Received: 8 November 2021 | Revised: 11 May 2022 | Accepted: 13 May 2022
DOI: 10.1111/fog.12594

ORIGINAL ARTICLE

FISHERIES OCEANOGRAPHY WILEY

Fisheries-based approach to disentangle mackerel (*Scomber scombrus*) migration in the Cantabrian Sea

Augusto Rodríguez-Basalo[1] | **Antonio Punzón**[1] | **Elvira Ceballos-Roa**[1] | **Gabriel Jordà**[2] | **José Manuel González-Irusta**[1] | **Enric Massutí**[2]

[1]Centro Oceanográfico de Santander, Instituto Español de Oceanografía (IEO-CSIC), Santander, Spain

[2]Centre Oceanogràfic de Balears, Instituto Español de Oceanografía (IEO-CSIC), Palma, Spain

Correspondence
A. Rodríguez-Basalo, Centro Oceanográfico de Santander, Instituto Español de Oceanografía (IEO-CSIC), Santander, Spain.
Email: augusto.rodriguez@ieo.csic.es

Funding information
CLIFISH, Grant/Award Numbers: CTM2015-66400-C3-1-R, CTM2015-66400-C3-2-R, CTM2015-66400-C3-2-RMINECO/FEDER

Abstract

Mackerel is an important commercial pelagic species present in the western and eastern North Atlantic. The Northeast Atlantic Mackerel (NEAM) stock has its southernmost spawning area mainly located western Iberian Peninsula and southern Biscay. This species performs extensive annual migrations. The present study is focused on the distribution of this species along the Cantabrian Sea, an essential area of the South Spawning Component (SSC), and the environmental drivers that can affect its migration phenology. We have used data from Vessel Monitoring System and Logbooks of the hand line fishery to estimate the catch per unit of effort (CPUE) as a proxy of its distribution and abundance. CPUEs data of fisheries targeting NEAM provided us with a tool to discriminate the most important predictors for both its prespawning and the postspawning behavior. Among the drivers that can affect mackerel migration, we have analyzed wind speed and direction, temperature at surface (SST) and at 200 m depth, chlorophyll *a*, mixed layer depth, upwelling intensity, and the most representative geographical variables: depth, slope of the seafloor, and distance to coast. We used generalize additive models to highlight the predictors most closely related to the phenology of the species and to shape the spatial–temporal abundance of NEAM in the southern Bay of Biscay waters. Temperature and wind speed and direction are the most important factors that affect prespawning and postspawning migration of NEAM SSC and shape its niche tracking leading to a gradual advance of the spawning season.

KEYWORDS
environment drivers, fisheries-based approach, mackerel, migration, NEAM, northeastern Atlantic

1 | INTRODUCTION

As the demand for living marine resources is constantly increasing (FAO, 2016), the improve of the knowledge of the fisheries and the biology of their target species is essential to approach the problem of resource conservation. It must be developed from an integrative point of view based on the inclusion of human activities in the management of ecosystems in what has been called Ecosystem-based Management

(Curtin & Prellezo, 2010). There is, therefore, a clear need to identify and integrate all socio-economic, physical, and biological aspects for critical assessment and maintenance of the productivity of ecosystems (Levin et al., 2009). This is especially important in the case of migratory species, which can be source of international disputes as they provide ecosystem services to populations from very different locations and countries (Semmens et al., 2011). Thus, the knowledge of the migratory behavior of pelagic species is essential to assess and manage their stocks, which necessarily will rely on considering the spatial–temporal changes in their distribution (Martin et al., 2007).

During the last decades, changes in the distribution and migration of marine species have been studied and associated to climate variability (Anderson et al., 2013; Dufour et al., 2010; Edwards & Richardson, 2004; Langan et al., 2021). Nowadays, there is a great concern about the extent to which marine ecosystems will change in response to oceanographic variables (Cheung et al., 2016) and how global warming will affect fishing resources and fisheries (Lehtonen, 1996; Sumaila et al., 2011). This is especially relevant in the case of migratory species, which are particularly vulnerable to the effects of climate change, mainly at high latitudes (Robinson et al., 2009). Giving that ocean warming has already affected the fisheries worldwide (Cheung et al., 2013), it is necessary to disentangle the environmental variables that most affect the highly valuable resources in order to understand the spatial–temporal changes that are taking place in the distribution and behavior of migratory species.

