

# Assessing the spatiotemporal persistence of fish distributions: a case study on two red mullet species (*Mullus surmuletus* and *M. barbatus*) in the western Mediterranean

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**ABSTRACT:** Understanding the spatiotemporal persistence of fish distributions is key to defining fish hotspots and effective fisheries-restricted areas (FRAs). Hierarchical Bayesian spatiotemporal models provide an excellent framework to understand these distributions, as they can accommodate different spatiotemporal behaviour in the data, primarily due to their flexibility. The aim of this research was to characterize the fundamental behavioural patterns of fish as persistent, opportunistic or progressive by comparing different spatiotemporal model structures in order to provide better information for marine spatial planning. To illustrate this method, the spatiotemporal distributions of 2 sympatric Mullidae species, the striped red mullet *Mullus surmuletus* and the red mullet *M. barbatus*, were analysed. The occurrence of each species, its conditional-to-presence abundance and median length were analysed using Mediterranean trawl survey data from the western Mediterranean between 2000 and 2016. Results demonstrate that there are various common hotspots of both species distributed along the Iberian coast. The convenient persistent spatiotemporal distribution of these hotspots facilitates the configuration of a network of connected FRAs for red mullets in the study area.

**KEY WORDS:** Fisheries management · Fisheries-restricted areas · Marine spatial planning · Spatiotemporal · Species distribution modelling

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## 1. INTRODUCTION

The identification of important fishery conservation areas, such as nurseries and spawning areas, has been linked to persistent hotspots (Fiorentino et al. 2003, Colloca et al. 2009), i.e. areas that repeatedly concentrate large abundances of fish. However,

assessing their persistence is a challenging task due to the inherent constraints of sampling at sea and the fact that fish distributions can vary over time. In this regard, spatiotemporal species distribution models (SDMs) may play a crucial role.

SDMs link species occurrence, abundance and other measures to environmental drivers (Costa et al.

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2017) and other unobserved spatial or spatiotemporal autocorrelation effects. SDMs are able to produce statistically robust predictions for previously unsampled locations (Zimmermann et al. 2010, Martínez-Minaya et al. 2018), which facilitates the identification of hotspots by, for example, using an upper percentile of the spatial predictions (Fiorentino et al. 2003, Nelson & Boots 2008, Colloca et al. 2009). However, spatiotemporal SDMs can be difficult to fit. A good option for fitting them is the Bayesian approach. This approach is convenient for tackling spatiotemporal SDMs given how spatial and temporal random effects statistics can be incorporated into a Bayesian hierarchical model (Banerjee et al. 2014). Indeed, development and implementation of Bayesian SDMs in fisheries ecology has widely increased in recent years, and these models can provide good insight to identifying important fisheries areas, such as nursery and spawning areas (Colloca et al. 2009, Paradinas et al. 2015).

A variety of research approaches have been suggested to assess persistence. Fiorentino et al. (2003) proposed the use of yearly hotspot frequency maps. Colloca et al. (2009) suggested the creation of annual Bayesian kriging maps and the application of aggregation curves to identify the level of persistence in different areas. Paradinas et al. (2015) proposed a Bayesian inference-based method to compare 2 spatiotemporal model structures, one to fit persistent scenarios, i.e. spatial distributions that do not change over time, and the other to accommodate opportunistic scenarios, i.e. spatial distributions that change independently across subsequent time events. Paradinas et al. (2017) enhanced the latter approach by including a third spatiotemporal structure to fit progressive spatiotemporal distributions, i.e. distributions confined between the fully persistent and the fully opportunistic scenarios that allow smooth spatial changes over time (see Section 2.2 for a more detailed explanation). However, the progressive and opportunistic spatiotemporal structures of Paradinas et al. (2017) assumed constant population sizes and disregarded any overall population size fluctuations.

The objective of our study was to characterize the spatiotemporal behaviour of fish distributions in order to assist marine spatial planning (MSP). To do so, we used 3 different spatiotemporal model structures to characterize the fundamental behavioural patterns of fish as either persistent, opportunistic or progressive, and to infer their relative population size trends. To demonstrate this approach, we applied it to 2 economically important fish species: the red mullet *Mullus barbatus* L., 1758 and the striped red mullet *M. surmuletus* L., 1758.

*M. barbatus* and *M. surmuletus* are sympatric demersal species that commonly inhabit the sandy and muddy bottoms of coastal areas and the continental shelf (Fischer et al. 1987). These 2 species have common feeding characteristics, as they are both benthic carnivores and primarily feed on small invertebrates (crustaceans, molluscs, polychaetes, etc.) (Gharbi & Ktari 1979). Both mullets are commercially valuable species throughout the Mediterranean (Reñones et al. 1995, Stergiou 2002). In Spain, trawlers represent 80 % of landings, of which almost 70 % are *M. barbatus* (García-Rodríguez et al. 2011).

Various studies have examined the distribution of *M. barbatus* and *M. surmuletus* in Mediterranean areas and have commented on variations in their bathymetrical distribution and abundance (e.g. Tserpes et al. 1999, Lombarte et al. 2000, Machias & Labropoulou 2002). However, these studies only focussed on estimating the relationship between species abundance and bathymetry and not on mapping and explicitly predicting species spatial patterns over time. From a biological perspective, a recent study by Tserpes et al. (2019) that analysed EU-funded Mediterranean International Trawl Survey (MEDITS) data from both species using the generalized additive modelling technique in the Mediterranean Sea, found that the biomass of both species declined with depth. Fiorentino et al. (2008) suggested that sea surface temperature increases northwest of Sicily during the pre-recruitment phase of *M. barbatus* could have had a positive effect on the stock and contributed to the benefits derived from trawling bans. Although there is a lack of relevant physiological studies, the differences in spatial distribution patterns among the species suggest that *M. barbatus* is more thermophilic than *M. surmuletus* (Kaschner et al. 2016). Finally, past studies have suggested that seafloor characteristics can affect the distribution of red mullets. Whereas *M. surmuletus* prefers rough substrates and narrow continental shelves, *M. barbatus* is more abundant in muddy bottom areas (Hureau 1986, Fischer et al. 1987, Lombarte et al. 2000). Indeed, eco-morphological studies suggest the existence of adaptive morphological and anatomical characteristics that allow *M. barbatus* to better exploit resources from muddy and turbid bottoms than its congener (Lombarte & Aguirre 1997).

