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Identifying fish spawning grounds by combining catch declarations and scientific survey data

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13

Abstract

14 Identifying and protecting essential fish habitats like spawning grounds requires an accurate knowledge of 15 fish spatio-temporal distribution. Data available through commercial declarations provide valuable 16 information covering the whole year and consequently they could prove useful to identify spawning grounds. 17 We developed an integrated framework to infer fish spatial distribution on a monthly time step by combining 18 scientific and commercial data while explicitly considering the preferential sampling of fishermen towards 19 areas of higher biomass. Over the spawning period, we applied a method to identify areas of persistent 20 aggregation of biomass and interpret these as spawning areas. The model is applied to infer monthly maps 21 of three species (sole, whiting, squids) in the Bay of Biscay on a 9-years period. Integrating several 22 commercial fleets in inference provide a good coverage of the study area and improves model predictions. 23 The preferential sampling parameters give insights into the temporal dynamics of the targeting behavior of 24 the different fleets. Persistent aggregation areas reveal consistent with the available literature on spawning 25 grounds, highlighting that our approach allows to identify potential areas of reproduction. 26 Keywords: Species distribution model, Spatio-temporal model, Hierarchical model, VMS and logbook data,

27 Fish reproduction areas, Template Model Builder (TMB)

28 **1** INTRODUCTION

Integrating fisheries into Marine Spatial Planning (MSP) to preserve ecosystem functions and ensure a sustainable exploitation requires an accurate knowledge of fish spatiotemporal distribution and more specifically of fish essential habitats such as reproduction and nursery grounds (Janßen et al. 2018). However, such knowledge is still missing for many species due to a lack of data with sufficient spatial, temporal or demographic resolution (Delage and Le Pape 2016; Regimbart et al. 2018).

35 The available data to map fish distribution and identify essential habitats mainly rely on 36 either scientific survey data (fishery-independent data) or commercial data available 37 through on-board observer programs (fishery-dependent data) (Pennino et al. 2016). Both 38 data sources benefit of direct on-board recording of catches and are usually considered 39 as high quality data. Furthermore, both data sources were proved to be complementary 40 (Rufener et al. 2021). Scientific data benefit from a standardized sampling plan, a constant 41 catchability and occur each year at the same period. Consequently, they provide 42 standardized data on a large spatial extent for the most species and size classes (Hilborn 43 and Walters 2013; Nielsen 2015). On the other hand, observer data potentially provide data over the full year for all caught species, even though they do not follow a standardized 44 45 protocol as survey data. Both are characterized by a relatively low sampling intensity in 46 space and time. Because of material limitations, surveys occur only once or twice a year 47 and provide a limited number of sample each time (ICES 2005) and observer programs 48 only cover a limited fraction of the entire fleet (e.g. only 1% of all sea trips are covered by 49 the French observer programs - Cornou et al., 2021). The low sampling density of both 50 data sources may lead to imprecise predictions (ICES, 2005; Alglave et al., 2022) and

51 constrains to consider only rough temporal resolution (e.g. semesters, quarters or 52 seasons – see for instance Kai et al., 2017; Pinto et al., 2019; Rufener et al., 2021) to 53 ensure a satisfying spatial coverage of the data at each time step. Nevertheless, the 54 temporality of key biological events, such as the reproduction peak, may be much tighter 55 than the temporal resolution of data (Biggs et al. 2021). Hence, those data alone are likely 56 not to provide accurate inferences on essential fish habitats such as spawning grounds.

57 Commercial catch declarations combined with their fishing locations available from VMS 58 (Vessel Monitoring System) were proven to be an interesting alternative to obtain catch 59 per unit effort (CPUE) data with fine spatial and temporal resolution (Pedersen et al. 2009: 60 Bastardie et al. 2010; Gerritsen and Lordan 2010; Hintzen et al. 2012; Murray et al. 2013; 61 Azevedo and Silva 2020). However, considering commercial fisheries data to infer fish 62 spatial distribution remains highly challenging. Among other challenges, this implies 63 accounting for fishermen sampling behavior. Fishermen typically tend to preferentially 64 sample areas of higher biomass (a process referred to as preferential sampling, PS -65 Diggle et al. 2010) which can lead to biased spatial predictions if not accounted for in 66 inference (Conn et al. 2017; Pennino et al. 2019; Alglave et al. 2022).

In a recent paper, Alglave et al. (2022) developed an integrated modelling framework to infer spatial distribution of fish abundance by combining scientific survey and commercial CPUE data from different fishing fleets while accounting for PS in the distribution of fishing effort. They applied their framework to commercial data of a single month to match with the scientific survey, and did not consider any temporal dimension in their model.