One of the best known and most studied migratory species in the North Atlantic is the mackerel (*Scomber scombrus* Linnaeus, 1758), a species that performs spawning and feeding migrations (Iversen, 2002). It has become of great importance for supporting a highly valuable European fishery (ICES, 2015), which have seen their landings increased since the beginning of the present century (ICES, 2019a). Currently, mackerel provides a total catch of approximately 1 million tonnes, with a first sale value over €1 billion (ICES, 2019b) and nowadays is a key component of high-latitude Atlantic ecosystems due to its expansion towards the central North Atlantic from the Nordic seas (Astthorsson et al., 2012; Jansen et al., 2016; Jansen & Gislason, 2011; Nøttestad et al., 2015), which was concluded to be mainly triggered by climate change (Bruge et al., 2016; Hughes et al., 2014; Trenkel et al., 2014), also affected by density-dependent effects (Olafsdottir et al., 2019). This expansion of the resource began in 2007, when mackerel started to migrate into Icelandic waters, circumstance that caused the disagreement of some countries with the maintenance of the traditional distribution of quotas that lasted until 2014 and the repeated noncompliance of the recommended TACs during the following years (Hannesson, 2013; ICES, 2019b). The southern area of the Northeast Atlantic Mackerel (NEAM) distribution, affected by the southern spawning component, was also object of quotas infringement, which derived in 2010 on a deduction, by the European Commission, of the mackerel quota assigned to Spain due to overfishing (EC, 2009).

In mackerel, distributed along the whole northern Atlantic, it has been traditionally considered two independent stocks, the western and the eastern (Trenkel et al., 2014), which are divided in five different spawning components, two in the western Atlantic and the other three belonging to the NEAM. The spawning components of the NEAM are the North Sea component, located at the North Sea and Skagerrak (ICES areas IIIa and IV); the western component, from northwestern Scotland to the Bay of Biscay (ICES areas VI, VII, and VIIIabde), and the southern component, distributed along the northern Iberian Peninsula (ICES areas VIIIc and IXa) (Iversen, 2002). Nevertheless, this traditional perception of the spawning division has been questioned by some authors that consider the North Sea spawning component as a "dynamic cline" (Jansen, 2014; Jansen & Gislason, 2013) or those who remark that southern and western spawning components are hardly distinguishable (Borja et al., 2002). As for the southern spawning component, it is mainly located in the Cantabrian Sea, where spawning tends to be in the first half of the year, reaching its higher rates in March–April. Juveniles remain in the spawning area until they reach sexual maturity at 2–3 years of age. From the analysis of fishery data, a shift in the timing of this migration has been observed during last decade (Punzón & Villamor, 2009; Villamor, Lanzós, et al., 2011).

The studies aiming to analyze migration patterns and distribution of mackerel have been based mainly on egg surveys (Borja et al., 2002; Bruge et al., 2016; Brunel et al., 2017) or pelagic ecosystem surveys (Astthorsson et al., 2012; Nikolioudakis et al., 2019), but few studies have relied on fisheries. However, vessel monitoring system (VMS), combined with logbook data, can be a very useful tool not only to develop fishing activity monitoring (Russo et al., 2019; Witt & Godley, 2007) or to study the state of the resources (Lambert et al., 2017) but also for the studies on the behavior of the commercial migratory species and its response to temperature variations (Lemos et al., 2016) through the estimation of catch per unit of effort (CPUE) data, as proxy of their abundance.

In northern Spain, the main fisheries targeting mackerel are bottom otter trawl (OTB), bottom pair trawl (PTB), handline (LHM), and purse seine (PS) (ICES, 2015), most of them tracked by VMS as they are larger than 15 m (European Commission, 2009). Fisheries-based studies have different issues that are difficult to control throughout the process of dealing with fisheries data, so it is necessary to disentangle reliable information after an intensive data cleaning process, as detailed Hintzen et al. (2012). In general terms, these fisheries have great adaptability both in terms of target species and gear types, but at the time of the spawning, they keep mackerel as the target species (Castro et al., 2010; ICES, 2015). However, the effort measurements for some of these fishing gears generate uncertainties. Thus, Gaertner and Dreyfus-Leon (2004) warn that the use of PS CPUEs is not adequate to reflect changes in the trends of the species abundances. This is not the case of trawl gears, in which the swept area has proven to be an effective descriptor of trawling effort (Mills et al., 2007). Regarding LHM, Punzón et al. (2009) reported that vessel length and fishing days are some of the effective measures of effort in studies to estimate the abundance of this species.

