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Bayesian spatio-temporal CPUE standardization: Case study of European sardine (*Sardina pilchardus*) along the western coast of Portugal

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Abstract

Understanding the key factors influencing population dynamics of fish stocks requires knowledge of their spatial distribution and seasonal habitat selection, but these spatio-temporal dynamics are often not explicitly included in ecological studies and stock assessment models. This study standardized the data of sardine fishery-dependent catch-per-unit- effort (CPUE) from the west coast of Portugal using Bayesian hierarchical spatio-temporal models (BHSTM) with the integrated nested Laplace approximation (INLA). Sardine CPUE was best explained by length of the vessel, vessel ID, month, year, and location (latitude, longitude). In terms of spatio-temporal distribution, sardine biomass prediction maps showed a constant pattern that changed every quarter of the year. In addition, sardine CPUE index showed a cyclical trend along the year with minimum values in July and maximum peak in November. This approach provided insights on variables and corresponding modelling effects that may be relevant in spatio-temporal fishery-dependent data standardization, and that could be applied to other fish species and areas.

KEYWORDS
Atlantic Ocean, Bayesian hierarchical spatio- models (BHSTM), integrated nested Laplace approximation (INLA), relative biomass, spatial, temporal

1 | INTRODUCTION

Three primary types of data are commonly used in fish stock assessment models: catch, biomass and biological data (ICES, 2019). Fishery-independent data from standardized surveys are often difficult to collect for economic and technical reasons (Maunder & Punt, 2004). Furthermore, scientific surveys usually occur during specific months or seasons, and provide no information about the stock during the rest of the year. For this reason, the most common source of data for assessment methods is fishery-dependent data (Maunder et al., 2006). Many ecological studies and stock assessments use relative biomass indices based on commercial catch-per-unit-effort (CPUE) data, which can be influenced by several factors, including environmental conditions, fishing methods, season, area fished, vessel size, fishing restrictions, and economics (Hilborn & Walters, 2013; Maunder & Langley, 2004). Note that relative biomass (i.e. CPUE) is hereinafter referred to as biomass. In stock assessments, each biomass index is associated with a fishing fleet that has an associated selectivity and defines the catchability relative to the age (or size) of the fish stock (Hoyle et al., 2014). However, the standardization of CPUE can be challenging and frequently involves separate steps, in which the standardization process and population dynamics are fitted independently (Maunder, 2001).

Various methods are used to standardize CPUE, the most common of which is the use of generalized linear models (GLM) for linear relationships between the response variable and the covariates (Glazer & Butterworth, 2002; Hazin et al., 2007) and generalized additive models (GAM) which also allow for fitting non-linear relationships between variables (Li et al., 2013; Tian et al., 2009). Most of these studies usually incorporate geo-reference or time information as explanatory variables, whereas Bayesian spatial models allow the inclusion of an explicit stochastic structure for underlying dependency among observations (Campbell et al., 2017). Fishery-dependent data are frequently characterized by a space–time structure, because species biomass and availability change continuously in space over time (Zhou et al., 2019). Thus, both spatial and temporal correlation must be considered during the modelling process because observations of species at geographically close locations are subject to similar life habits and environmental characteristics (Hefley et al., 2017).

Typically, commercial fishery data are records of a specific vessel at a given time and location. For this type of nested data, spatial models using hierarchical approaches are known to perform well. Several authors have applied Bayesian hierarchical spatio-temporal models (BHSTM) fitted through the integrated nested Laplace approximation (INLA) (Rue et al., 2009) in single-species CPUE standardization (Cao et al., 2011; Monnahan & Stewart, 2018; Mourato et al., 2019). BHSTM have an advantage over common CPUE standardization models (e.g. GLM or GAM) by accounting for spatio-temporal autocorrelation through spatially structured random effects and autoregressive terms, thereby reducing uncertainty of estimated biomass indices (Cosandey-Godin et al., 2015; Zhou et al., 2019). In addition, fishing efficiency may differ among vessels of different technical characteristics that can be modelled as independent identical random effects (Pennino et al., 2014; Monnahan & Stewart, 2018) or as random walk effects to deal with vessel and time variables (Cavieres & Nicolis, 2018). It is worth mentioning that BHSTM also allow to include smoothed (non-linear) terms for environmental covariates (e.g. chlorophyll-a, bathymetry, sea surface temperature, etc.), which can be crucial to explain spatio-temporal species distribution and biomass (Muñoz et al., 2013; Paradinas et al., 2020; Rufener et al., 2017).

European sardine (*Sardina pilchardus*, Walbaum, 1972), hereafter referred to as sardine, is the most abundant small pelagic species of the northeast Atlantic Ocean. In European Atlantic waters, the International Council for the Exploration of the Sea (ICES) conducts sardine assessment for three different stocks (ICES, 2019). The United Kingdom fishes the southern Celtic Sea and English Channel stock, France and Spain the Bay of Biscay stock, while Spain and Portugal manage the Cantabrian Sea and Atlantic Iberian waters stock (hereafter referred to as the Iberian stock), which is distributed around the Iberian Peninsula and is mainly caught using purse-seines (ICES, 2017a). In Portugal (Figure 1), sardine landings account for more than 70% of all commercial catches (Stratoudakis & Marçalo, 2002). Different regulatory measures, such as, minimum landing size, closed areas, and limitations on the number of fishing days, have been applied to this stock since 1997 (ICES, 2011). In the recent past, the biomass of age 1 and older fish decreased from 2006 to 2018 and the lowest level of recruitment on record occurred in 2017 (ICES, 2018). However, the Iberian stock has recently increased its biomass (ICES, 2021), which in part is attributable to strict fishing limitations (number of fishing days and total catch), in addition to favourable environmental conditions.