In this paper, we extend the modeling framework from Alglave et al. (2022) with a temporal
dimension to estimate fish spatio-temporal distribution at a monthly time step. Our new
model accounts for the variation over time (monthly time step) in the biomass field as well

75 as in the intensity of PS of the distinct fishing fleets. To illustrate the value of the method, 76 we selected and applied the model to 3 demersal species in the Bay of Biscay (common 77 sole, whiting and squids) characterized by contrasted configurations regarding the 78 available knowledge of their spawning grounds. We used those applications to reinforce 79 results obtained in Alglave et al. (2022) demonstrating how the integrated framework 80 benefit from the huge amount of spatio-temporal CPUE data to produce accurate maps of 81 spatio-temporal biomass. To illustrate the capacity of the framework to identify potential 82 spawning grounds, we processed model outputs to identify areas of recurrent aggregation 83 occurring during the reproduction season and confronted these to literature information.

85 2 MATERIAL AND METHODS

86 In this section, we first present the different species, the datasets and how we process 87 and combine them to produce CPUE data in space and time. Second, we extend the 88 model proposed by Alglave et al. (2022) to introduce a temporal dimension on a discrete 89 monthly time step. Then, we illustrate how integrating several fleets in the analysis 90 improves models predictions, how the PS component modifies model predictions and can 91 be interpreted. Last, we illustrate how we investigate spatio-temporal dynamics from 92 model outputs and identify reproduction grounds based on the aggregation patterns of 93 each 3 species. The models were fitted to data from 2010 to 2018 on a monthly time step 94 (108 time steps).

95 2.1 Case studies

96 Sole is a data-rich case. Direct information about reproduction grounds is available 97 through egg and larvae surveys (Arbault et al. 1986). Discard rates is also very low, which 98 makes the landings data a good proxy of the catch (ICES 2019a). Whiting is a data-poor 99 case study where only indirect information of reproduction period exists through spring 100 trawl surveys (Houise and Forest 1993). Discard rates can be high (about 30 %) and thus 101 landings data may provide a biased picture of the real catches (ICES 2019b). Squids 102 represent a mixture of several species: Loligo Vulgaris (Lamarck, 1798), Loligo forbesii 103 (Steenstrup, 1856) and Alloteuthis sp (Lamarck, 1798). They are declared under a 104 common denomination in the catch (Loliginidae here referred as squids). Overall scientific 105 survey suggest that the predominant species in the Bay of Biscay is Loligo Vulgaris (ICES, 106 2020a, p.17). All 3 species are data-poor: no information exist regarding their reproduction 107 grounds but some information of the reproduction period exist for Loligo Vulgaris (Moreno 108 et al. 2002).

109 **2.2 Data**

110 2.2.1 High spatial resolution catch per unit effort data for the mature component111 of the populations

We pre-processed the VMS and catch declaration (logbook) data to obtain high spatial resolution CPUE data for the mature component of those three stocks, for three different fishing fleet, and for each month of the 2010-2018 time series. In the text, CPUE is used but no discard information is available at the scale of the fishing sequence.

116 We selected data of three trawlers métiers OTB_DEF (bottom otter trawl targeting 117 demersal species), OTB_CEP (bottom otter trawl targeting cephalopods) and OTT_DEF 118 (multi-rig otter trawl targeting demersal species). Here the term fleets is used to refer to 119 these groups. They refer to distinct component that have overall similar targeting 120 behaviors and similar technical characteristics. These fleets were selected (1) so as to 121 cover the full spatial domain (Figure 1) and (2) because fishing time of trawlers is a good 122 proxy of effort which allows to compute reliable CPUE for biomass (Hovgerd and Lassen 123 2008).

Because one of our primarily goal is to identify spawning grounds, we filtered only the mature fraction of the landings. This was done by crossing the landings data with length class and maturity data (see details in SM1). Note that this procedure was not possible for squids, as there are no data on maturity and size classes in this case.

Landing data were then combined with VMS data to finally obtained high spatial resolution
CPUE data discretized on a 0.05°x0.05° grid on a monthly time step (see the detailed
procedure for this combination in Alglave et al. (2022) and SM2).

131 2.2.2 Scientific data

We also integrated scientific data in the analysis. For hake and squids we used the survey data from the EVHOE survey. The Orhago survey was used for sole (ICES, 2020 - see SM, Figure S3). The data were extracted from the DATRAS database on the period 2010 - 2018. Only the mature fraction of the survey catches were kept in the analysis to make it comparable with commercial data. Some details on the surveys are given in SM3.

137 **2.3 Spatio-temporal integrated model**

We build on the integrated hierarchical model proposed by Alglave et al. (2022) by incorporating a temporal component to model the evolution of the latent field of biomass across the monthly time steps (Figure 2). The PS of commercial data for the different fleets is modelled explicitly through inhomogeneous Poisson point processes for the fishing locations.