In the present study, the use of fisheries data provides a way to monitor mackerel from its arrival to the southern spawning area at the end of the winter, to its departure during spring time. We analyze the

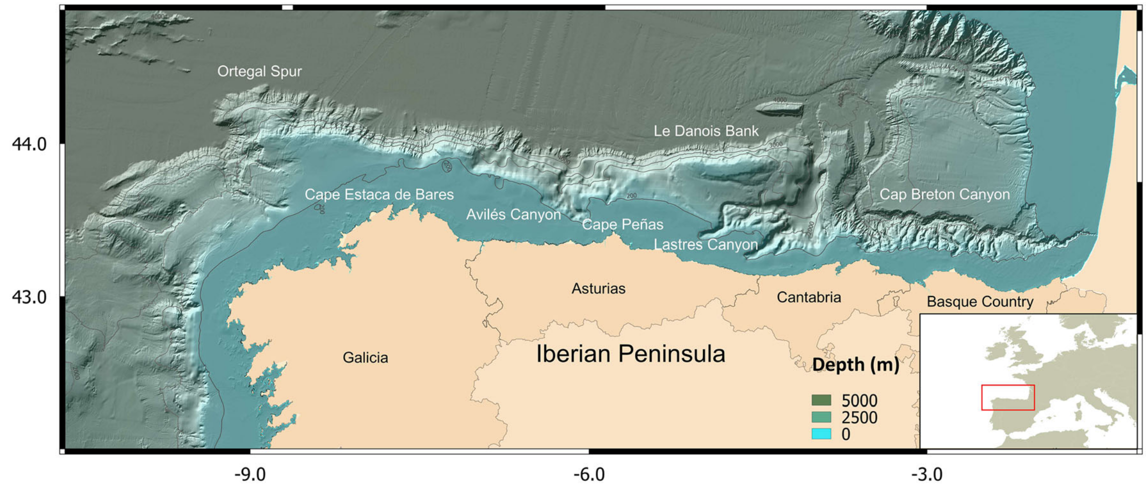

FIGURE 1 Study area. Northern Iberian Peninsula, showing its main geomorphological features of the seafloor

drivers that shape spatial–temporal abundance of NEAM in the southern Bay of Biscay waters, as well as those that trigger its migration to and from this area. This analysis has been developed through spatial distribution models. We also search the optimal sea surface temperature (SST) range and how important is this environmental variable on the spawning southernmost latitude of this species. Finally, we characterize the thermal niche from 1992 to 2018, both for its pre-spawning and trophic migrations.

2 | MATERIAL AND METHODS

2.1 | Study area

The study area is located on the south of the Bay of Biscay, the Cantabrian Sea, along the northwestern Iberian Peninsula waters (Figure 1). The Cantabrian Sea is characterized for having a great structural heterogeneity, with long submarine canyons, such as Cap Breton and Aviles canyons, as well as seamounts like Le Danois Bank. The area occupied by NEAM fisheries from late winter to spring is the continental shelf covering the west of Galicia and the coast of Iberian Peninsula facing Cantabrian Sea, in the southernmost area of the ICES subdivision VIIIb and most of ICES subdivision VIIIc. The continental shelf is a little wider on the west side, the coast of Galicia, and gets narrower as soon as it gets close to Basque Country. The area can be divided in two zones according to important upwelling episodes, one that affects the northwestern Iberian coast, the Canary-Iberian Peninsula upwelling system, that occurs between the months of April and September, and that reaches its maximum during the summer (Casabella et al., 2014; Fraga, 1981) and another in the southern Bay of Biscay, off the Central Cantabrian coast (Botas et al., 1990). Cape Estaca de Bares marks the limit of influence of both areas (Prego et al., 2012).

