch declaration), rather than artificially reallocating 674 uniformly catch declarations on related VMS pings. Doing so, the quantity of information 675 provided by commercial data would be more representative of the information they really 676 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, 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).

#### 697

#### 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).

#### 702

#### **ACKNOWLEDGMENTS**

The authors are grateful to the Direction des pêches maritimes et de l'aquaculture (DPMA)
and Ifremer (Système d'Informations Halieutiques - SIH) who provided the aggregated
VMS data. The findings and conclusions of the present paper are those of the authors.

The authors thank David Eme who provided tidy environmental covariates data as well as Kasper Kristensen, Jean-Baptiste Lecomte, Louise Day and Pierre-Yves Hernvann for their feedbacks and their highly valuable advice. The authors thanks also Maxime Olmos, John Best, and two anonymous reviewers whose feedbacks greatly improved the manuscript.

#### 711 DATA AVAILABILITY STATEMENT

712 Survey data are available through the DATRAS portal (https://www.ices.dk/data/data-713 portals/Pages/DATRAS.aspx) with the package 'icesDatras' (https://cran.r-714 project.org/web/packages/icesDatras/index.html). Logbooks and VMS data are 715 confidential data and they are available on specific request to DPMA. Codes that support 716 the findings of this study are on gitlab and can be given access on request at the address: 717 baptiste.alglave@agrocampus-ouest.fr.

#### **FIGURES AND TABLES**



Figure 1. Diagram of the spatial integrated model including preferential sampling for

723 commercial data. Locations of scientific trawls do not contribute directly to the likelihood.



Figure 2. Maps of simulated commercial sampling points obtained for three values of preferential sampling (b=0, b=1, b=3). Blue scale: values of the simulated biomass field. Dots: fishing points. For b = 0, the targeting metric  $T_i(x) = 1$ . For b = 1,

728	$\arg\max T_j(x)=12,$	$q_{50\%}\{T_j(x)\} = 0.4$ . For $b = 3$ , arg max $T_j(x) = 80$ , $q_{50\%}\{T(x)\}$	=
729	x	0.002 (SM 1.3).	





732 733 Figure 3. Map of scientific samples (black dot) and commercial sampling distribution 734 (red color scale – unit: fishing hours). Note that all scientific hauls last around 30 735 minutes. Black lines - limits of the spatial domains covered by the scientific survey 736 (Orhago and EVHOE) that delineate the study area. Left – Hake, November 2014 (EVHOE; commercial data from otter bottom trawls targeting demersal species 737 738 OTB\_DEF). Middle – Sole, November 2017 (Orhago; commercial data from otter bottom 739 trawls targeting demersal species OTB\_DEF). Right – squid, year 2015 (EVHOE; 740 commercial data from otter bottom trawls targeting cephalopods OTB\_CEP).



743	Figure 4. Performance metrics obtained for various commercial and scientific data
744	sample size. Column: intensity of the preferential sampling in simulated data. x-axis: 5
745	combinations of commercial and scientific sample size. 'com' stands for commercial, 'sci'
746	stands for scientific, S stands for small sample size (50), M stands for medium sample
747	size (400), L stands for large sample size (3000). Colors: model configurations.
748	Integrated_q.com: integrated model with catchability fixed to 1 for commercial data;
749	Integrated_q.sci: integrated model with catchability fixed to 1 for scientific data. Boxplots
750	represent the variability among the 100 replicates.
751	



753 754

755 Figure 5. Performance metrics obtained in different data and model configurations. Red 756 points: mean value. 1<sup>st</sup> column: no discrepancy between simulation and estimation. 2<sup>nd</sup> column: commercial data do not cover a 9 x 9 zone of the grid.  $3^{rd}$  column: b is 757 arbitrarily fixed to 0 in the estimation models. 4<sup>th</sup> column: data simulated with a random 758 759 effect n in the sampling intensity process. In all configurations, simulations are conducted for three levels of preferential sampling (x-axis: b = 0, b = 1, b = 3). Colors: 760 data sources used in the integrated model for inferences. Integrated q.com: integrated 761 762 model with catchability fixed with commercial data. Boxplots represent the variability 763 764 among the 100 replicates.