143 **2.3.1 Biomass field**

As a notable extension of Alglave et al. (2022), the biomass field (eq.1) is modelled as a spatio-temporal Gaussian Random Field (GRF) through a log link as:

146
$$\log(S(x,t)) = \alpha_S(t) + \delta(x,t) \quad (1)$$

147 where $x \in D \subset R^2$ stands for the spatial locations and $t \in [1, T]$ the monthly time steps. 148 The term $\alpha_s(t)$ is a time varying intercept modelled as a fixed effect and $\delta(x, t)$ is a GRF 149 spatio-temporal process which represents the spatio-temporal correlation structure of the 150 biomass field. As commercial data may not always cover the full area, the temporal 151 correlation component allows to interpolate between time-steps. Here, the spatio-temporal 152 term has a classical stationary first-order autoregressive form (eq.2) following (Cameletti 153 et al. 2013):

154
$$\delta(x,t) = \varphi \cdot \delta(x,t-1) + \omega(x,t) \quad \text{for } t = 2, \dots T$$
 (2)

155 The autocorrelation coefficient φ is a scalar with $\varphi \in]-1,1[, \omega(x, t)$ represents the spatial 156 innovation and is a 0 mean GRF (with no temporal correlation).

Note that no covariate is included in the latent field to keep the model as simple as possible. If any, the covariates effects are captured through the spatio-temporal term $\delta(x, t)$. Similarly, the intercept $\alpha_S(t)$ was modelled through a simple fixed effect but more complex specifications including some seasonal, yearly and interaction effect could be adopted such as in Thorson et al. (2020).

162 **2.3.2 Sampling process for the commercial fishing points**

As the scientific survey sampling plan is designed independently from the biomass field, scientific sampling locations do not need to be modelled explicitly (Diggle et al. 2010). By contrasts, the dependence between the fishing locations and the biomass field has to be modelled to capture preferential sampling. We extended the model proposed by Alglave et al. (2022) to account for temporal variations in PS. Fishing locations are modelled as an inhomogeneous point process (X_{comj} in the Figure 2) whose intensity $\lambda_j(x, t)$ (eq.3) controls the expected number of fishing points within a given area:

170
$$\log(\lambda_j(x,t)) = \alpha_{Xj}(t) + b_j(t) \cdot \log(S(x,t)) + \eta_j(x,t)$$
(3)

171 where:

172 - the time varying intercept $\alpha_{Xj}(t)$ quantifies the average fishing intensity on the 173 whole area; as the biomass intercept $\alpha_{S}(t)$, it is modelled as a fixed effect;

174 - the time varying $b_j(t)$ quantifies the strength of PS; it is modelled as a fixed effect 175 too. If $b_j(t) = 0$, then PS is null. If $b_j(t) > 0$, then PS occurs and the greater, the 176 stronger PS; 177 - the pure spatial GRF $\eta_j(x, t)$ captures the remaining spatial variability in the fishing 178 point pattern not captured by the PS term (for instance, dependence of the fishing 179 locations towards management regulations, distribution of other targeted species, 180 habits/tradition).

181 **2.3.3 Observation process**

All observations for both scientific and commercial data of any fleet *j* are assumed all mutually independent conditionally on the latent field of biomass and the sampling locations. The observation model allows to distinguish several fleets with specific catchabilities. As data (both scientific and commercial) eventually present a high proportion of zero values, we model the observations through a Poisson-link zero-inflated model introduced by Thorson (2018) and already used in Alglave et al. (2022) (see detailed description of the observation model in SM4).

189 2.3.4 Maximum likelihood estimation

The estimation of the spatio-temporal model is achieved through maximum likelihood estimation. We used the SPDE approach Lindgren et al. (2011) and Template Model Builder (TMB - Kristensen et al., 2016) for a fast estimation of the spatial and spatiotemporal random effects. Details on estimation are provided in SM 5, 6 and 7.

194 **2.4** Evaluating the Interest of integrating multiple fleets

195 Integrating several fleets in inference allows to cover the whole area (Figure 1) and is 196 expected to improve inferences. To illustrate the value of integrating the data from multiple 197 fleets within a single integrated model, we compared the spatial predictions obtained by 198 fitting the model to all available data with those obtained by integrating only one fleet. In 199 addition, we investigated if integrating all the fleets in inference increased the correlation between scientific data and model predictions. We also compared the coefficient of
variation of the prediction between each model (for November 2018).

202 **2.5** Evaluating the value of modelling PS

We first assessed the impact of PS on the distribution of biomass by comparing estimations obtained from integrated models (i.e. models fitted to all data sources) accounting for PS with those obtained when ignoring PS. We computed the log-likelihood related to each data source (commercial and scientific data) to assess if there is an improvement in model goodness-of-fit when accounting or not for PS. Note that fitting a model without PS is straightforward as it only requires to remove the sampling process component from the likelihood function.

210 **2.6** Interpreting the intensity of preferential sampling

The estimates of PS parameters may bring valuable information on the dynamics of the fishery as they inform on the strength of the relationship between commercial sampling distribution and species distribution. We investigate the variability of the PS parameters (*b*) by representing the variability of the different *b* parameter estimates for the three case studies and the different fleets. Then, focusing on the sole case study, we highlight the insights brought by the model on the temporal evolution of PS and its seasonal variations.

217 2.7 Investigating spatio-temporal dynamics and identifying reproduction 218 grounds

The spatio-temporal model provides some insight on the temporal dynamics of species distribution both at inter- and intra-annual levels. Based on the maps of abundance inferred at each time steps, we applied a method to identify recurrent aggregation areas.