2.2 | Fisheries data

We have analyzed data from the following fisheries targeting mackerel in the study area: OTB, PTB, LHM, and PS (Figure 2). VMS and logbook data, provided by the Secretaría General de Pesca Marítima of the Spanish Ministry of Agriculture, Fisheries and Food, covering a period between 2007 and 2017, were used to estimate the CPUE, a proxy of the abundance of this species. We decided to work with these data, instead of fishing/navigation as presence/absence data, because the use of absences is not recommended in pelagic species (Boyce et al., 2002; Guisan & Thuiller, 2005). The clustering technique CLARA (Clustering Large Applications), a nonhierarchical method prepared to deal with a large number of data (Rousseeuw & Kaufman, 2009), was used to obtain the fishing trip targeting mackerel from the logbook data (Punzón et al., 2016). The silhouette coefficient was considered to validate the goodness of this clustering (Lengyel & Botta-Dukát, 2018), which indicates the homogeneity of the group and how different it is from the nearest groups (Castro et al., 2010). We have considered the levels indicated by Kaufman and Rousseuw (1986): 0.71–1, consistent pattern; 0.51–0.70, reasonable pattern; 0.26–0.50, weak pattern; and <0.26, no pattern concluding that the discrimination approach is much better in LHM (highly consistent pattern) than in trawling gears (OTB and PTB) and PS (Table 1), thus allowing us to delimit very accurately the part of the fleet that is targeting mackerel during its spawning migration. After selecting logbooks data of LHM fisheries targeting mackerel, they were merged with VMS records using VMStools R package (Hintzen et al., 2012). According to the gear and the speed, we obtained the fishing activity allowing us to extract the records where the boats were fishing. The weight of the landing was equitably distributed to the pings in which the fishing boats were detected as fishing. Finally, to get CPUE of LHM, fishing days and the length of the vessel were used as a measure of fishing effort (Punzón et al., 2004):

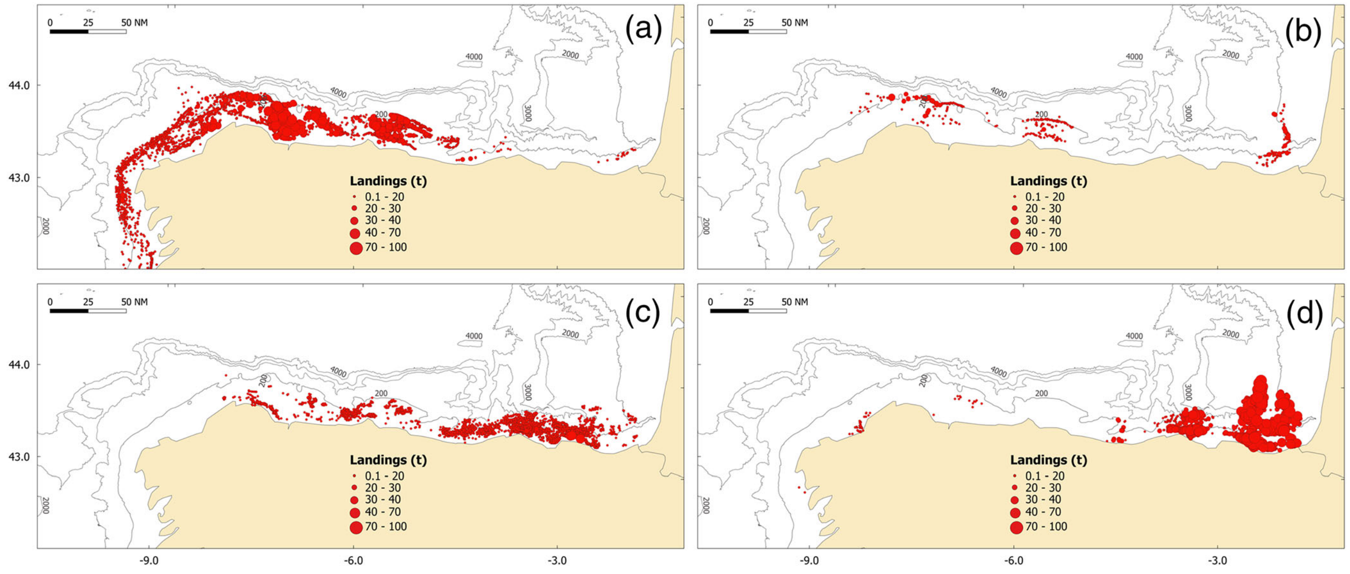

FIGURE 2 Spatial distribution of the different fisheries obtained from bottom otter trawl (OTB) (a), bottom pair trawl (PTB) (b), handline (LHM), (c), and purse seine (PS) (d) landings

TABLE 1 Average silhouette width and discrimination capacity of the different fisheries targeting mackerel from the clustering technique clustering large applications (CLARA)

Analysis	OTB	PTB	LHM	PS
Average silhouette width	0.60	0.74	1.0	0.72
Mackerel in cluster group (%)	86.6	76.7	99.9	84.1

Abbreviations: LHM, handline; OTB, bottom otter trawl; PS, Purse seine; PTB, bottom pair trawl.

$$\text{CPUE} = \frac{C}{L * D}$$

where C is the catch, L is the vessel length, and D are the days of the fishing trip.