Figure 6. Prediction of the relative biomass for each case study. 1<sup>st</sup> column: model
 fitted to scientific data only; 2<sup>nd</sup> column: integrated model accounting for PS; 3<sup>rd</sup>
 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 integrated model so that all maps are in the same scale.



773Figure 7. Comparison of relative difference in biomass spatial predictions (calculated as774 $(S_{b_{fix}}(x) - S_{b_{est}}(x))/S_{b_{est}}(x))$  in space (left) and of total biomass (sum on the spatial775domain; right) obtained with the integrated models from the 3 case studies when776accounting or not for preferential sampling. b\_est: PS is estimated. b\_fix: PS is not777accounted for.

#### Table 1: Simulations

General simulations description												
Biomass field	Depends on one continuous covariate ( $\Gamma_{S}$ ) and one random spatial effect ( $\delta$ ). Simulated within a 25 x 25 grid. Both are simulated independently through a GRF with Matérn covariance function. Their range ( $\rho$ ) 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 <i>et al.</i> (2011).											
Scientific data	Random stratified plan within 4 strata (see Figure S2.1) Catchability fixed					to 1 Simulated with 10% of zeroes $(\xi_i = 0)$						
Commercial data	Simulated according to three PS levels (i.e. three values for <i>b</i> - see Figure 2). - <i>b</i> = 0: commercial sampling is not preferential; - <i>b</i> = 1: preferential sampling is moderate, commercial vessels mainly target areas where fish biomass is high; - <i>b</i> = 3: commercial sampling is highly preferential and vessels strongly target zones where biomass is high. $\eta$ is set to 0 for Q1, Q2, Q3. For Q4, $\eta$ is set to tailor the sole case study. The range of $\eta$ is set to 40 (4 times the range of $\delta$ ), the marginal variance is set to 5 (5 times the marginal variance of $\delta$ ). 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				
<b>Question 1:</b> How do each data source contribute to inferences?	0,1,3	50	50, 400, 3000	Full	No	Scientific only, commercial only, both	yes	Scientific or Commercial				
	0,1,3	50, 400, 3000	3000	Full	No	Scientific only, commercial only, both	yes	Scientific or Commercial				
<b>Question 2</b> : How does a partial coverage of the study area by the commercial data affect the quality of the estimation?	0,1,3	50	3000	No fishing in a 9x9 cells box	No	Scientific only, commercial only, both	yes	Commercial				
<b>Question 3</b> : What is the cost of ignoring PS in estimation when sampling is preferential?	0,1,3	50	3000	Full	No	Scientific only, commercial only, both	no ( <i>b</i> fixed at 0)	Commercial				
<b>Question 4</b> : How does the estimation perform when additional processes other than PS drive the fishing locations?	0,1,3	50	3000	Full	Yes	Scientific only, commercial only, both	yes	Commercial				