222 2.7.1 Aggregation index

223 We used the Getis and Ord index $G_d(x, t)$ (Getis and Ord 1992; Ord and Getis 1995) to 224 determine persistent aggregation areas (see for instance Milisenda et al., (2021)). The 225 generalized version of the Getis and Ord index is given in Bivand and Wong (2018) and 226 Ord and Getis (1995). Basically, $G_d(x, t)$ is a normalized version of the ratio between the 227 sum of the log-biomass (denoted s(x,t)) within a fixed neighborhood d and the sum of 228 s(x, t) on the entire area (for a fixed time step) (Getis and Ord 1992). We computed these indices on $s(x,t) = \log(S(x,t))$ so that the s(x,t) are Gaussian, which makes G_d 229 230 Gaussian too. In the application, we used a neighborhood distance d=7.5 km which 231 defines a small neighborhood of 8 cells (the direct neighbors of each cell grid) and allows to identify very localized aggregation areas. Positive values for the aggregation index G_d 232 indicates that s(x, t) fall within a local patch of high values while negative G_d indicates 233 that s(x, t) fall within a local patch of low values. Near 0 values G_d , indicates that s(x, t)234 235 does not fall in some local aggregation patch. As G_d follows a standardized Gaussian 236 distribution, the comparison between the value of the index and the quantiles of a standard 237 Gaussian distribution can be used to evaluate whether or not the latent field of biomass 238 fall within a statistically significant high or low aggregation patch. We used the quantile 239 99% (2.58) as a threshold to ensure a high level of significance for patch detection (only 240 local patch of positive values are considered) and applied the Bonferroni correction to 241 account for the multiple statistical tests that are conducted.

Then, we define the persistence indices IP(x, m) as the proportion for which a point *x* falls significantly within an aggregation area for a specific month/season *m* (can be either a month or several months) among several years. *IP* allows to define the persistent

aggregation areas during reproduction throughout the time series. They are used in thefollowing to identify reproduction grounds.

247 **2.7.2** Confronting the results with the available literature

We compare the information available from the literature (for sole and whiting) with the persistence indices on their reproduction periods.

Arbault et al. (1986) investigated the reproduction of sole along the Bay of Biscay based on several egg surveys occurring in 1982. Five surveys were conducted between January and May. Egg density was sampled in different locations from Hendaye to Pointe du Raz (43°30N-48°N) and allowed to map the distribution of egg production on the full study domain. The pic of reproduction occurred in February; thus we compare the maps obtained from the February survey with the persistence index we obtained for February.

For whiting, only two EVHOE trawl surveys occurred during spring (considered as the reproduction period of whiting) between 1987 and 1992 in the Bay of Biscay (Houise and Forest 1993). For each haul, the individuals were counted and aged. Individual up to two years were all considered mature. We compare the distribution of age-2 individuals obtained with these surveys (there were very few age 3-individuals) and the index of persistence from our model during spring (March to May).

No available information exists regarding the reproduction grounds of squids in this area, however the study from Moreno et al. (2002) investigated the reproduction period for *Loligo vulgaris* in the Eastern Atlantic and highlighted that their reproduction falls in winter and spring with a pic from January to April. We compute the persistence index for this period to evidence if some spatial aggregation patterns emerge from the model outputs and could be considered as spawning grounds.

- 268 To assess whether the aggregation patterns within the reproduction period are stable over
- the time period, we iteratively computed the persistence index over a 5-year mobile time-
- span while pushing forward one year each time.

271 **3 Results**

3.1 Assessing the contribution of each data sources to inference

273 Results highlight how combining several commercial fleets in the framework brings a 274 better picture of the spatial distribution on the whole domain. For instance, when 275 comparing model prediction the month of the survey and survey outputs, integrating 276 several fleets into the analysis improves correlation with scientific data (Figure 3). It also 277 allows to reduce the standard deviation of the predictions on the full domain (Figure S8). 278 When looking at the predictions within the spatial range of the fleets, single-fleet models 279 logically provide similar spatial predictions compared with the integrated model (Figure 4; 280 red dots). However, predictions realized outside the spatial range of the fleet largely depart 281 from the ones realized through the integrated models (black dots, Figure 4), emphasizing 282

that the other fleets bring additional information to inference in these areas. This is particularly evidenced with the OTB_CEP and OTT_DEF fleets that partially cover the study area compared with OTB_DEF that better cover the whole study area (Figure 1).

285 **3.2** Interpreting estimates PS intensity

286 Estimates of the PS intensity (b parameters) for the different species, the different fleets 287 and the different time steps provide information on the targeting behavior which are 288 consistent with expertise. Estimates of b are positive for each species and each fleet 289 (Figure 5, left column). For squids, PS is the strongest for OTB_CEP followed by 290 OTB_DEF and OTT_DEF. This is consistent with the expert knowledge of the targeting 291 behavior of these fleets: OTB_CEP target cephalopods and catch on average 15% of 292 squids while OTB_DEF and OTT_DEF catch respectively 5% and 1% of squid). A similar 293 pattern can be identified for whiting $(b_{OTB CEP} > b_{OTB DEF} > b_{OTT DEF})$; this is consistent 294 with species spatial distribution as whiting (like squids) are found in coastal areas where the OTB_CEP fleet is operating. For sole, the strength of PS is on average higher for OTB_CEP and OTT_DEF than for OTB_DEF but with less contrast between the three commercial fleets.