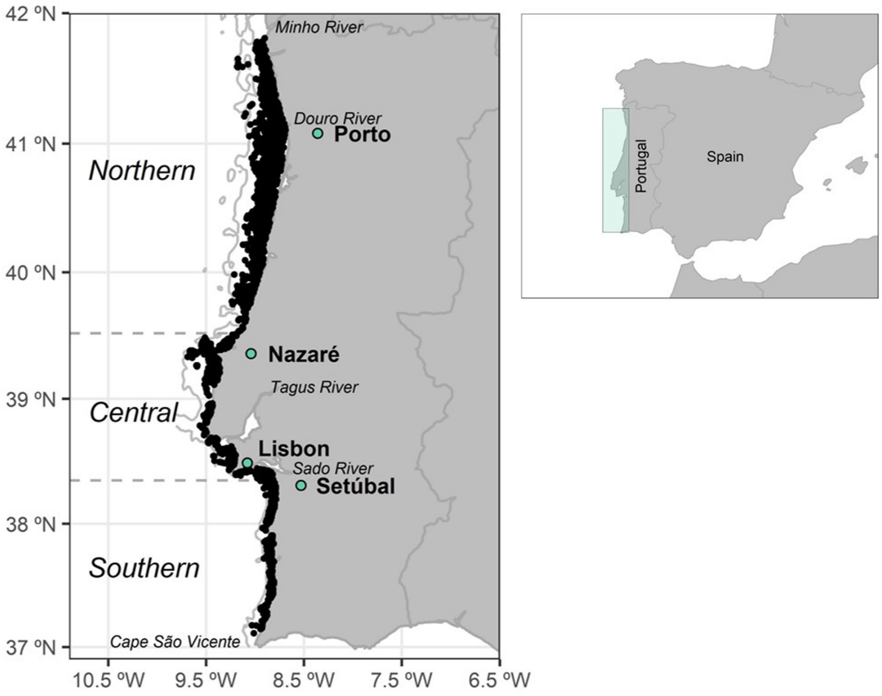


FIGURE 1 Map of the study area showing the sampling locations (black dots) of European sardine (*Sardina pilchardus*) from the purse-seine commercial fleet within the period 2011–2013. Note that the northern, central, and southern regions have been defined based on the morphology of the continental shelf (Zwolinski et al., 2010). Bathymetric line indicates the 100 m depth contour

Previous studies have found significant relationships between the spatio-temporal distribution of sardines and environmental covariates. For example, in the Mauritanian Sea, chlorophyll-a (Chl-a), upwelling index and SST significantly explained the spatio-temporal CPUE index of sardine (Bacha et al., 2017). For sardine in the Mediterranean, bottom depth and sea surface temperature explained most of the presence of the species (Tugores et al., 2011), and the Meridional Current was related to landings (Quattrocchi & Maynou, 2017). For the Iberian sardine stock in Portuguese waters, decreasing recruitment corresponded to an increase of the upwelling index during winter (Santos et al., 2001, 2012). Other research has shown that temperature and food availability, estimated as satellite-derived SST and chlorophyll-a during the spawning season, were related to recruitment success for the two main recruitment areas off the Iberian Peninsula (Bernal et al., 2007; Garrido et al., 2017). Satellite-derived chlorophyll-a data can be used to infer sardine distribution and feeding intensity (Garrido et al., 2008), whereas adult sardines preferred depths <100 m and waters with a high chlorophyll-a content but low temperature in spring and autumn (Zwolinski et al., 2010). The spatio-temporal dynamics of this species has been less studied, but it is likely to have a large influence on migration patterns (Silva et al., 2019).

Most of the existing studies on the spatial distribution and biomass of adult sardine along the Portuguese coast refer to specific seasons or months of the year. To the authors' knowledge, this is the first study in the area that implements a spatio-temporal component that allows predicting sardine biomass maps for every month of the year. Our study has two objectives: (1) to assess where and when sardine biomass is distributed in the study area and (2) to derive a standardized CPUE index that could be used as input to stock assessment models. To this end, we apply BHSTM via INLA to map sardine biomass accounting for vessel-related variables, spatio-temporal autocorrelation, and possible relationships with environmental covariates, such as SST, Chl-a, bathymetry, current intensity, and current direction. The presented approach enables the inclusion of different variables through various types of random effects and to consider spatio-temporal dependence for data sets with consecutive time units (e.g. months or years). This approach can be applicable to other commercial species.

2 | METHODS

2.1 | Purse-seine fishery data

This study analysed data from the sardine purse-seine fishery off the Portuguese west coast. As we were interested in monthly frequency data (i.e. high temporal resolution), only the years 2011–2013 were selected, a period where restrictions on sardine fishing were lower and similar between years than in subsequent years (ICES, 2018).