Several studies agree that *M. barbatus* stocks have grown throughout most Mediterranean geographic sub-areas (GSAs) over the last decade (Vasilakopoulos et al. 2014, Tserpes et al. 2016, 2019, Cardinale et al. 2017, GFCM 2018). Sieli et al. (2011) hypothesized that the additional trawling prohibitions imple-

mented through EC No 1967/2006 (Council of the European Union 2006) have contributed to this increase. However, stock assessments of *M. barbatus* over the last decade have consistently classified it as an overfished species in the GSA06 (study area, see below) and suggested a reduction of the fishing effort (WGSAD 2019). Although *M. surmuletus* has not been evaluated in the GSA06, results from Tserpes et al. (2019) seem to show rather stable population sizes over the last years. Given that *M. surmuletus* prefers rough bottoms, we hypothesized that trawling prohibitions have had less impact on it and that other measures such as fisheries-restricted areas (FRAs) could have a greater impact.

## 2. MATERIALS AND METHODS

### 2.1. Red mullets in the Mediterranean

Data on *Mullus barbatus* and *M. surmuletus* (hereafter referred to as 'red mullet') were collected during the EU-funded MEDITS (Bertrand et al. 2002) carried out between spring and early summer (April to June) between 2000 and 2016. The MEDITS project follows a stratified sampling design based on coverage of 5 bathymetric strata (10–50, 51–100, 101–200, 201–500 and 501–700 m) in each Mediterranean GSA and uses a GOC-73 net with a 20 mm mesh size. Sampling stations were randomly placed within each stratum at the beginning of the project. In all subsequent years, sampling was carried out in similar locations. The duration of the hauls was fixed to 30 min in depths of <200 m and to 1 h in deeper waters. This study covers the trawlable grounds of the GSA06, which borders the northern Iberian Mediterranean coast. A total of 1448 trawl operations were observed over a period of 17 yr, averaging 80 fishing hauls per year. Presence of *M. barbatus* was recorded in 55% of the hauls and of *M. surmuletus* in 38% of the hauls. Mean abundance was approximately 33.4 and 4.8 ind. haul<sup>-1</sup> for *M. barbatus* and *M. surmuletus*, respectively. It should be noted that MEDITS cannot sample over rocky seabed, where *M. surmuletus* is more abundant (Tserpes et al. 2002). With respect to length, the smallest *M. barbatus* specimens were 5 cm in length, the largest were 30 cm, and the median observed length was 15 cm. For *M. surmuletus*, the smallest specimens were 3 cm in length, the largest were 39 cm, and the median observed length was 18 cm.

We analysed 3 different response variables to characterize the distribution of both species. First, we

considered the presence/absence variable to measure the occurrence of each species. Second, we used the total number of individuals captured per 30 min of trawling (i.e. number per unit effort, NPUE) for positive observations only as an indicator of the conditional-to-presence abundance of the species. While kilograms per unit effort is a more common indicator of abundance, NPUE does not vary according to the length of the fish, which may be especially relevant when analysing the abundance of recruits measured in different months of the year. Finally, to assess the spatiotemporal segregation of both species by length, we considered a third variable by calculating the median length of specimens caught in each haul.

A descriptive analysis of the data indicated spatially structured distributions for both species (Fig. 1). Therefore, all 3 response variables were modelled using both a smooth bathymetric effect and the different spatiotemporal structures described in Section 2.2. The bathymetry map was obtained from the European Marine Observation and Data network (EMODnet, [www.emodnet.eu/](http://www.emodnet.eu/)), developed for marine spatial ecology, and has a spatial resolution of  $0.002 \times 0.002$  decimal degrees (i.e. 20 m).

### 2.2. Spatiotemporal modelling

Point-referenced spatial models (Cressie 1993) are suitable in situations where observations are carried out within a defined continuous spatial domain. The main purpose of spatial modelling is to infer the unobserved spatial structure of the data to enhance predictions in unsampled locations (Cressie 1993). Trawl fisheries spatial studies have traditionally relied on point-referencing the data into the centroid of the fishery transect, which neglects within-haul variability. Unfortunately, MEDITS does not collect video footage of the trawl and, therefore, there is no information on what is caught along the transect to account for the catch distribution throughout the fishing operation.

As with the spatial domain, observations collected at similar times tend to be more related than temporally distant ones (Cressie & Wikle 2015) and, therefore, lead to temporally autocorrelated data. SDMs commonly include temporal trends as fixed effects to infer overall temporal patterns. However, temporal trends may not account for temporal autocorrelation in the data. Thus, a better approach may be to include time in a spatiotemporal covariance function (Cameletti et al. 2013). Hierarchical Bayesian models