Interestingly, some of the *b* parameters time series emphasize seasonal patterns (Figure 6, top). For instance in the sole case study for the OTB_CEP fleet, the *b* parameters are higher in summer and autumn emphasizing relatively stronger PS, while being lower in winter and early spring (but see section 3.4 below for a more detailed interpretation of this seasonality pattern).

303 3.3 Evaluating the influence of PS on spatial distribution

304 Because estimates of b are positive, spatial density of fishing points is positively correlated 305 with biomass density. Hence, considering PS revises downwards the biomass estimates 306 in areas not sampled by the commercial fleets compared to estimates obtained while 307 ignoring PS (Figure 5, right column, black points), but does not strongly affect predictions 308 in locations within the range of the fleets (blue points). Considering PS only slightly 309 improves the fit of the model to the data. For the Sole case study, some improvement of 310 the likelihood occurred in both the commercial and the scientific likelihood values (Table 311 1). For whiting and squids, there are no strong modifications in both scientific and 312 commercial likelihoods.

313 **3.4** Investigating spatio-temporal dynamics of fish biomass

Results provide biomass density maps on a monthly time step that allow for evaluating seasonal distribution patterns, and from which aggregation index were calculated. The temporal correlation parameter (φ) is estimated around 0.8 for all the species emphasizing strong temporal correlations in the biomass field values. The range parameters are

estimated to 55 km for sole and squids while being estimated to 67 km for whiting
emphasizing wider spatial autocorrelation for this species.

320 Concerning the Sole case study, model predictions highlight the relatively offshore 321 distribution from November to April and its coastal distribution from June to October 322 suggesting some migrations happen between these 2 periods (Figure 6, bottom). In 323 particular, the migration in June/July conducts to a contraction of the sole distribution 324 around the Vendée coast, the Gironde Estuary and the Landes coast (45.5°N-46°N) while 325 the migration in November leads to an expansion of the species distribution towards the 326 offshore areas all along the Bay of Biscay. Interestingly such seasonality coincides with 327 the seasonality of PS intensity for the OTB_CEP (Figure 6, Top). Higher PS parameters 328 corresponds to coastal distribution of sole while lower PS parameters corresponds to 329 offshore distribution of sole.

330 Similar maps can be computed for the other species and are presented in SM10.

331 **3.5** Aggregation index and reproduction grounds

Regarding spawning grounds, both sole and squids emphasize strong aggregation patterns that match the available knowledge of their reproduction grounds. For sole, the aggregation areas globally match with the observed area of maximum egg concentration (Figure 7), although reproduction grounds are slightly eastern in the case of egg maps. This slight discrepancy could be interpreted as an effect of the larval drift as the maps provided by Arbault et al. (1986) are concentration of eggs and not reproduction grounds per se. Overall, these aggregation areas are stable over time (Figure 8).

For whiting, similar patterns can be identified during the reproduction period (Figure 7);
they match with previous studies investigating the spatial distribution of mature whitings

341 (Houise and Forest 1993). In particular, the Northern (3°W-47°N) and the Southern (2°W-342 45.5°N) aggregation patches are almost systematically significantly considered as 343 aggregation areas (aggregation index equals 1) while the other middle one (2.5°W-344 46.5°N) is classified as an aggregation area that appears less frequently. An additional 345 persistent aggregation area can be identified in the North of the Bay of Biscay (4.5°W-346 48°N) suggesting that reproduction may also occur in this area which was not identified in 347 the report of Houise and Forest (1993). Interestingly the Northern aggregation area (3°W-348 47°N) is more pronounced at the end of the period (Figure 8).

For squids, no literature information related to any reproduction ground exist, only the time period of the reproduction is known (the pic fall between January to April). On this time period, some persistent aggregation areas can be evidenced in coastal areas (Figure 7) along the Vendée coast (2.5°W-46.5°N), the Landes coasts (1.5°W-44°N to 45°N) and around Belle-Île-en-Mer (3°W-47.25°N). Interestingly the two Northern aggregation areas are more pronounced at the end of the time series compared to the beginning of the time series (Figure 8).

Similar maps of persistent aggregation areas are available for each month and evidence
some other aggregation areas outside of the reproduction period (SM11). For instance,
for sole a persistent patch can be identified offshore the Gironde Estuary (1.5°W – 45.5°N)
from August to December.