#### 782 **REFERENCES**

783

- Abbott, J., Haynie, A., and Reimer, M. 2015. Hidden Flexibility: Institutions, Incentives, and the Margins of Selectivity in Fishing. Land Economics, 91: 169–195.
   Banerice, S., Carlin, B. P., and Colfand, A. F. 2014. Hierarchical modeling and analysis for
- Banerjee, S., Carlin, B. P., and Gelfand, A. E. 2014. Hierarchical modeling and analysis for
   spatial data. CRC press.
- Bourdaud, P., Travers-Trolet, M., Vermard, Y., Cormon, X., and Marchal, P. 2017. Inferring
  the annual, seasonal, and spatial distributions of marine species from
  complementary research and commercial vessels' catch rates. ICES Journal of Marine
  Science, 74: 2415–2426.
- Bourdaud, P., Travers-Trolet, M., Vermard, Y., and Marchal, P. 2019. Improving the
  interpretation of fishing effort and pressures in mixed fisheries using spatial overlap
  metrics. Canadian Journal of Fisheries and Aquatic Sciences, 76: 586–596.
- Cameletti, M., Lindgren, F., Simpson, D., and Rue, H. 2013. Spatio-temporal modeling of
   particulate matter concentration through the SPDE approach. AStA Advances in
   Statistical Analysis, 97: 109–131.
- Cheung, W. W., Lam, V. W., Sarmiento, J. L., Kearney, K., Watson, R., and Pauly, D. 2009.
   Projecting global marine biodiversity impacts under climate change scenarios. Fish and fisheries, 10: 235–251. Wiley Online Library.
- Conn, P. B., Thorson, J. T., and Johnson, D. S. 2017. Confronting preferential sampling when
   analysing population distributions: diagnosis and model-based triage. Methods in
   Ecology and Evolution, 8: 1535–1546.
- 804 Cornou, A.-S., Quinio-Scavinner, M., Sagan, J., Cloâtre, T., Dubroca, L., and Billet, N. 2021.
  805 Captures et rejets des métiers de pêche francais Résultats des observations à bord 806 des navires de pêche professionnelle en 2019. Ifremer.
- 807 Cressie, N. A. 1993. Statistics for spatial data. John Willy and Sons. Inc., New York.
- B08 Delage, N., and Le Pape, O. 2016. Inventaire des zones fonctionnelles pour les ressources
  B09 halieutiques dans les eaux sous souveraineté française. Première partie: définitions,
  B10 critères d'importance et méthode pour déterminer des zones d'importance à
  B11 protéger en priorité. Rapport de recherche. Pôle halieutique AGROCAMPUS OUEST,
  B12 Rennes.
- Deporte, N., Ulrich, C., Mahévas, S., Demanèche, S., and Bastardie, F. 2012. Regional métier
  definition: a comparative investigation of statistical methods using a workflow
  applied to international otter trawl fisheries in the North Sea. ICES Journal of Marine
  Science, 69: 331–342. Oxford University Press.
- B17 Diggle, P. J., Menezes, R., and Su, T. 2010. Geostatistical inference under preferential
  B18 sampling. Journal of the Royal Statistical Society: Series C (Applied Statistics), 59:
  B19 191–232.
- Biggle, P. J. 2013. Statistical analysis of spatial and spatio-temporal point patterns. CRC
   press.
- Bucharme-Barth, N. D., Grüss, A., Vincent, M. T., Kiyofuji, H., Aoki, Y., Pilling, G., Hampton, J.,
   *et al.* 2022. Impacts of fisheries-dependent spatial sampling patterns on catch-per-

- 824 unit-effort standardization: A simulation study and fishery application. Fisheries 825 Research, 246: 106169.
- 826 Erisman, B. E., Grüss, A., Mascareñas-Osorio, I., Lícon-González, H., Johnson, A. F., and López-827 Sagástegui, C. 2020. Balancing conservation and utilization in spawning aggregation 828 fisheries: a trade-off analysis of an overexploited marine fish. ICES Journal of Marine 829 Science, 77: 148–161. Oxford University Press.
- 830 Ferraris, J. 2002. Fishing fleet profiling methodology. Food & Agriculture Org.
- 831 Fletcher, R. J., Hefley, T. J., Robertson, E. P., Zuckerberg, B., McCleery, R. A., and Dorazio, R. M. 832 2019. A practical guide for combining data to model species distributions. Ecology, 833 100: e02710.
- 834 Francis, R. C. 2017. Revisiting data weighting in fisheries stock assessment models. 835 Fisheries Research, 192: 5–15.
- Gelfand, A. E., Diggle, P., Guttorp, P., and Fuentes, M. 2010. Handbook of spatial statistics. 836 837 CRC press.
- 838 Gerritsen, H., and Lordan, C. 2010. Integrating vessel monitoring systems (VMS) data with 839 daily catch data from logbooks to explore the spatial distribution of catch and effort 840 at high resolution. ICES Journal of Marine Science, 68: 245–252.
- 841 Gimenez, O., Buckland, S. T., Morgan, B. J. T., Bez, N., Bertrand, S., Choquet, R., Dray, S., et al. 842 2014. Statistical ecology comes of age. Biology Letters, 10: 20140698. Royal Society.
- 843 Girardin, R., Hamon, K. G., Pinnegar, J., Poos, J. J., Thébaud, O., Tidd, A., Vermard, Y., et al. 844 2017. Thirty years of fleet dynamics modelling using discrete-choice models: What 845 have we learned? Fish and Fisheries, 18: 638-655.
- 846 Grüss, A., Thorson, J. T., Carroll, G., Ng, E. L., Holsman, K. K., Aydin, K., Kotwicki, S., et al. 847 2020. Spatio-temporal analyses of marine predator diets from data-rich and data-848 limited systems. Fish and Fisheries, 21: 718–739.
- 849 Guisan, A., and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. 850 Ecological modelling, 135: 147–186. Elsevier.
- 851 Haynie, A. C., Hicks, R. L., and Schnier, K. E. 2009. Common property, information, and 852 cooperation: Commercial fishing in the Bering Sea. Ecological Economics, 69: 406-853 413.
- 854 Hilborn, R., and Walters, C. J. (Eds). 1992. Quantitative Fisheries Stock Assessment: Choice, 855 Dynamics and Uncertainty. Springer US. 856
  - https://www.springer.com/gp/book/9780412022715 (Accessed 14 June 2021).
- 857 Hintzen, N. T., Bastardie, F., Beare, D., Piet, G. J., Ulrich, C., Deporte, N., Egekvist, J., et al. 2012. 858 VMStools: Open-source software for the processing, analysis and visualisation of 859 fisheries logbook and VMS data. Fisheries Research, 115: 31–43. Elsevier.
- 860 Hintzen, N. T. 2021. Zooming into small-scale fishing patterns: The use of vessel monitoring 861 by satellite in fisheries science. Wageningen University.
- 862 Hintzen, N. T., Aarts, G., Poos, J. J., Van der Reijden, K. J., and Rijnsdorp, A. D. 2021. 863 Quantifying habitat preference of bottom trawling gear. ICES Journal of Marine Science, 78: 172-184. 864
- 865 ICES. 2005. Report of the Workshop on Survey Design and Data Analysis (WKSAD). Sète, 866 France.
- 867 ICES. 2012. Manual for the international bottom trawl surveys. SISP 1-IBTS Copenhagen, 868 Denmark.