The deduction of the quota in 2010, due to penalty caused by the Spanish fleet overfishing, resulted in an irregular behavior of this fleet, which in subsequent years exhausted the quote before April. The normal patterns of the fleet were not recovered during the studied period. Therefore, in order to avoid the anomalous situation that lasted between 2010 and 2017, this period was discarded for the months of March and April, the most affected by the regulations. Finally, a total of 4677 registrations of CPUEs belonging to 200 vessels were finally used for the analysis: 2146 recorded in February between 2007 and 2017, 1284 recorded in March between 2007 and 2009, and 1247 recorded in April from 2007 to 2009.

2.3 | Environmental data

We used the bathymetry and its derivatives slope and roughness, extracted from a $0.002 \times 0.002^\circ$ resolution Digital Terrain Model (DTM) provided by EMODnet Bathymetry Consortium 2016 (https://doi.org/10.12770/c7b53704-999d-4721-b1a3-04ec60c87238). Distance to coast (DtC) was also considered as a variable that may affect mackerel distribution during its migration as well as to the CPUEs. The inclusion of geographic variables in the phenological study of migratory species is relevant for the knowledge of spawning habitats, since it can be an indicator of geographical attachment probably produced by localized environmental conditions sustained over time (Reglero et al., 2012). Furthermore, the hydrographical variables considered as possible causes of changes in the spatial–temporal abundance of mackerel in the study area were SST), temperature at 200 m depth (T200), mixed layer depth (MLD), sea surface salinity (SSS), and chlorophyll *a* (Chl*a*) as a proxy of the productivity. The T200 is limiting in the sense that information from shallower areas is lost, but its importance in certain periods of the migration has led to its inclusion in this study. Monthly fields of those variables with a spatial resolution of $1/12^\circ$ were obtained from the IBI Ocean Reanalysis Systems (Sotillo et al., 2015) for the period 1992–2018 (doi: 10.48670/moi-00029, accessed on 6/6/2018). The core of the reanalysis is the NEMO v3.6 ocean general circulation model and assimilates altimeter data, in situ temperature, and salinity vertical profiles and satellite SST. Additionally, the wind speed and direction expressed in terms of orthogonal velocity components: west–east (UWI) and south–north (VWI) wind components and the upwelling index (Borja et al., 2002; Brunel et al., 2017) were also considered. In particular, two different upwelling indices have been computed, one using the wind parallel to west Galician coast and other using the wind parallel to Cantabrian coast. To that end, monthly wind fields with a spatial resolution units of $1/20^\circ$ from 1980 to 2018 were obtained from the MERRA2 global atmospheric reanalysis (Gelaro et al., 2017), provided by the Global Modeling and Assimilation Office (GMAO, accessed on 6/6/2018 on doi: 10.5067/VJAFPLI1CSIV).