361 **4 DISCUSSION**

362 Main findings

363 In this paper, we develop a framework to infer fish spatio-temporal distribution on a monthly time step while combining scientific survey data and commercial catch 364 365 declarations from several fleets. Commercial catch data constitute a valuable data source 366 that complement scientific survey or onboard sampling programs by providing much 367 higher spatio-temporal sampling density. Those complementary sources of data were 368 integrated through a spatio-temporal hierarchical model taking into account spatio-369 temporal variation within the biomass field and PS on a monthly time step. We fitted the 370 model to VMS-logbooks data filtered and processed over the period 2010-2018 for 3 371 demersal species (sole, squids and whiting) in the Bay of Biscay.

372 We emphasize the benefit of integrating several spatially complementary fleets to infer 373 fish distribution throughout the year. We demonstrate how the within year dynamic of the 374 PS parameters can be interpreted in regards to the joint dynamics of species distribution 375 and effort distribution and to the overall targeting behavior of the fleets (e.g. OTB_CEP for 376 the squids case study). Even though PS parameters are not fishing intention per se 377 (Bourdaud et al. 2019), these could advantageously complement information provided by 378 landing profiles to estimate the targeting behavior of any group of vessels (either 379 métier/fleet or any group that would seem appropriate).

Interestingly, although interpretation of the PS parameters provide insight into the spatiotemporal fleet dynamics, accounting for PS in the inferences does not significantly improve model fitting even when some fleets emphasize strong PS (e.g. squids, OTB_CEP). These results contrasts with Alglave et al. (2022), and could result from the integration of several

fleets in the analysis that allow a full coverage of the area. Indeed, in Alglave et al. (2022), the fleet emphasizing strong PS only covered a restricted (and coastal) part of the area. As introducing PS mainly affects inferences on poorly sampled areas, predictions in the offshore areas where mostly affected. Here, as the fleets are all estimated to have a positive PS and cover the whole area, PS only downscale the predictions in the few areas areas that remain unsampled.

390 Filtering the mature fraction of the population in both the scientific and the commercial 391 data allow us to infer the spatio-temporal distribution of the mature fraction of the biomass 392 through the year on a monthly time step. We developed an index to infer aggregation 393 areas of the mature fraction of the biomass that are persistent across years. When 394 calculated on a temporal window predefined following the available information on the 395 reproduction period for each species, the aggregation index allow us to identify the main 396 recurrent spatial aggregation areas within the reproduction period. Results demonstrate 397 that the recurrent aggregation areas identified from our method for Sole and Whiting were 398 highly consistent with those already identified in the literature. Our results demonstrate 399 how the aggregation index can provide new insights on the spawning grounds for species 400 like squids for which no information on the spawning grounds is available on the literature. 401 Areas of high aggregation persistent across years were identified during the expected 402 period of reproduction and could be interpreted as spawning grounds. This opens perspectives for applying more systematically the approach for species where no 403 404 information of reproduction grounds is available to fill the gaps in our knowledge with 405 minimum cost (Delage and Le Pape 2016; Regimbart et al. 2018).

406

408 Combining our results with other data sources to refine inferences on spawning409 grounds

410 Although the mature fraction of the biomass was filtered in the data, our maps do not 411 directly inform whether individuals are actually reproducing or not. Persistent aggregation 412 areas should be considered as potential spawning areas rather than actual spawning 413 areas. To get information on actual reproduction zones and support our findings, other 414 kind of data could complement our analysis. Typically, our maps could be of great help to 415 design surveys recording eggs, larvae and spawning individuals that would provide direct 416 information of species reproduction (Fox et al. 2008). Because developing such additional 417 surveys would be highly expensive, our maps could provide valuable a priori information 418 to optimize the survey design and potentially find a compromise between the cost, the 419 spatial extent, the temporal coverage of the survey and the accuracy of the expected 420 estimates/predictions. Similar ideas were already applied to the sole case study to 421 investigate more precisely the space-time variation of sole reproduction. Arbault et al. 422 (1986) work provided a priori information of reproduction grounds that allowed designing 423 more localized surveys to study inter- and intra-annual variability of one specific sole 424 spawning area (Petitgas 1997). Several statistical methods have been developed since 425 and are suitable to optimize such adaptive sampling design; see for instance the recent 426 work of Leach et al. (2021).

Our results could also be combined with fishermen expert knowledge (Yochum et al. 2011) to complement our knowledge of fish reproduction (Delage and Le Pape 2016). For instance, Bezerra et al. (2021) and Silvano et al. (2006) proved the usefulness of fishers knowledge to determine the temporality of fish spawning and to identify some spawning grounds by crossing the information of aggregation areas provided by several fishermen.

These were proved complementary with scientific data as they can be available at lowcost and provide local knowledge of fish ecology.