Vessel monitoring system (VMS) and logbook data from purse-seine vessels (>15 m) were merged based on trip start and ending dates but also location to determine fishing activity (net sets). Fishing activity was identified by analysing vessel speed patterns. The start of the fishing activity was signalled by a rapid decrease in velocity and the end of the fishing activity is signalled by a rapid increase in velocity. When the difference between consecutive points were >5 wind speed knots, these were marked as the beginning and end of fishing sets (Katara & Silva, 2017). Fishing vessel characteristics (e.g. overall length, main engine power) were available from the EU Fleet Register database (https://webgate.ec.europa.eu/fleet-europa/index_en). Fishing trips with a single net set (hereinafter referred to as fishing set) were selected to avoid bias, because the algorithm divided the catch quantity equally when more than 1 haul was performed. We found no large spatial differences in catches before or after this filtering process. The final data subset consisted of $N = 3461$ fishing sets and contained information for vessel tonnes (mean 65.31 t), vessel length (mean 22.26 m), main engine power (mean 307.7 KW), vessel ID ($n = 66$), landing harbour ($n = 13$), region ($n = 3$), year ($n = 3$), month ($n = 12$), and location (latitude, longitude) (see Figure 1 and Figures S1–S3).

2.2 | Environmental variables

Environmental variables influence habitat preferences, which in turn influence catchability (Alonso-Fernández et al., 2019). To study the relationship between sardine catch, locations, and habitat conditions at these locations, we considered five environmental variables: sea surface temperature (SST in °C), chlorophyll-a (Chl-a in mg/m^3), intensity (m s^{-1}) and direction of currents. These variables were selected for analysis because they were shown to be strongly related to marine system productivity that affect nutrient availability and water stratification (Bacha et al., 2017; Fernández-Corredor et al., 2021; Garrido et al., 2008; Quattrocchi & Maynou, 2017). In addition, bathymetry (in metres) was also tested (Zwolinski et al., 2010).

Daily satellite maps of SST, Chl-a, intensity, and direction of currents were retrieved from the COPERNICUS server (https://www.copernicus.eu/es). The bathymetry map was retrieved from the GEBCO database (https://www.gebco.net/). To ensure the same spatial resolution, all environmental data were aggregated to the lowest common resolution (0.06 × 0.06 decimal degrees) using the raster package (Hijmans, 2021) in R Core team (2021). Finally, the values of the environmental variables at each fishing set location were extracted from the corresponding daily variable maps.

2.3 | CPUE modelling process

Total sardine catch (kg) from a single fishing set per trip was used as the response variable to characterize spatio-temporal sardine biomass. To standardize CPUE, variables related to fishing activity time (Maunder & Punt, 2004), such as time searching fish or net size would have been needed for the purse-seine fishery (Stratoudakis & Marçalo, 2002), but were not available. Therefore, we analysed other variables regarding effort capacity as explanatory variables following Maunder and Punt (2004).

Model selection was performed as an additive process divided into four sequential steps. The first step corresponded to the selection of effort variables, which included vessel length, tonnes, and main engine power, all tested as linear and second-order random walk (RW2) effects, which is the Bayesian way to perform smoothing splines through different time knots (Fahrmeir & Lang, 2001). Note that effort variables are often correlated, so they were tested in separated models and only one of them was selected. In the second step, the variables vessel ID, harbour, region, and their nested combinations were analysed as covariates that could explain extra variability related to effort (i.e. fishing behaviour) via independent identical random effects (iid) (Blangiardo & Cameletti, 2015). This term is an effective way to account for unstructured variability of a given variable as independent associated error for each level. In the third step, we tested the five environmental variables Chl-a, SST, current intensity, current direction, and bathymetry as linear and smoothed (RW2) effects (Fahrmeir & Lang, 2001). Finally, in the fourth step, different spatio-temporal components were included for a more accurate detection of changes in the spatio-temporal biomass trend (Campbell, 2015). Year was included as an iid term to allow the model to link the information for 3 years as if they were a single one, with the objective of predicting in a single year (i.e. not all vessels were fishing in all years but we had information from all of them when doing the prediction). The progressive spatio-temporal structure for the variable month was included (Paradinas et al., 2017). This is an autoregressive structure of the first order (AR1), which has demonstrated good performance for processes where spatial realizations change in a correlated way over consecutive time units (Pennino et al., 2022). Moreover, the variable month was also included as a RW2 term with and without the option cyclic to detect possible biomass trend behaviour.

An exploratory analysis of the covariates was performed following the approach of Zuur et al. (2010), including collinearity, outliers, and missing values before their inclusion in the models. In particular, correlation between variables was tested using the Spearman's correlation, whereas collinearity was tested by computing the generalized variance-inflation factors (GVIF) (Fox, 2015) (see Table S1). When more than one environmental variable was present in the same model, they were standardized to avoid numerical confounding (difference of the mean divided by the corresponding standard deviation) (Gelman, 2008). Model selection was performed using the Watanabe-Akaike information criterion (WAIC) (Watanabe & Opper, 2010), the deviance information criterion (DIC) (Spiegelhalter et al., 1999) as the criteria for goodness of fit, and the leave-one-out cross-validated Conditional Predictive Ordinate score (CPO) (Geisser, 1993) computed by its mean logarithm (LCPO) (Gneiting & Raftery, 2007) as a predictive quality measure. For all measures, the smaller the score, the better the model.