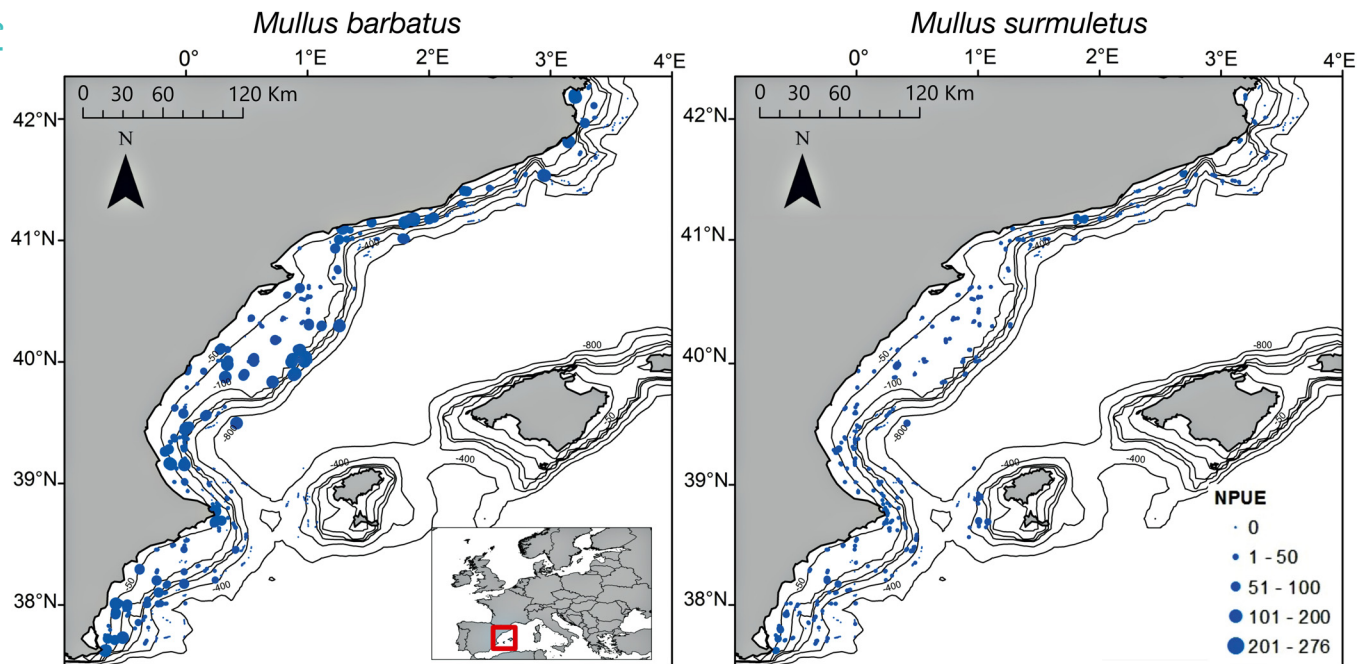


Fig. 1. Mediterranean trawl survey data distribution from 2000 to 2016 for *Mullus barbatus* and *M. surmuletus*. The sizes of the circles are proportional to the numbers per unit effort (NPUE)

are flexible and, therefore, enable diverse spatio-temporal structures to accommodate different types of spatiotemporal patterns in order to evaluate whether these patterns are persistent or change over time, and if they do change, to what extent (Paradinas et al. 2017).

This study applied Bayesian spatiotemporal geostatistical models using the integrated nested Laplace approximation approach (Rue et al. 2009) for R (R Core Team 2019) and its stochastic partial differential equations (SPDE) module (Lindgren et al. 2011). The SPDE approach approximates continuous Matérn spatial Gaussian fields through Gaussian Markov Random Fields that are efficiently exploited under the R-integrated nested Laplace approximations (INLA) software. R-INLA is a very flexible and relatively user-friendly software that enables the user to fit complex spatiotemporal SDMs (Blangiardo et al. 2013, Muñoz et al. 2013). This is done through a so-called mesh, a Delaunay triangulation of the spatial domain, where each knot represents an integration point in space. As opposed to a regular grid, the distance between mesh nodes is irregular. For this study, we chose a minimum distance between knots that is equal to the minimum distance between yearly hauls so that inferred spatial effects could account for the shortest distances in the data.

#### 2.2.1. Modelling occurrence and NPUE distribution

Collecting fisheries abundance data spatiotemporally often results in a large proportion of zeros observed, i.e. zero-inflated data. These data are generally analysed using 2-part models, also known as hurdle models (Jones 1989). Generally, occurrence and NPUE are modelled independently. However, abundance and detection probability (occurrence) are often related (Kéry et al. 2005, 2009), which violates the independence assumption of common hurdle models. In this study, shared bathymetric effects were incorporated following Paradinas et al. (2017) in order to incorporate information on both the occurrence and the NPUE to better fit informed environmental effects. Shared spatiotemporal effects were not fitted because they do not perform well in trawl fisheries spatial effects (Quiroz et al. 2015, Paradinas et al. 2017). Paradinas et al. (2017) hypothesized that this could be due to reasonably small spatial presence-absence variability compared to that of abundance. As a result, very different spatial covariance functions were fitted in the occurrence and NPUE models.

Let  $Y_{st}$  and  $Z_{st}$  be the spatiotemporally distributed occurrence and NPUE, respectively.  $s = 1, \dots, nt$  refers to the spatial location and  $t = 1, \dots, m$  to the temporal index. Occurrence ( $Y_{st}$ ) was modelled using a Bernoulli distribution, and NPUE ( $Z_{st}$ ) was modelled

using a negative binomial distribution, which is a probability distribution that captures the overdispersion of count data. The means of both variables were modelled through the logit and log link functions, respectively, to the bathymetric and spatiotemporal effects

$$\begin{aligned} Y_{st} &\sim \text{Be}(\pi_{st}) \\ Z_{st} &\sim \text{NB}(\mu_{st}, \sigma_{st}) \\ \text{logit}(\pi_{st}) &= \alpha^{(Y)} + f(d_s) + V_{st}^{(Y)} \\ \log(\mu_{st}) &= \alpha^{(Z)} + \theta f(d_s) + V_{st}^{(Z)} \end{aligned} \quad (1)$$

where  $\pi_{st}$  represents the probability of occurrence at location  $s$  at time  $t$  and  $\mu_{st}$  and  $\sigma_{st}$  are the mean and variance of the NPUE, respectively. The linear predictors, which contain the effects that link the parameters  $\pi_{st}$  and  $\mu_{st}$  include:  $\alpha^{(Y)}$  and  $\alpha^{(Z)}$ , terms that represent the intercepts of each respective variable;  $f(d_s)$  is the bathymetric effect modelled as a second-order random walk smooth function parametrised as unknown values  $f = (f_0, \dots, f_{i-1})^T$  at  $i = 25$  equidistant values of  $d_s$ , with hyperparameter  $\rho_d$  representing the variance of the  $f(d_s)$  model.  $f(d_s)$  is shared between both predictors and multiplied by  $\theta$  in the NPUE model to allow for different scales between both predictors, i.e. the logit transformed probability and the logarithm of the NPUE.  $V_{st}^{(Y)}$  and  $V_{st}^{(Z)}$  refer to the spatiotemporal structures of fish occurrence and NPUE, respectively, and can follow any of the 3 spatiotemporal structures described in Section 2.2.