869 ICES. 2020a. International Bottom Trawl Survey Working Group (IBTSWG). ICES Scientific 870 Reports. ICES. http://www.ices.dk/sites/pub/Publication 871 Reports/Forms/DispForm.aspx?ID=37066 (Accessed 28 May 2021). 872 ICES. 2020b. Working Group for the Bay of Biscay and the Iberian Waters Ecoregion 873 (WGBIE). ICES Scientific Reports. ICES. http://www.ices.dk/sites/pub/Publication 874 Reports/Forms/DispForm.aspx?ID=36841 (Accessed 28 May 2021). 875 Kai, M., Thorson, J. T., Piner, K. R., and Maunder, M. N. 2017. Spatiotemporal variation in 876 size-structured populations using fishery data: an application to shortfin mako 877 (Isurus oxyrinchus) in the Pacific Ocean. Canadian Journal of Fisheries and Aquatic 878 Sciences, 74: 1765-1780. 879 Kristensen, K., Thygesen, U. H., Andersen, K. H., and Beyer, J. E. 2014. Estimating spatio-880 temporal dynamics of size-structured populations. Canadian Journal of Fisheries and 881 Aquatic Sciences, 71: 326–336. 882 Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. 2016. TMB: Automatic Differentiation and Laplace Approximation. Journal of Statistical Software, 70: 1–21. 883 884 Le Pape, O., Chauvet, F., Mahévas, S., Lazure, P., Guérault, D., and Désaunay, Y. 2003. 885 Quantitative description of habitat suitability for the juvenile common sole (Solea 886 solea, L.) in the Bay of Biscay (France) and the contribution of different habitats to 887 the adult population. Journal of Sea Research, 50: 139–149. 888 Lindgren, F., Rue, H., and Lindström, J. 2011. An explicit link between Gaussian fields and 889 Gaussian Markov random fields: the stochastic partial differential equation 890 approach. Journal of the Royal Statistical Society: Series B (Statistical Methodology), 891 73: 423–498. Wiley Online Library. Martínez-Minaya, J., Cameletti, M., Conesa, D., and Pennino, M. G. 2018. Species distribution 892 893 modeling: a statistical review with focus in spatio-temporal issues. Stochastic 894 environmental research and risk assessment, 32: 3227–3244. Springer. 895 Moriarty, M., Sethi, S. A., Pedreschi, D., Smeltz, T. S., McGonigle, C., Harris, B. P., Wolf, N., et al. 896 2020. Combining fisheries surveys to inform marine species distribution modelling. 897 ICES Journal of Marine Science, 77: 539–552. Oxford University Press. 898 Murray, L. G., Hinz, H., Hold, N., and Kaiser, M. J. 2013. The effectiveness of using CPUE data 899 derived from Vessel Monitoring Systems and fisheries logbooks to estimate scallop 900 biomass. ICES Journal of Marine Science, 70: 1330–1340. 901 Nielsen, J. R. 2015. Methods for integrated use of fisheries research survey information in 902 understanding marine fish population ecology and better management advice: 903 improving methods for evaluation of research survey information under 904 consideration of survey fish detection and catch efficiency. Wageningen University. 905 Ocean Studies Board, and National Research Council. 2000. Improving the collection, 906 management, and use of marine fisheries data. National Academies Press. 907 Okamura, H., Morita, S. H., Funamoto, T., Ichinokawa, M., and Eguchi, S. 2018. Target-based 908 catch-per-unit-effort standardization in multispecies fisheries. Canadian Journal of 909 Fisheries and Aquatic Sciences, 75: 452–463. 910 Paradinas, I., Conesa, D., Pennino, M., Muñoz, F., Fernández, A., López-Quílez, A., and Bellido, 911 J. 2015. Bayesian spatio-temporal approach to identifying fish nurseries by 912 validating persistence areas. Marine Ecology Progress Series, 528: 245–255. 913 Parent, E., and Rivot, E. 2012. Introduction to hierarchical Bayesian modeling for ecological 914 data. CRC Press.