2.4 | CPUE model formula

Z_{stkj} denotes the spatio-temporally distributed sardine biomass for a given vessel k, where $s = 1, \ldots, n_{tj}$ is the spatial location and $t = 1, \ldots, 12$ is the month index. Furthermore, X_{istj} identifies the i^{th} environmental variable in location s, month t, and year j. We chose the gamma distribution from the exponential family because it is a continuous probability distribution adequate to model positive right-skewed data. In addition, the $\epsilon = 0.00001$ value was added to the response variable to avoid zero values. The mean of the CPUE variable was then related via the link log function to the smoothed covariates and the spatio-temporal effects:

$$\begin{gathered} Z_{st} \sim \mathrm{Gamma}(\mu_{st},\ \varphi_{st}) \\ \log(\mu_{stkj}) = \alpha + \sum_{i=1}^{I} f_i(X_{istj}) + Y_j + V_k + U_{st} \\ k = 1, \ldots, 66,\ \ j = 2011,\ 2012,\ 2013 \\ U_{st} = W_t + \rho U_{st-1} \end{gathered} \tag{1}$$

where μ_{st} and ϕ_{st} represent, respectively, the mean and dispersion of the estimated biomass. The linear predictor $\log(\mu_{stkj})$ considers the following components: α representing the intercept; $f_i(X_{istj})$ which allows fitting of any possible non-linear relationship of the environmental variables (Fahrmeir & Lang, 2001), corresponding to the second-order random walk functions for Chl-a, SST, bathymetry, current intensity and direction, and the time variable month. All the environmental variable values were aggregated in 10 time knots (i.e. constant group increments) to avoid overfitting the shapes (except month, which had 12 time knots); Y_j is the component of the temporal unstructured (iid) random effect for year and V_k is the random effect corresponding to the vessel ID. The final term, U_{st}, represents a latent spatial field W_t for each month t, corresponding to a spatially structured random effect for each location. Furthermore, ρ is a temporal (autoregressive) correlation parameter bounded by [0,1]. U_{st} refers to the progressive spatio-temporal structure of the biomass that is described in the work of Paradinas et al. (2017).

For the fixed effects and variance of the biomass process, vague prior distributions with a zero-mean and a standard deviation of 100 were set (Krainski et al., 2018). Penalized complexity (PC) priors (Fuglstad et al., 2019) were used to describe prior knowledge of hyperparameters of the spatial effect terms, and the precision parameters of the second-order random walks (RW2). These priors were set to satisfy P(prior.range < 0.5) = 0.05 and P(prior.sigma > 0.6) = 0.05. Therefore, we consider as prior information a spatial range greater than 0.5 degrees (around 66.6 km) and a standard deviation less than 0.6. The choice of the informative priors for the precision of the different variable RW2 effects was performed by means of a sensitivity analysis to ensure that the posterior distributions concentrated well within the support of the priors (Zuur et al., 2017).

All models were fitted using the integrated nested Laplace approximation (INLA) via the R-INLA software (https://www.r-inla.org/). Final model spatio-temporal predictions were carried out for a given mean vessel length (22.40 metres) over the study area, where the $\epsilon = 0.00001$ value was subtracted from the CPUE. Standardized monthly CPUE index was obtained from the median of the posterior predictive distribution biomass maps. The R code for the modelling process applied in this study can be found at this GitHub repository (https://github.com/FranIzquierdo).

3 | RESULTS

3.1 | CPUE modelling process

The best model for standardizing sardine biomass included vessel length, vessel ID, the spatio-temporal component, year, and month (Table 1; Tables S2 and S3). For the first modelling step, smoothed vessel length was the best effort capacity variable in terms of goodness of fit (Table 1). We selected only this variable because all of them were highly correlated (>0.7). Smoothed effects showed a better fit than linear effects for all cases (Table 1). In the second step, vessel ID was selected as the best variable because it showed the lowest DIC, WAIC, and LCPO values (Table 1). Vessel ID and harbour differed little, and the different nested combinations did not improve the goodness of fit (Table S1). In the third step, Chl-a and current intensity smoothed variables showed a small improvement in goodness of fit over the best model from Step 2 (Table 1). Different numbers of time knots tested to improve the variable performance had a negligible impact on the model and therefore were not selected. Note that the correlation of environmental variables with sardine catch was less than 0.1 in all cases. In the fourth step, the greatest reduction in DIC, WAIC, and LCPO was associated with year and the spatio-temporal component (Table 1). Moreover, inclusion of month to detect the cyclic temporal trend improved these indicators.