The Bayesian approach requires prior distributions for each parameter of the model. We used R-INLA default vague prior distributions for the variance of the NPUE, the fixed effects and the scaling parameter of the shared effects. However, we chose different prior distributions for the hyperparameters of the geostatistical terms and the  $\rho_d$  hyperparameter of the second-order random walks. The reason for this is because those parameters were embedded in our Bayesian hierarchical model, and it was not easy to find non-informative priors for them. In line with Simpson et al. (2017) and Fuglstad et al. (2019), we used penalised complexity priors, also known as PC priors, i.e. weak informative priors, that can leverage prior knowledge and are appropriate for hierarchical models when model components are combined linearly in the latent part of the model, like the ones used here. Specifically, we used PC priors that followed the following criteria: (1) the probability that the spatial effect range was smaller than 150 km was 0.15, to avoid very small spatial autocorrelation ranges, (2) the probability that the spatial effect variance was greater than 1 was 0.20, to avoid masking the bathymetric effect through the spatial effect, and (3) the

probability that  $\rho_d$  was greater than 0.5 in the occurrence model and greater than the observed NPUE standard deviation in the NPUE model was 0.01. We also performed a sensitivity analysis of the choice of priors by testing different priors and verifying that the posterior distributions were consistent and concentrated well within the support of the priors.

### 2.2.2. Modelling median length distribution

In addition to the corresponding occurrence and NPUE models, we also fit a conditional-to-presence median specimen length model to provide insight into the habitat use of different life stages. Median length was modelled using a Gaussian distribution, as is customary in age-class analyses (Markatou 2000). If  $U_{st}$  denotes the spatiotemporally distributed median specimen length, then:

$$\begin{aligned} U_{st} &\sim N(\mu_{st}, \sigma_{st}) \\ \mu_{st} &= \alpha^{(U)} + f(d_s) + V_{st}^{(U)} \end{aligned} \quad (2)$$

where  $\mu_{st}$  and  $\sigma_{st}$  represent mean and variance, respectively.  $\mu_{st}$  was modelled using a usual identity link, and the remaining model components follow the same structures as in Eq. (1). Selected priors were the same as in the NPUE model.

## 2.3. Assessing the persistence of the red mullet distribution

The spatiotemporal behaviour of the data can vary depending on the nature of the fish being studied and the available data resolution. Here, we propose that 3 spatiotemporal structures,  $V_{st}$ , be studied based on a geostatistical term  $W$  that accounts for the spatial autocorrelation in the data in continuous space. Each of these  $V_{st}$  structures builds a different type of spatiotemporal pattern over  $W$  to characterize the level of persistence in persistent, opportunistic or progressive distributions (see summary in Table 1).

### 2.3.1. Fully persistent fish distributions

A fully persistent distribution implies that spatial preference is the same at different moments in time, regardless of the overall population size of the species at the observed moment. Therefore, modelling persistent scenarios requires a structure that fixes the spatial distribution over time but allows mean intensity changes to absorb overall population dynamics:



Table 1. Explanation of the 3 different spatiotemporal structures compared in the models.  $V_{st}$  is the generalized term used to denote a spatiotemporal structure in Eqs. (1) & (2);  $W$  is the geostatistical field of  $V_{st}$ ;  $f(t)$  is a temporal trend effect; and  $\rho W_{st-1}$  is a first-order autoregressive relationship between subsequent spatial realizations

Model	Notation	Description
Opportunistic	$V_{st} = W_{st} + f(t)$	$V_{st}$ is decomposed in different and uncorrelated realizations of the spatial field $W_{st}$ for each year $t$ and an additive temporal trend $f(t)$
Persistent	$V_{st} = W_s + f(t)$	$V_{st}$ is a common realization of the spatial field $W_s$ for each year ( $t$ ) and an additive temporal trend $f(t)$
Progressive	$V_{st} = W_{st} + \rho W_{st-1} + f(t)$	$V_{st}$ is decomposed in correlated spatial realizations $W_{st}$ that change over subsequent time events using a first order autoregressive model $\rho W_{st-1}$ . The model includes an additive temporal trend $f(t)$

$$V_{st} = W_s + f(t) \quad (3)$$

where the spatiotemporal structure  $V_{st}$  modelled through a single geostatistical term  $W_s$  is inferred using all observations from different time events  $t$ , and accommodates mean intensity changes through a function of time  $f(t)$ . This study applied a second-order random walk effect to  $f(t)$ , but a simple random effect could also be implemented. In summary, this structure benefits those distributions that do not change throughout time.

### 2.3.2. Opportunistic fish distributions

An opportunistic distribution describes a situation where a fish distribution shows substantial fluctuations from time event to time event with no apparent relation between them. The overall population size may also change with time. Thus, a sensible opportunistic structure must accommodate very different spatial distributions at different time events:

$$V_{st} = W_{st} + f(t) \quad (4)$$

where the spatiotemporal structure is decomposed into different geostatistical terms  $W_{st}$  for each time event, as proposed by Paradinas et al. (2015). Therefore, the species distribution is able to change independent of each time event. We also included an extra temporal trend effect  $f(t)$  using a second-order random walk effect to infer any mean intensity changes over time.

### 2.3.3. Progressive fish distributions

A progressive distribution describes fish distributions that are neither fully persistent nor fully oppor-

tunistic, i.e. distributions that change smoothly over time, and whose overall population size changes over time. Therefore, a progressive spatiotemporal structure must allow smooth transitions in the distribution of fish from one time event to another and, if possible, quantify the level of change between time events:

$$V_{st} = W_{st} + \rho V_{st-1} + f(t) \quad (5)$$

where  $V_{st}$  and  $V_{st-1}$ , are the fitted spatial distributions in time  $t$  and time  $t-1$ ,  $W_{st}$  is a combination of the distribution observed at time  $t$  and the fitted spatial distribution in  $t-1$  weighted by  $\rho$ , i.e. a first-order autoregressive parameter that assesses the level of similarity between subsequent geostatistical fields. Therefore,  $\rho$  also provides information on the degree of persistence in the process. The closer the  $\rho$ -value is to 1, the more persistent the process (i.e. very high correlation between subsequent years), whereas  $\rho$ -values closer to 0 suggest more opportunistic distributions (i.e. uncorrelated distributions). We also included an extra temporal effect  $f(t)$  using a second-order random walk effect to infer any mean intensity changes over time.