434 Limits and perspectives for the approach

435 Our framework has several limitations that are all material for future research avenues.

436 First, our model remains relatively simple in regards to all the temporal processes that 437 actually occur within a fishery. It is both a strength and a weakness: such way the model 438 remains relatively generic, but one might want to extend it further to account for other 439 temporal and spatio-temporal processes affecting fisheries dynamics. For instance, we 440 opted for a non-seasonal representation of the model, however one could make it 441 seasonal by decomposing the intercepts $\alpha_{S}(t)$ and $\alpha_{Xi}(t)$ as well as the random effects 442 $\delta(x,t)$ and $\eta(x,t)$ into seasonal and yearly terms in addition to some 'season x year' 443 interaction terms as is performed in Thorson et al. (2020). In their work, such specification 444 mainly allowed to provide information over the time-steps where data was lacking. In the 445 configuration of our case studies, data is available for all time steps and have a relatively 446 good coverage of the study domain. Consequently, such model specification should not 447 modify the overall inference of the biomass field we obtain even though it provide a nice 448 conceptual view of seasonality. Alternatively, our framework could integrate orthogonal 449 spatio-temporal terms in the latent field to capture the main mode of variability of the 450 biomass field (Thorson et al. 2020b). Such orthogonal terms would allow to capture the 451 main spatial patterns that structure the latent field as well as their variation in time. These 452 could prove very useful to identify the structuring processes that affect species distribution 453 and could give a valuable insight in the space-time dynamics of the species. Another 454 exciting research avenue would consist in integrating population dynamics in the latent

455 field of biomass (Cao et al. 2020). This would require to refine further the demographic 456 resolution of the VMS-logbooks data (see for instance Azevedo and Silva 2020), but once 457 done, it would give access to huge data for inferring the space-time dynamics of fish 458 populations. Finally, our model considers fishermen preferentially sample areas where the 459 biomass is higher (preferential sampling), but does not consider any other drivers and 460 specifically the temporal and spatio-temporal relations that can affect fishers behavior. 461 These can be highly complex and may depend on the distribution of the resource, 462 tradition/habits, management regulations (Abbott et al., 2015; Girardin et al., 2017; Salas 463 and Gaertner, 2004; Hintzen, 2021). These drivers are rarely studied in both space and 464 time (although see Tidd et al., 2015). Our framework could allow to jointly model the 465 dynamics of the species, the distribution of the effort, the link that relates species 466 distribution and effort in space/time and all the other spatial and/or temporal drivers that 467 affect the distribution of fishing effort. For instance, we could relate the fishing intensity to 468 the biomass field from the previous time steps, or alternatively consider that the locational 469 choice depend on the catches of the previous time steps. Adding such covariates and 470 spatio-temporal dependencies in the sampling equation (eq.3) will probably not modify the 471 overall pattern of biomass distribution, but it would allow to quantify the drivers of 472 fishermen behavior and give valuable insight in the functioning of the fishery.

Second, including discards would potentially improve our approach. Indeed, logbooks data are landings declarations data which means they inform on the landings and not on the true catch. Thus, by assuming the observations we derive from logbooks data are representative of the biomass, we make the hypothesis that the discard rate is constant in space and time and does not affect model predictions. This should not be a problem for sole and squids as the discards are low and TAC have not been really binding during the

479 studied period. However, the issue might be more stringent for whiting and/or other 480 species with a high and non stationary level of discards. Integrating discards data in the 481 analysis could help solving this issue. Stock et al. (2019) and Yan et al. (2022) used 482 observer data to model bycatch in both space and time and Breivik et al. (2017) used 483 bycatch data from onboard surveys to predict the temporal evolution of bycatch realized 484 in the full commercial data. Similarly, we could integrate into the same analysis the 485 logbooks and the observer data by assuming that the catch of observer data is a 486 summation of both landings (which is also observed in the logbooks data) and discards 487 (which is unobserved in the logbooks data). This way, the discards information available 488 from observer data would be shared with the logbooks data and would allow correcting 489 for the missing portion of catch declarations data while possibly accounting for possible 490 space or time variation in the discard rate.

Last, our analysis rely on the hypothesis that the spawning season is known a priori. Extending the approach to infer the spawning season based on the temporal dynamic of the aggregation patterns could improve our knowledge of species spatio-temporal distribution. In particular, identifying the main species phenomenological phases and their consistency (or shift) in time is crucial in the context of global change (Thorson et al. 2020a).

In our study, we computed the aggregation index on a period we assumed to be the reproduction period based on literature (Arbault et al. 1986; Houise and Forest 1993; Moreno et al. 2002). Hence, our results are sensitive to this a priori hypothesis, or our approach can even be inapplicable for species when no information is available in the literature. Several methods exist and could be adapted to extract the spatial patterns that shape model outputs, their related temporal variation and identify from these the main

phenological phases that characterize species distribution (e.g. reproduction, feeding see for instance Empirical Orthogonal Functions or Principal Oscillation Patterns - Cressie
and Wikle 2015; Wikle et al. 2019).