TABLE 1 Sequential model selection process for the European sardine (*Sardina pilchardus*) biomass (CPUE) standardization in the west coast of Portugal within the period 2011–2013

Selection of models	DIC	WAIC	LCPO	Rank
Step 1				
L_s	**665.42**	**670.23**	**6.02**	**1**
L_l	677.41	676.50	6.02	2
P_s	686.06	684.67	6.02	3
Step 2				
L + V	**642.42**	**619.24**	**6.01**	**1**
L + V + VH	642.78	618.02	6.01	2
L + H + HR	645.41	633.94	6.01	3
Step 3				
L + V + Chl-a$_s$	**639.75**	**612.56**	**6.01**	**1**
L + V + Int$_s$	640.89	613.90	6.01	2
L + V + Bath$_l$	642.96	620.18	6.01	3
Step 4				
L + V + Y + St + M$_c$	**550.30**	**509.24**	**5.99**	**1***
L + V + Y + St + M$_s$	556.86	517.01	5.99	2
L + V + Y + St	557.74	521.62	5.99	3

Note: Selection criteria is based on DIC, WAIC, and LCPO scores. Only the three best models of each step are presented. Capital letters represent variable names where L = vessel length, P = main engine power, V = vessel ID, H = harbour, R = region, Bath = bathymetry, Chl-a = chlorophyll-a, int = currents intensity, Y = year, St = progressive spatio-temporal structure and M = month. Subscript letters represent modelling effects where l = linear, s = smoothed (RW2), c = cyclic (RW2). Best model of each step is highlighted in bold and the best selected model is indicated by *.

3.2 | Best selected model

The presence of an autoregressive spatio-temporal term indicated a high degree of temporal persistence in the spatial distribution of adult sardines over the study area. The high temporal correlation parameter (ρ) of the progressive spatio-temporal structure (0.985) supported these results. The mean posterior value for the spatial effect range was 1.095 degrees, while the standard deviation was 0.751.

The smoothed effect for the variable vessel length showed that the relationship between catch biomass and vessel length was not strictly linear, especially for lengths of 21–26 m (see Figure 2). Moreover, the smoothed month effect captured the temporal cyclic trend well throughout the year, with a minimum effect in July and a maximum effect in November (see Figure 2). Vessel ID indicated important specific and random differences among the 66 vessels during the study period (Figure 2). In addition, mean biomass of the Iberian sardine decreased over the 3 years (Figure 2). The approximate difference between 2011 and 2013 of −0.5 (in log-scale) suggested that the overall mean biomass decreased by approximately 60% in the area.

The posterior distribution mean of the biomass spatial effect showed a homogeneous spatial pattern throughout the year (see Figure S4). This term represented the intrinsic variability associated with the spatial effect (removing the rest of model effects). Therefore, the differences between the mean spatial effect and the predicted biomass show the variability contributed by the other components of the model (see Figure 3 and Figure S4).

The median of the posterior predictive distribution for sardine biomass revealed areas with a persistent high concentration of fish throughout the whole year, being the central region the one with maximum values, whereas a moderate biomass area was seen in the south (Figure 3). The northern area was highest in biomass variability, with moderate biomass in the first quarter of the year, lower biomass in the second quarter, and highest values in the last quarter (Figure 3).

Regarding the uncertainty of the posterior predictive distribution for sardine biomass, high values in the first quartile indicate areas where biomass was high, while lower values in the third quartile indicate areas where biomass was low (Figure 4). In addition, the second quartile shows that the central region was the area with the highest annual values of sardine biomass (Figure 4).

Finally, the derived sardine CPUE index showed a cyclical trend with moderate values at the beginning of the year decreasing to a minimum value in July and increasing to a maximum peak in November (See Figure 5).

4 | DISCUSSION

The present study provided estimates of monthly spatio-temporal variability of sardine biomass distribution along the western coast

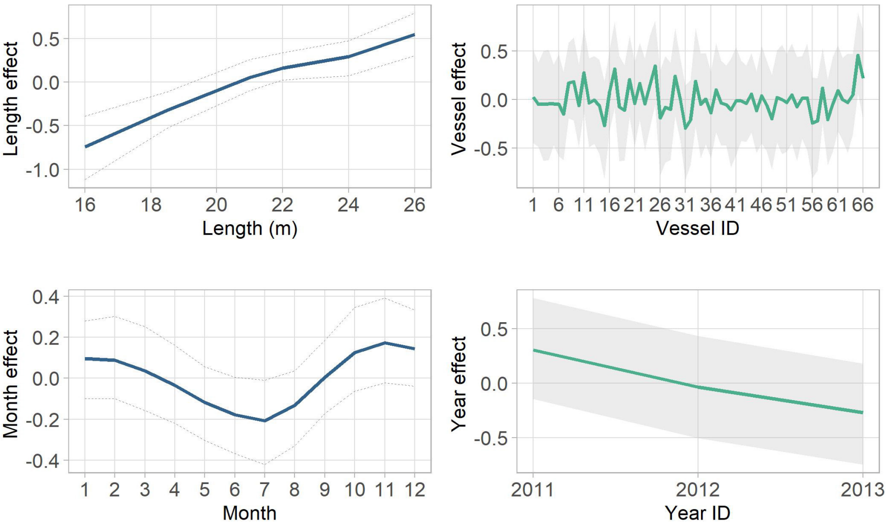


FIGURE 2 Marginal smoothed (RW2) effects of vessel length, month, and random (iid) effects of vessel ID (n = 66) and year (n = 3) on the linear predictor scale (logarithmic link) of the Iberian sardine biomass (CPUE) best model. Shaded regions represent the approximate 95% credibility interval