## 2.4. Model selection

The models were selected by testing all possible structures using the Watanabe Akaike's information criterion (WAIC) (Watanabe 2010) for goodness of fit and the log-conditional predictive ordinate (LCPO) (Gneiting & Raftery 2007) for predictive quality measures. WAIC and LCPO scores are inversely related to the compromise between fit, parsimony and predictive quality, i.e. higher scores denote worse models. Models were fitted using the 'INLA' package (Martins et al. 2013) in R version 3.6.1 (R Core Team 2019).

## 2.5. Identification of hotspots

Identification of red mullet hotspots was based on the 90<sup>th</sup> percentile of the NPUE in each year at depths of between 0 and 700 m. The 90<sup>th</sup> percentile selects the most abundant 10% of the study area. We chose this value by using the 10% marine protection goal set in different international agreements, e.g. CBD Aichi target 11 (<https://www.cbd.int/doc/publications/cbd-ts-78-en.pdf>), UN sustainable development goal 14 (<https://sustainabledevelopment.un.org/sdg14>), EU common fisheries policy target 14.5 ([https://ec.europa.eu/sustainable-development/goal14\\_en](https://ec.europa.eu/sustainable-development/goal14_en)), etc. This percentile cut-off value could be changed at any time to meet required management policies.

## 3. RESULTS

According to model selection scores (Table 2), the occurrence and NPUE distributions of both species were progressive. Persistent model scores were quite close to the progressive structure, suggesting that distributions were relatively persistent between 2000 and 2016. These results were supported by the strong temporal correlation parameters in the progressive spatiotemporal model (0.98 and 0.97, for the occurrence and NPUE, respectively, of *M. surmuletus* and 0.96 and 0.97, respectively, for *M. barbatus*).

Yearly median length patterns were different for both species (Table 2). *M. barbatus* results follow a progressive distribution, with a temporal correlation of 0.74, meaning that the spatial structure significantly changed from year to year. By contrast, *M.*

*surmuletus* median length spatial distribution was persistent.

The predicted bathymetric distribution of both species' occurrence and NPUE revealed a clear decrease with depth (Fig. 2). By contrast, median length increased with depth, to a maximum observed depth of 325 m for *M. barbatus* and 300–450 m for *M. surmuletus*.

The overall abundance of both red mullets increased over the course of study period, as shown in Fig. 3. The marginal temporal effects of Fig. 3 are in the log scale. Thus, a difference of +0.75 and +0.3, which are the approximate differences between 2000 and 2016 for *M. barbatus* and *M. surmuletus*, respectively, suggests that the overall abundance has increased by approximately 110% in the case of *M. barbatus* and 35% in the case of *M. surmuletus*.

As presented in Eqs. (1) & (2), posterior mean maps (1 km × 1 km resolution) are driven by a combination of bathymetric and spatiotemporal effects (Figs. 4 & 5). Occurrence maps highlight that the most suitable habitats for both species are located over the continental shelf along the Iberian Mediterranean coast (Fig. 4). The locations of *M. barbatus* and *M. surmuletus* hotspots were similar, but overall, the predicted hotspots for *M. surmuletus* were larger than those for *M. barbatus*. Zone A in Fig. 5 shows a large joint hotspot around Islas Hormigas and another around Tabarca, which was not identified as a hotspot for *M. barbatus*, despite NPUEs being relatively high. Both locations have been marine reserves since 1995 and 1986, respectively. Zone B highlighted 3 joint hotspots in the central part of the study area between Valencia and the Ebro delta, including a marked hotspot around Columbretes, which has been a marine reserve since 1989. Additional smaller hotspots were found near Valencia and off the coast of the Ebro delta, near the edge of the continental shelf. Finally, several smaller hotspots were identified in the northern part of the study area, along the Catalanian shelf and its canyons (Zone C in Fig. 5). These canyons are highly productive areas that could favour the aggregations of recruits (Lloret & Leonart 2002). The NPUE maps also appear to show that the southern part of Ibiza constitutes an important hotspot for both species. However, the reality is that occurrence probability is very low for *M. barbatus*.

Table 2. Model comparison for the different response variables based on the Watanabe Akaike's information criterion (WAIC) and the log-conditional predictive ordinate (LCPO) scores. Due to the joint modelling of NPUE and occurrence, we obtained a single joint model score for both predictors. Rank 1 stands for the best model and 3 for the worst.  $\Delta$ WAIC and  $\Delta$ LCPO represent the deviations of these model selection scores from the best model, which is represented as the reference level '–'

Model	NPUE occurrence			Median length		
	Rank	$\Delta$ WAIC	$\Delta$ LCPO	Rank	$\Delta$ WAIC	$\Delta$ LCPO
<b><i>Mullus barbatus</i></b>						
Opportunistic	3	+728	+0.98	2	+15	+0.01
Progressive	1	–	–	1	–	–
Persistent	2	+56	+0.02	3	+32	+0.02
<b><i>Mullus surmuletus</i></b>						
Opportunistic	3	+188	+0.17	3	+18	+0.02
Progressive	1	–	–	2	+5	+0.01
Persistent	2	+48	0	1	–	–