- Pati, D., Reich, B. J., and Dunson, D. B. 2011. Bayesian geostatistical modelling with
  informative sampling locations. Biometrika, 98: 35–48.
- Pelletier, D., and Ferraris, J. 2000. A multivariate approach for defining fishing tactics from
  commercial catch and effort data. Canadian Journal of Fisheries and Aquatic
  Sciences, 57: 51–65. NRC Research Press.
- Pennino, M. G., Conesa, D., Lopez-Quilez, A., Munoz, F., Fernández, A., and Bellido, J. M. 2016.
   Fishery-dependent and-independent data lead to consistent estimations of essential habitats. ICES Journal of Marine Science, 73: 2302–2310. Oxford University Press.
- Pennino, M. G., Paradinas, I., Illian, J. B., Muñoz, F., Bellido, J. M., López-Quílez, A., and Conesa,
  D. 2019. Accounting for preferential sampling in species distribution models.
  Ecology and evolution, 9: 653–663.
- Peterson, C. D., Courtney, D. L., Cortés, E., and Latour, R. J. 2021. Reconciling conflicting
  survey indices of abundance prior to stock assessment. ICES Journal of Marine
  Science, 78: 3101–3120.
- Pinto, C., Travers-Trolet, M., Macdonald, J. I., Rivot, E., and Vermard, Y. 2019. Combining
  multiple data sets to unravel the spatiotemporal dynamics of a data-limited fish
  stock. Canadian Journal of Fisheries and Aquatic Sciences, 76: 1338–1349. NRC
  Research Press.
- Planque, B., Loots, C., Petitgas, P., LINDSTRØM, U. L. F., and Vaz, S. 2011. Understanding what
  controls the spatial distribution of fish populations using a multi-model approach.
  Fisheries Oceanography, 20: 1–17.
- 936 Punt, A. E. 2017. Some insights into data weighting in integrated stock assessments.
  937 Fisheries Research, 192: 52–65.
- Punt, A. E., Dunn, A., Elvarsson, B. Þ., Hampton, J., Hoyle, S. D., Maunder, M. N., Methot, R. D., *et al.* 2020. Essential features of the next-generation integrated fisheries stock
  assessment package: A perspective. Fisheries Research, 229: 105617.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation
   for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
- Rivoirard, J., Simmonds, J., Foote, K. G., Fernandes, P., and Bez, N. 2008. Geostatistics for
  estimating fish abundance. John Wiley & Sons.
- Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., and Le Pape, O. 2010. Effect of
  nursery habitat degradation on flatfish population: Application to Solea solea in the
  Eastern Channel (Western Europe). Journal of sea Research, 64: 34–44. Elsevier.
- Rufener, M.-C., Kristensen, K., Nielsen, J. R., and Bastardie, F. 2021. Bridging the gap between
   commercial fisheries and survey data to model the spatiotemporal dynamics of
   marine species. Ecological Applications: e02453.
- Salas, S., and Gaertner, D. 2004. The behavioural dynamics of fishers: management
  implications. Fish and Fisheries, 5: 153–167.
- Saunders, S. P., Farr, M. T., Wright, A. D., Bahlai, C. A., Ribeiro Jr., J. W., Rossman, S., Sussman,
  A. L., *et al.* 2019. Disentangling data discrepancies with integrated population
  models. Ecology, 100: e02714.
- Schaub, M., and Abadi, F. 2011. Integrated population models: a novel analysis framework
  for deeper insights into population dynamics. Journal of Ornithology, 152: 227–237.
  Springer.
- Schmitten, R. A. 1999. Essential fish habitat: opportunities and challenges for the next
   millennium. *In* American Fisheries Society Symposium, p. 10.