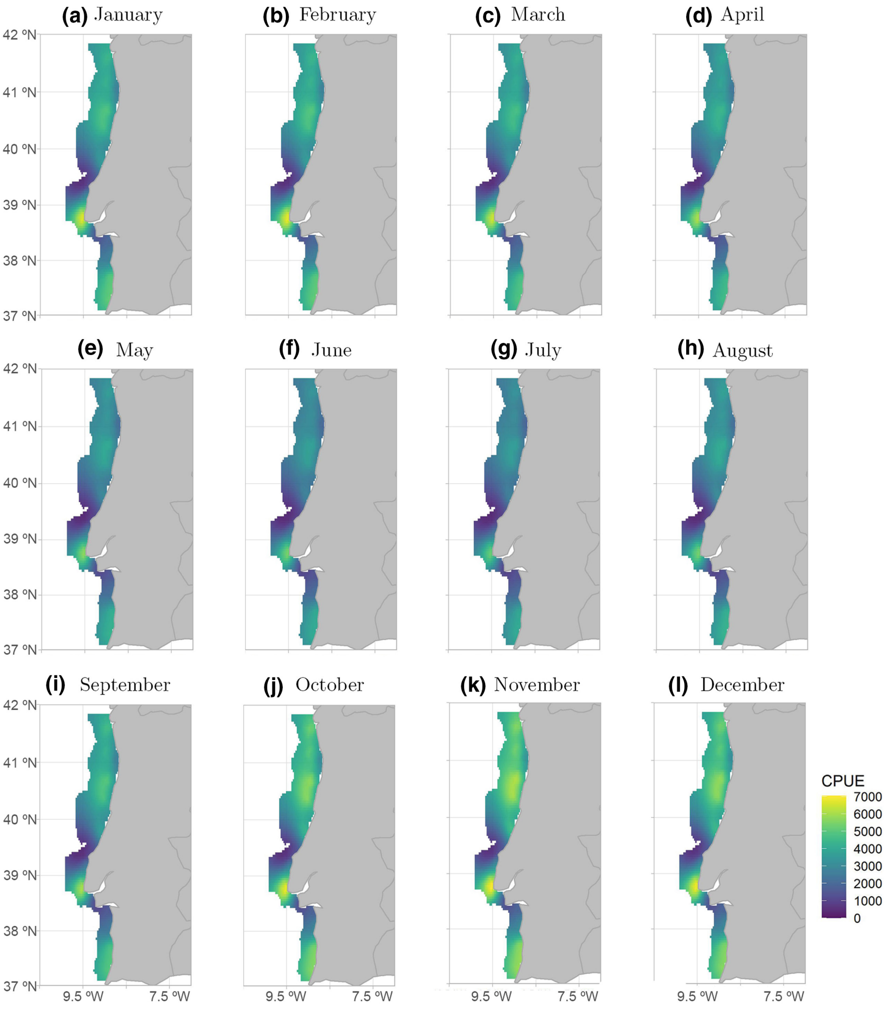


FIGURE 3 Median biomass (CPUE) maps of the posterior predictive distribution for European sardine (*Sardina pilchardus*) along the west coast of Portugal over the different months of the year. Note that the predicted sardine biomass (CPUE) corresponds to the catches (kg) taken for a given vessel length of 22.40 m within the period 2011–2013

of Portugal derived from commercial fishery data. The application of Bayesian models allowed the implementation of vessel characteristics, spatio-temporal dynamics, and environmental variables through fixed, smoothed, and various types of random effects, with a measure of the associated parameter uncertainty.

The use of the variable effort as a ratio of the response variable or included as an offset, assumes a linear relationship 1:1 between the catch and the effort. However, in some fleet-specific cases this may not be correct (Alonso-Fernández et al., 2019; Ward et al., 2004). Our study case modelled effort as an explanatory variable where smoothed effects had better goodness of fit than linear effects, and vessel length was the effort capacity variable. Engine power was not expected to have great influence, because smaller vessels could reach all the fishing grounds in the study area. Vessel length was