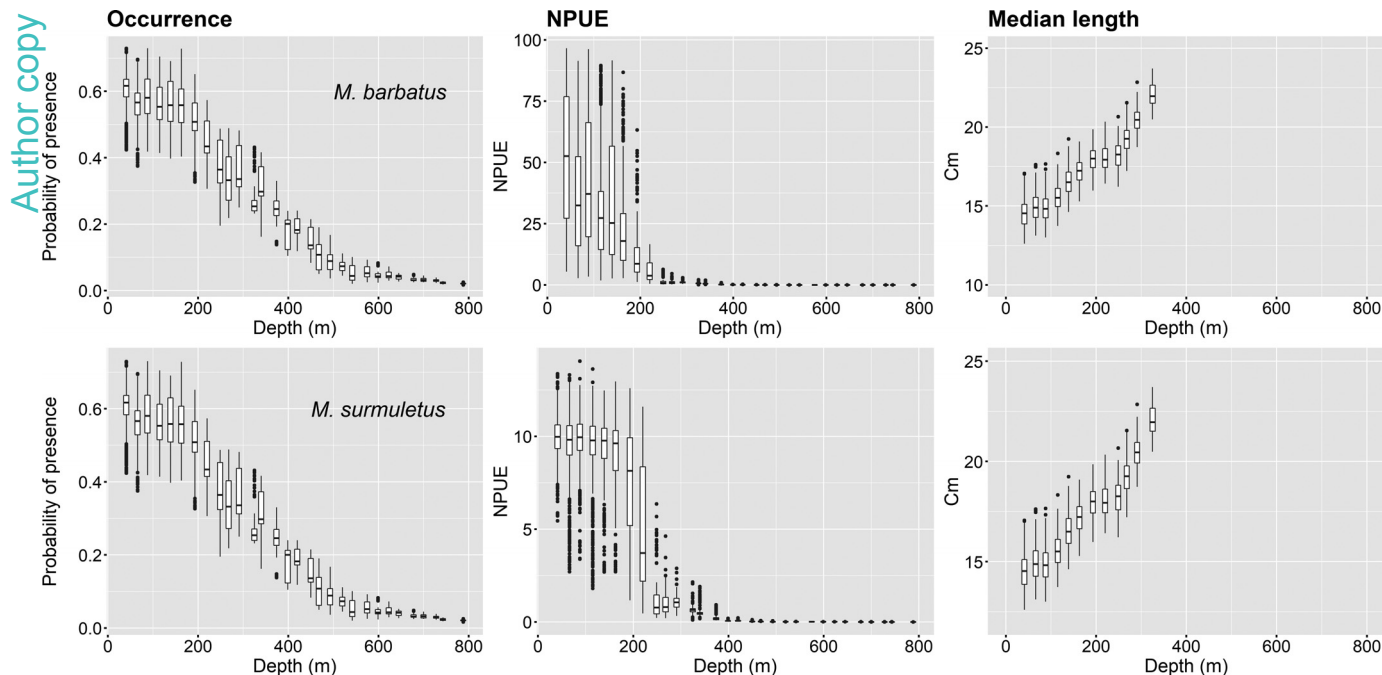


Fig. 2. Mean fitted value boxplots of the occurrence probability, number per unit effort (NPUE) and median length models at different depths for *Mullus barbatus* (top row) and *M. surmuletus* (bottom row). Each boxplot corresponds to an approximately 20 m depth interval. Each box represents the interquartile range of the mean fitted values, the central bold line represents the median value, and dots represent fitted values above 1.5 times and below 3 times the interquartile range beyond either end of the box

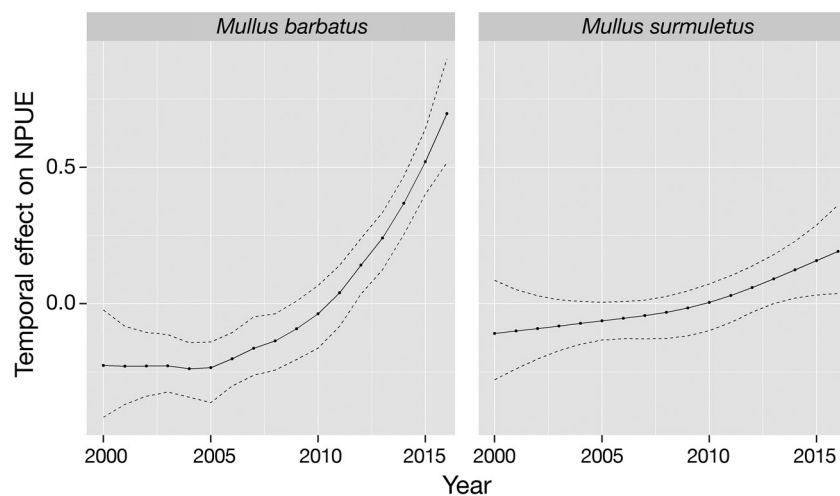


Fig. 3. Marginal temporal effects in the linear predictor scale (logarithmic link) of *Mullus barbatus* and *M. surmuletus* NPUE. Solid lines represent the mean of the effect while dotted lines represent the 95 % credible intervals

The median length distribution of *M. barbatus* changed progressively over time but, on average, as seen in Fig. 4, larger specimens were found around the deeper waters of the southern Catalanian shelf and near Valencia. The length distributions of *M. surmuletus* were rather persistent, with smaller

specimens concentrated in the central part of the study area and larger specimens found in the north, along the Catalanian shelf.

#### 4. DISCUSSION

SDM studies have often disregarded the importance of accounting for the time scale in fish spatial distributions (Dunn et al. 2016). Understanding the level of spatiotemporal persistence of fish is essential to identifying well informed hotspots (Warren 1998, Davoren 2007, Suryan et al. 2012) and key to MSP decision making. In fact, by only applying spatial techniques to analyse spatiotemporal data, it could generate misleading hotspot identification in non-persistent scenarios.