506 Future use for Marine Spatial Planning

507 Finally, our approach could reveal useful in the context of Marine Spatial Planning (MSP). 508 Janßen et al. (2018) highlighted that one of the main requirement for implementing MSP 509 while accounting for fish ecology is the availability of fine scale information on species 510 distribution and of their essential habitats. Here we propose a method which can provide 511 such information for the fraction of the population available through catch declarations (i.e. 512 mainly the adult fraction and in some cases part of the juvenile fraction). This knowledge 513 is typically needed to design Marine Protected Areas (MPA – see for instance Lambert et 514 al. (2017) or Loiselle et al. (2003)), Fishery Conservation Zones (Delage et Le Pape, 515 2016 ; Regimbart et al., 2018), or alternatively identify areas that should be kept for fishing 516 in a context were many other human activities are competing in space and time with 517 fishing (Campbell et al. 2014; Bastardie et al. 2015). This would require to open the 518 spectrum of the analysis to an economical dimension and possibly integrate our results 519 into ecological-economic models in order to evaluate alternative management regulations 520 and assess their tradeoffs in regards to all the sets of ecosystem services provided 521 through activities such as fishing, aquaculture, energy, shipping, recreation and 522 conservation (Nielsen et al. 2018).

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531 VMS and logbooks data. The findings and conclusions of the present paper are those of

532 the authors.

533 **DATA AVAILABILITY STATEMENT**

534 Survey data are available through the DATRAS portal (https://www.ices.dk/data/data-

535 portals/Pages/DATRAS.aspx) with the package 'icesDatras' (https://cran.r-

536 project.org/web/packages/icesDatras/index.html). Logbooks and VMS data are

537 confidential data and they are available on specific request to DPMA.

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- 741

TABLES

Table 1. Ratio between the negative log-likelihood values (either commercial or scientific) from the IM accounting for PS and the IM ignoring PS.

Species	Negative log-likelihood ratio	
	Scientific data	Commercial data
Sole	0.97	0.92
Squids	1.00	1.01
Whiting	0.99	1.00
<i>Note.</i> The ratio between negative log-likelihoods $(-log(lkl))$ is given as: $r = \frac{-log(lkl_{PS})}{-log(lkl_{nOPS})}$.		

If r < 1, the model accounting for PS better fits the data than the model ignoring PS (no PS).

749 **FIGURES CAPTION**

Figure 1. Spatial distribution of each fleet on the whole period (2010-2018). Unit: fishing for in fishing hour.

752

753 Figure 2. Diagram of the integrated spatio-temporal model.

754

Figure 3. Comparison between the observed scientific CPUE (y-axis) and the corresponding model predictions (x-axis) on the month of the survey, based on model integrating data from one commercial fleet only (either OTB_CEP, OTB_DEF, OTT_DEF) or from all commercial fleets (Integrated model). x-axis: model predictions. y-axis: scientific data observations (CPUE in kg/hour). Black line: linear regression 'log(scientific observations) ~ log(model predictions)'. r: Spearman correlation coefficient. Scientific data are integrated to inference for all models.

762

763 Figure 4. Sole case study. Comparison between predictions from the integrated model 764 (using all fishing fleets) and the model integrating only one commercial fleet for the 12 765 months of year 2018. Left: OTB CEP fleet, middle: OTB DEF fleet, right: OTT DEF fleet. 766 x-axis: integrated model predictions. y-axis: single-fleet model predictions. The prediction 767 values are log-scaled. Red points: predictions within the sampling area of the related fleets 768 (i.e. the cells sampled by the fleet). Black points: predictions outside the sampling area of the related fleets. Black line: x = y axis. Note that the intercept of the x-y line has been 769 770 scaled to account for differences in the intercept values between models. Scientific data 771 are integrated to inference for all models.

772

773 Figure 5. Estimates of PS parameters for each commercial fleet (left) and effect of PS 774 on model outputs (right). Left: boxplot represent the variability of maximum likelihood 775 estimates of parameters b across the monthly time steps. Right: log-predictions of the 776 integrated model accounting for PS (y-axis) versus log-predictions of the integrated model 777 ignoring PS (x-axis) for the 12 months of year 2018. Blue points: predictions within the 778 sampling area of the commercial fleets (i.e. the cells sampled by commercial fleets). Black 779 point: predictions outside the sampling area of the commercial fleets. Black line: x = y780 axis.

781

Figure 6. Sole case study. (Top) Temporal evolution of the *b* parameters for the three commercial fleets fitted to the integrated model. Blue vertical lines: January. (Bottom) Monthly biomass distribution averaged on the full period. Only quantile values are represented. Model predictions come from the integrated model accounting for PS.

786

Figure 7. Left: index of persistence during the reproduction period of sole (February), whiting (March-May) and squids (January-April). Reproduction period defined from

ecological expertise. Index were computed from 2010 to 2018. Right: literature information
on reproduction grounds when available. For sole, the map represents egg concentration
from an egg and larvae survey conducted in 1982 (Arbault et al., 1986). For whiting, the
map represents records of age-2+ whiting (i.e. mature individuals), from two spring trawl
surveys that occurred between 1987 and 1992 (Houise and Forest, 1993). Model
predictions come from the integrated model accounting for PS.

795

Figure 8. Persistence indices within the reproduction period computed on a 5-year mobile time-span for each 3 species (5-year time span indicated on the top of each map). Model predictions come from the integrated model accounting for PS.

799

FIGURES







Figure 4



Sole case study





Figure 6

Monthly mean distribution

- 819 820
- 821



Figure 7



APPENDICES