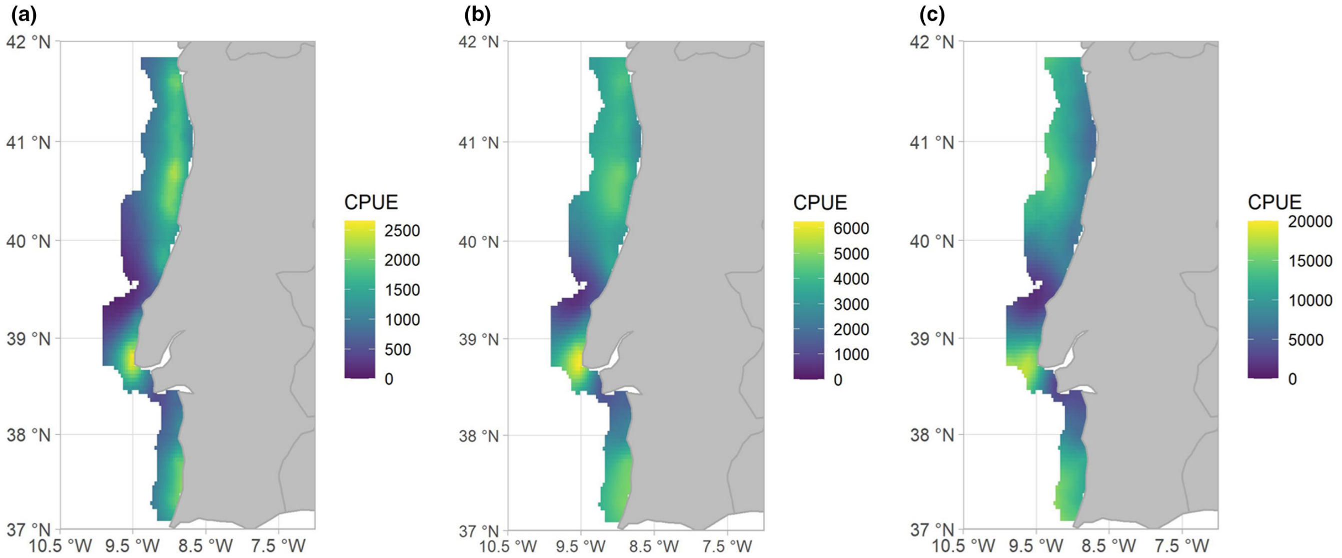
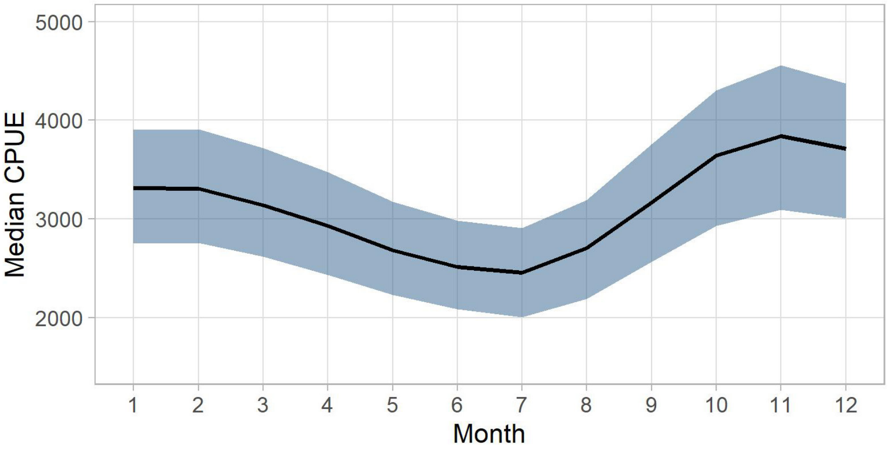


FIGURE 4 Total average for all months (January–December) corresponding to the first (a), second (b), and third (c) quartiles for the biomass (CPUE) of European sardine (*Sardina pilchardus*) posterior predictive distribution maps. These maps represent the uncertainty of the biomass (CPUE) prediction. Note that the predicted sardine biomass (CPUE) corresponds to the catches (kg) taken for a given vessel length of 22.40 m within the period 2011–2013

FIGURE 5 Spatio-temporal predicted biomass (CPUE) index of European sardine (*Sardina Pilchardus*) in the west coast of Portugal. Shaded lower and upper limits represent the first and third quartiles. This trend has been obtained by doing the median of the predicted biomass (CPUE) monthly maps. Note that the predicted sardine biomass (CPUE) corresponds to the catches (kg) taken for a given vessel length of 22.40 m within the period 2011–2013



also an important variable for the trawl fishery because longer vessels could catch more fish (Pennino et al., 2014). For the purse-seine fleet, vessel length differences were small, but were considered as a good proxy to explain effort capacity variability in the absence of other important factors (e.g. net size, number of workers) and effort time variables (e.g. haul duration, searching time).

Fishers may exhibit different fishing behaviour among regions, harbours and vessels, due to differences in fishing restrictions (ICES, 2018) or sardine abundance (Zwolinski et al., 2010). We found vessel ID to be the best variable to reflect these differences because a given vessel usually fished in the same region and landed in the same harbour. Furthermore, Vessel ID also may have helped to explain some intrinsic variability associated with a fisher's knowledge and behaviour. Therefore, the amount of catch in a given location logically depends more on the fishing vessel than on the region or harbour. Vessel was a fine-scale variable whose inclusion as a random effect allowed vessels to have different efficiencies and expected catches (Monnahan & Stewart, 2018).

For sardine CPUE data, Chl-a and the upwelling index and SST were significant for explaining the spatio-temporal abundance pattern in the Mauritanian sea (Bacha et al., 2017). Similarly, bottom depth and sea surface temperature were relevant variables that explained most sardine landing variability in the Mediterranean basin (Tugores et al., 2011). In our study, the only variables that influenced sardine catchability were Chl-a and current intensity, slightly improving the goodness of fit, although their improvement was too low to be selected in the modelling process. Sea surface temperature in the studied area/period ranged from around 11 to 22°C. The major variability of temperature was related to the seasonal cycle and not the spatial component. The optimal temperature for sardine larvae ranges from 13 to 17°C (Garrido et al., 2016) and thermal tolerance of small pelagic species increases throughout ontogeny (Peck et al., 2013). For this reason, the temperature experienced by sardines in this study was not expected to be a limiting factor that affected spatial distribution. Temperature might be significant over a longer period that includes extreme events (such as marine heatwaves and cold spells) or in areas where temperature falls outside or at the extremes of the species' range. Sardines are planktivorous throughout their life cycle, and are expected to prefer areas of high primary and secondary productivity. Recruitment strength correlated with years of higher Chl-a concentration during the spawning season (Garrido et al., 2017). In this study, Chl-a did not explain spatio-temporal variability of sardine catches. In the western Iberian area, the potential habitat for adult sardine was driven by a high chlorophyll-a concentration associated with mean or low salinity and both high and low temperatures (Zwolinski et al., 2010). The latter study used research survey data, which contains information about presence/absence and random sampling, while fishery data identifies mainly positive catches as a consequence of preferential sampling (Diggle et al., 2010; Pennino et al., 2019).