For example, a merely spatial analysis in an area that has had both high and low abundance observations over the years could infer high abundance estimates, whereas a spatiotemporal analysis, like the one performed in this study, would more appropriately infer high-low



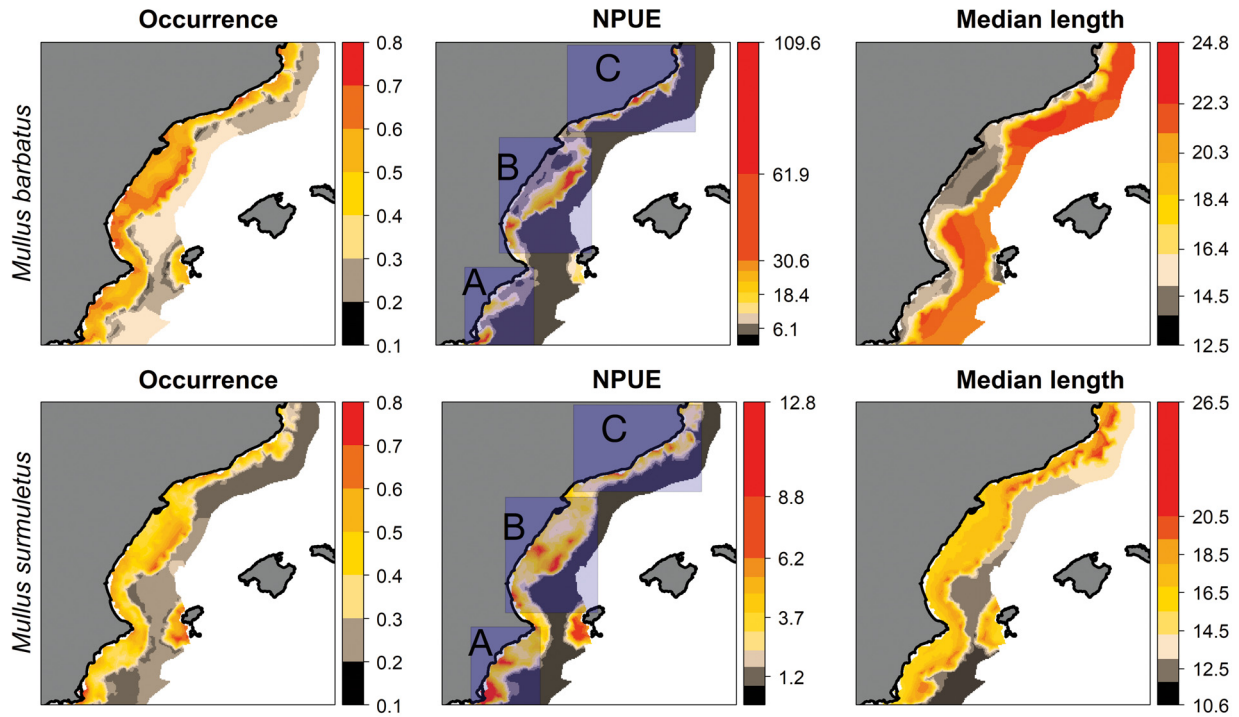


Fig. 4. Average spatial distributions of *Mullus barbatus* and *M. surmuletus* occurrence, NPUE and median length (cm) between 2000 and 2016. Blue rectangles represent zoomed sections (Zones A, B and C) in Fig. 5. See [https://iparperspective.shinyapps.io/pilot\\_atlas\\_MED\\_GSA06/](https://iparperspective.shinyapps.io/pilot_atlas_MED_GSA06/) for yearly maps

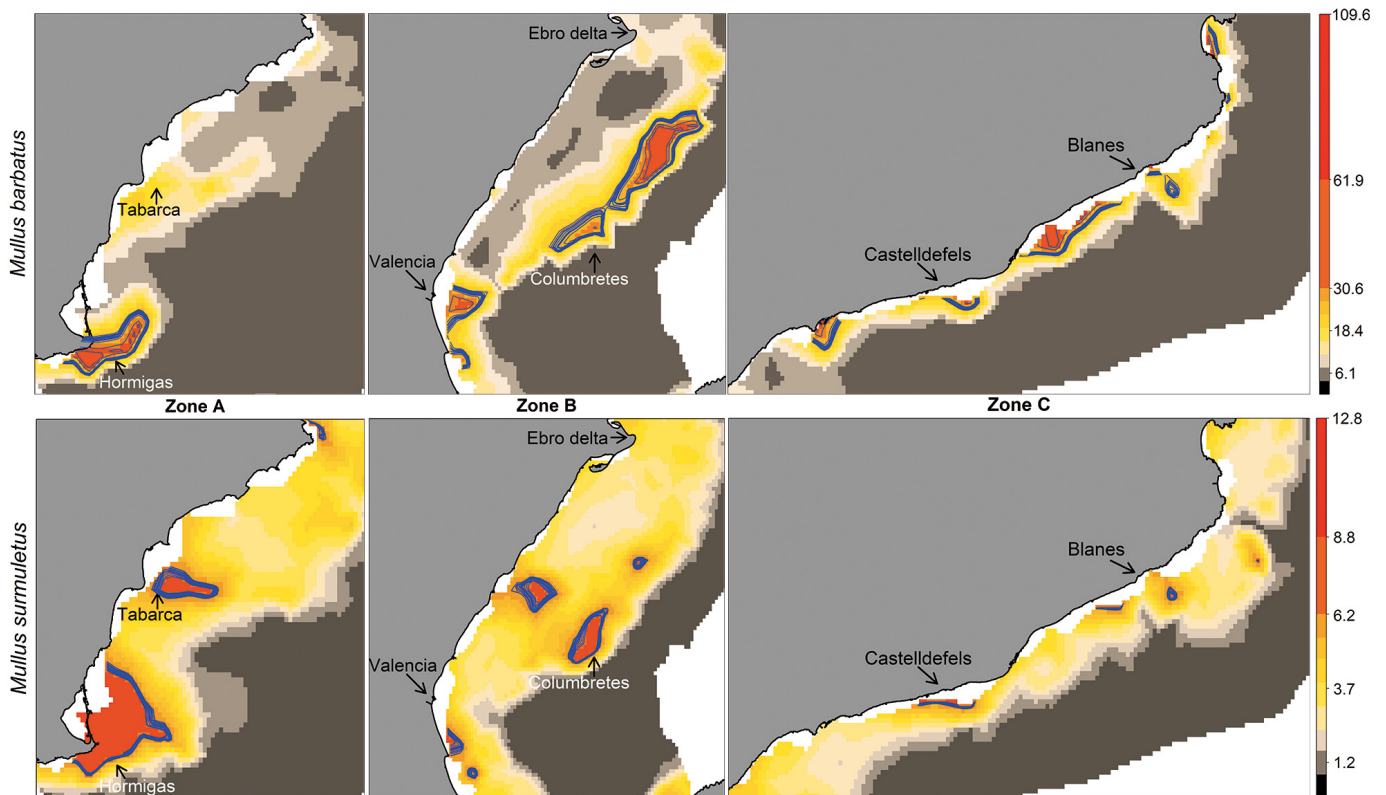


Fig. 5. Zoomed spatial distribution of *Mullus barbatus* and *M. surmuletus* NPUE in Murcia (Zone A), Valencia (Zone B) and Catalonia (Zone C). Hotspots, identified as areas with NPUE above the 90<sup>th</sup> percentile, are highlighted in blue