- Stephens, A., and MacCall, A. 2004. A multispecies approach to subsetting logbook data for
   purposes of estimating CPUE. Fisheries Research, 70: 299–310.
- Thorson, J. T., and Ward, E. J. 2014. Accounting for vessel effects when standardizing catch
   rates from cooperative surveys. Fisheries Research, 155: 168–176.
- 965 Thorson, J. T., Ianelli, J. N., Munch, S. B., Ono, K., and Spencer, P. D. 2015a. Spatial delay966 difference models for estimating spatiotemporal variation in juvenile production and
  967 population abundance. Canadian journal of fisheries and aquatic sciences, 72: 1897–
  968 1915.
- Thorson, J. T., Scheuerell, M. D., Shelton, A. O., See, K. E., Skaug, H. J., and Kristensen, K.
  2015b. Spatial factor analysis: a new tool for estimating joint species distributions and correlations in species range. Methods in Ecology and Evolution, 6: 627–637.
  Wiley Online Library.
- 973 Thorson, J. T. 2015. Spatio-temporal variation in fish condition is not consistently explained
   974 by density, temperature, or season for California Current groundfishes. Marine
   975 Ecology Progress Series, 526: 101–112.
- Thorson, J. T., Fonner, R., Haltuch, M. A., Ono, K., and Winker, H. 2016. Accounting for
  spatiotemporal variation and fisher targeting when estimating abundance from
  multispecies fishery data. Canadian Journal of Fisheries and Aquatic Sciences, 74:
  1794–1807.
- Thorson, J. T., Jannot, J., and Somers, K. 2017a. Using spatio-temporal models of population
  growth and movement to monitor overlap between human impacts and fish
  populations. Journal of Applied Ecology, 54: 577–587.
- Thorson, J. T., Johnson, K. F., Methot, R. D., and Taylor, I. G. 2017b. Model-based estimates of
  effective sample size in stock assessment models using the Dirichlet-multinomial
  distribution. Fisheries Research, 192: 84–93.
- 986 Thorson, J. T. 2018. Three problems with the conventional delta-model for biomass
  987 sampling data, and a computationally efficient alternative. Canadian Journal of
  988 Fisheries and Aquatic Sciences, 75: 1369–1382. NRC Research Press.
- Thorson, J. T., Adams, G., and Holsman, K. 2019. Spatio-temporal models of intermediate
  complexity for ecosystem assessments: A new tool for spatial fisheries management.
  Fish and Fisheries, 20: 1083–1099.
- Thorson, J. T., Cunningham, C. J., Jorgensen, E., Havron, A., Hulson, P.-J. F., Monnahan, C. C.,
  and von Szalay, P. 2021. The surprising sensitivity of index scale to delta-model
  assumptions: Recommendations for model-based index standardization. Fisheries
  Research, 233: 105745.
- Trenkel, V. M., Beecham, J. A., Blanchard, J. L., Edwards, C. T., and Lorance, P. 2013. Testing
   CPUE-derived spatial occupancy as an indicator for stock abundance: application to
   deep-sea stocks. Aquatic living resources, 26: 319–332. EDP Sciences.
- Winker, H., Kerwath, S. E., and Attwood, C. G. 2013. Comparison of two approaches to
  standardize catch-per-unit-effort for targeting behaviour in a multispecies hand-line
  fishery. Fisheries Research, 139: 118–131.
- 1002 Witman, J. D., and Roy, K. 2009. Marine Macroecology. University of Chicago Press. 442 pp.
- Zipkin, E. F., Inouye, B. D., and Beissinger, S. R. 2019. Innovations in data integration for
   modeling populations. Ecology, 100: e02713.