Sardine biomass decreased steadily within the study period (2011–2013), in accordance with the assessment of the state of the stock (ICES, 2018). The spatio-temporal progressive term explained most of the variability in sardine biomass, similar to the European hake (*Merluccius merluccius*) recruits in the northern Iberian Peninsula (Izquierdo et al., 2021) and to the different species of tuna (albacore, bigeye, and yellowfin) but also dolphin fish and broadbill swordfish in Australia analysed by Zhou et al. (2019). In our study, a high correlation parameter indicated that sardines were spatially persistent in the study area. This means that sardine biomass at a given location depends on the biomass that was present in the previous month and repeats itself throughout the year (Paradinas et al., 2017). Moreover, the addition of an extra smoothed cyclic effect for month allowed us to identify a temporal biomass trend with a noticeable improvement of the final model. This extra temporal term was also present in the best abundance model for mullet (*Mullus surmuletus* and *M. barbatus*) distribution in the Mediterranean (Paradinas et al., 2020).

The spatio-temporal distribution of predicted sardine biomass increased from north to south through the year. Similar to Zwolinski et al. (2010), we found higher biomass in the northern and central regions, followed by the southern area. In addition, our results confirmed that sardine occurrence was higher in autumn than spring in the northern area (Zwolinski et al., 2010). The northern part of the study area, where sardine biomass was higher, coincided with the main recruitment area for this species (Santos et al., 2012). Adult sardine catch variability could act as a proxy for recruitment with a lag of 1 year for a short-lived species (Borges et al., 2003). This could be one of the reasons why this area had the highest sardine biomass for both recruits and adults. Actually, northern and central regions had high sardine recruits, whereas only adults were encountered in the south (ICES, 2017b). We have found the southern area to be the one with the lowest biomass of sardines, with the lowest values in the first quarter of the year and highest values during the last quarter. This follows the above-mentioned hypothesis that recruits and adults are strongly related for the three regions in the study area. Finally, the central region is a high concentration area for all months, although lower in the middle half of the year. This result also matches the findings of Zwolinski et al. (2010), who reported a significant increase in sardine prevalence from autumn to spring.

Most stock assessment models use yearly indices to represent annual levels of relative biomass of species (Maunder & Harley, 2002). It is important to state that misspecification of these indices can lead to a significant weakness in the performance of the assessment models when linking the stock trend to the biomass index (Methot Jr & Wetzel, 2013; Tagliarolo et al., 2021). In our case study, we standardized a CPUE with a monthly temporal resolution, but the same approach could be applied for years. Despite the progressive monthly differences in the sardine biomass, the distribution pattern of the species could be grouped by year quarters. This information may be useful to managers to select the best season when planning a scientific survey or a spatially explicit management plan (Szalaj et al., 2018). Thus, we argue that the use of the spatio-temporal progressive term is one of the main strengths of the present study. This component represents the model uncertainty associated with space over time. In an ideal study case, if we had perfect explanatory variables in the model, the spatio-temporal mean effect map would be zero. As was shown in a study of sardine distribution in the north of Spain, the assumption that a single process was most important led to biased results because the environment in which fish lived was explicitly complex and multidimensional (Carrera & Porteiro, 2003). Therefore, the inclusion of a spatio-temporal component in CPUE standardization helps to explain spatio-temporal variability of unknown environmental covariates and fishing influencing factors (e.g. food availability or fisher's knowledge) that are not explicitly included in the model.

In conclusion, the CPUE standardization process plays a fundamental role in the study of commercially exploited species, as fishery-dependent indices influence the calibration of stock assessment models. For this type of data, the consideration of spatio-temporal dependence in the standardization process may have a great relevance, especially when there is a lack of information on environmental covariates or fishing-related variables. The use of a Bayesian spatio-temporal approach to model CPUE data allowed us to understand the distribution of sardine biomass along the west coast of Portugal throughout the year. The presented approach is a flexible modelling method, as it accounts for vessel characteristics, spatial variability over time and environmental covariates, providing a relative biomass index and its associated uncertainty. This methodology is applicable to a wide range of commercial fishery species and can contribute to improve our knowledge of the spatio-temporal distribution and biomass trends for ecological studies and stock assessments.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Portuguese fisheries authority "DGRM - Direcção Geral dos Recursos Marinhos, Segurança e Serviços Marinhos". Restrictions apply to the availability of these data, which were used under license for this study. Data are available from Susana Garrido with the permission of DGRM.

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