estimate transitions over the years. In this regard, the spatial-temporal structure comparison applied in this study provides an SDM approach to quantitatively assess the persistence level of the hotspots through inference, i.e. by comparing the goodness of fit of different models and the inferred temporal autocorrelation parameter, rather than using post-modelling analysis as in previously proposed methods (Colloca et al. 2009). Moreover, the extra marginal temporal trends included in these models provide substantial information on the overall population dynamics after accounting for the spatial variability of the data, which constitutes an important refinement over previous hotspot persistence identification approaches (Colloca et al. 2009, Paradinas et al. 2015, 2017).

The case study allowed us to assess the distributional behaviour of red mullets in the western Mediterranean, and to confirm the positive population size trend in both species between 2000 and 2016. Both species occurrence and NPUE spatial distributions showed very little spatial variation, as inferred by the temporal correlation parameters. The high persistence in the spatial distribution of red mullets is particularly convenient for MSP purposes, as it implies that hotspot locations are also persistent, which allows us to designate fixed FRAs to protect red mullet stocks.

Persistent hotspots were identified throughout the study area, and many of them were shared by both species. Six high-abundance convergence areas were identified. From south to north, the identified shared hotspots were as follows: a hotspot located around Islas Hormigas marine reserve, a hotspot in the coastal region south of Valencia, a large hotspot around the Columbretes Islands marine reserve, a small joint hotspot off the coast of the Ebro delta and near the edge of the continental shelf, and several more small hotspots in the surroundings of Casteldelfs and Blanes Canyons in Catalanian waters. With respect to non-shared hotspots, 2 *Mullus surmuletus* hotspots were identified: one around Tabarca marine reserve and the other in coastal waters halfway between Columbretes and the Ebro delta.

The overlap between existing FRAs and red mullet hotspots is apparent. In fact, 3 out of 4 long-term FRAs in the study area, i.e. Islas Hormigas, Tabarca archipelago and Columbretes islands, showed high NPUE for both red mullet species. While quantifying the impact of FRAs on red mullets is beyond the scope of this study, *M. surmuletus* seems to benefit more from them than *M. barbatus*. The 3 largest *M. surmuletus* hotspots were linked to marine reserves,

whereas for *M. barbatus*, 2 medium-sized hotspots were linked to Islas Hormigas and Columbretes, with relatively high NPUEs in Tabarca.

These red mullet hotspots in the vicinity of marine protected areas (MPAs) suggest that MPAs have a positive influence and act as source areas. Spawners and recruits can benefit from these fishing restriction measures and configure a suitable habitat. This MPA effect has been reported by other authors in the study area (Mendoza et al. 2014). Additionally, another MPA effect is the concentration of fishing effort in areas surrounding the MPA. Some fishing boats operate as close as possible to MPA borders and take advantage of the exported MPA production. These fishing operations generate bottom disturbance and turbidity, which makes some small crustaceans, which are an important part of the red mullet diet, available to them. In other words, the fishing operations generate suitable feeding resources for red mullets. Hence, a combination of the positive exportation MPA effect and the suitable feeding habitat due to turbidity could be the explanation of these red mullet hotspots close to the MPA limits.

Although the small distances between red mullet shared hotspots appear to be an excellent example of the efficiency of current FRAs and support new initiatives on MPA connectivity, these measures should be considered in a broader multispecies context. An ecosystem based management strategy requires that at least all important fisheries species be considered in the study area (Gislason et al. 2000, Morishita 2008), i.e. red mullets, but also other important species, such as hake *Merluccius merluccius*, monkfish (*Lophius* sp.) and red shrimp *Aristeus antennatus*, among others. MPA connectivity must compromise in terms of the characteristics of species whose territorial range and dispersion rates differ considerably.

Bellido et al. (2019) reported depth as the key factor for conservation measures in the marine environment. Regarding red mullets, the resulting bathymetric niche characterization is in line with the results of past studies (Golani 1994, Lombarte et al. 2000), where red mullet NPUE decreased significantly below the 200 m depth stratum and striped red mullet were relatively common until the 300–350 m stratum. By contrast, specimen length for both species increased with depth (Fig. 2). In line with Macpherson & Duarte (1991), we observed that small specimens tend to aggregate in larger numbers and are associated with shallower waters, whereas larger specimens are more scattered and inhabit deeper waters. This ontogenetic distribution is common to many marine species, with specimens in their early ontogeny preferring shall-

lower waters and those in the adult stages preferring to colonize deeper habitats. Hence, protecting a combination of both shallow and deep waters is needed to guarantee that different size fractions of the population, particularly juveniles and spawners, are protected (Bellido et al. 2019, 2020).

Similarly, a thoroughly planned FRA network should recognize the economic conditions of fishermen by quantifying the level of overlap between identified productive fishery areas and their fishing grounds (Pennino et al. 2018). A combination of partial protection areas and no-take areas could be the best solution (Sciberras et al. 2015) to reduce the short-term negative economic impact on fishers.

It is important to bear in mind that the MEDITS survey covers only a short season from late spring to early summer. Consequently, the maps produced only reflect a snapshot of the expected relationships and distribution of these species. An effective MSP should incorporate seasonal spatiotemporal dynamics. These dynamics could be included by adding findings from fisheries-dependent data, which potentially provide higher spatiotemporal coverage. However, integration of the 2 data sources is not a trivial matter, given that fisheries-dependent data are collected based on preferential sampling schemes (Bellido et al. 2019, Pennino et al. 2019). Other options include (1) extending the MEDITS survey to include more seasons or (2) creating a reference fleet (Pennington & Helle 2011), i.e. use commercial vessels to sample MEDITS locations with the appropriate gear to collect scientific data in different seasons.

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