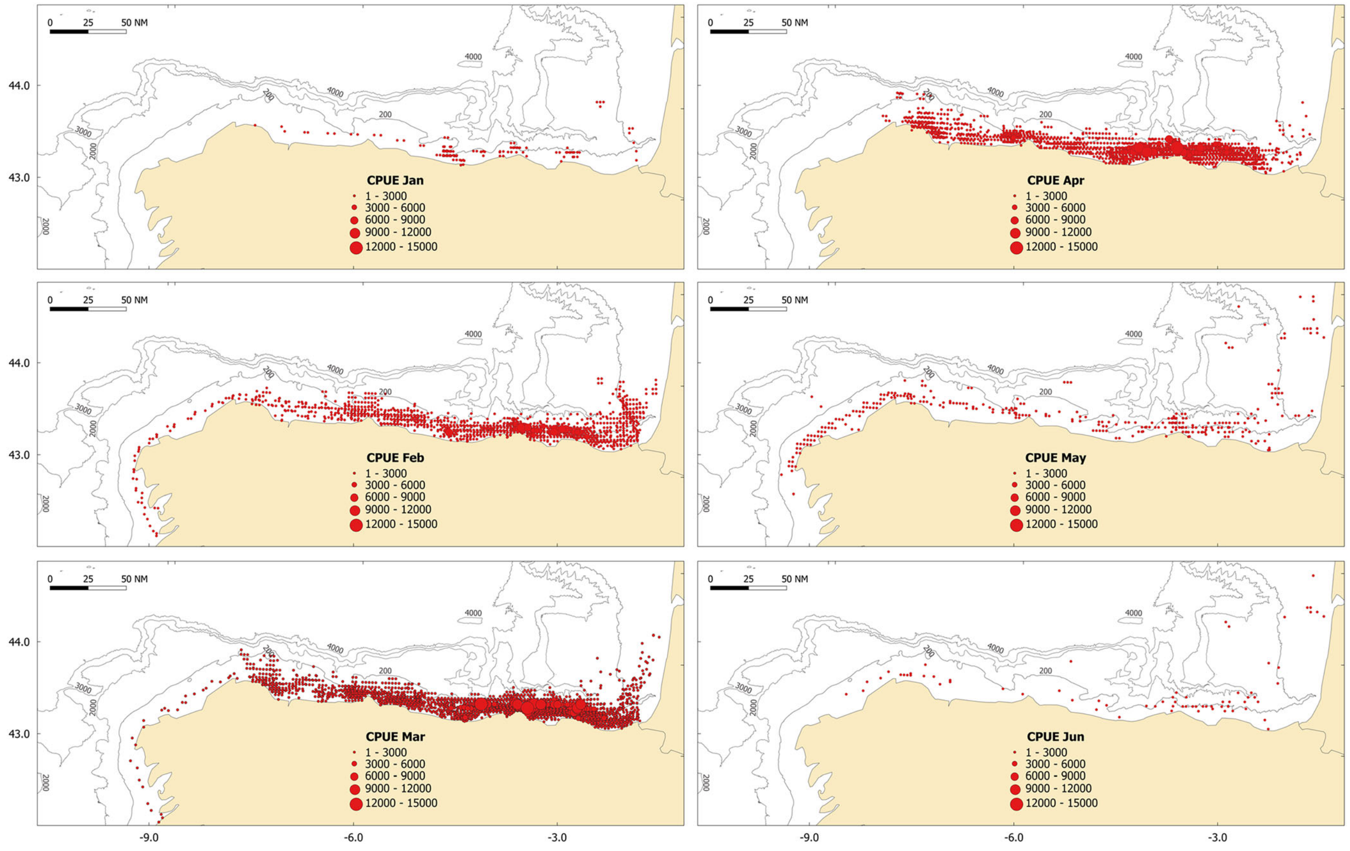

FIGURE 3 Monthly catch per unit of effort (CPUEs) of mackerel along the northwestern Iberian Peninsula and Cantabrian Sea, estimated from the hand line fishery during the half part of the year (January–June) for the period 2007–2009

The collinearity between each pair of variables has been verified by means of a correlation matrix, discarding those that present a Spearman rank correlation greater than 0.7 and that were also significant (*p*-value <0.05). As a result, the upwelling indices were removed from the analysis as they were correlative with the currents: Cantabrian index negatively correlated with westerly wind, and Galician upwelling index negatively correlated with southerly wind. To avoid multicollinearity between predictors, a variance inflation factor (VIF) test has been performed. This measure allows us to eliminate those variables that have redundant information when integrating them in general models (Robinson & Schumacker, 2009). All VIF values were under 3, so no more predictors were removed from the study.

2.4 | Data analysis

Due to the lack of data available for the months of January, May, and June, when fishing effort is negligible, only the months of February, March, and April were considered, being March the month with highest values of CPUEs (ICES, 2019b). To discriminate the predictors that may contribute to trigger the spawning and feeding migration of mackerel, we assumed that most catches produced in February occur during the spawning migration, while catches of April occurred while most of the mackerel moves to the feeding grounds in the north. This was determined from the studies of Punzón and Villamor (2009), who proved that in the 2000s the peak of catches had moved forward to the month of March. Accordingly, the study was disaggregated by months separately (Figure 3).

Generalized additive models (GAM), a modeling technique in which the relationships between response and predictor variables are shaped by smooth functions that not need to be linear (Hastie & Tibshirani, 1987), were developed by month to determine to what extent each variable has contributed to the distribution patterns of mackerel in the study area. For the GAMs, we finally considered the whole period for February analysis and the years 2007, 2008, and 2009 for March and April. In order to normalize CPUEs data and decrease variability, logarithmic transformation was used. To get started, Gaussian distribution univariate models were performed for each response variable (Table 2). The selection of the variables was developed using the forward-backward stepwise selection, adding predictors that best improve the *r*-square according the univariate models until all were selected and removing them according to the maximum *p*-value until we get the null model. Among all the models, the one with the lowest AIC (Akaike Information Criterion) was selected. The smoothed knots were set to a maximum of 4 to avoid overfitting. Moran's I test was used to check the autocorrelation of the data, showing that values where significantly higher (>0.1) than the expected, with *p*-values lower than 0.005, 0.01, and 0.04 for

TABLE 2 Explained variance of univariate models

	Univariate models			Full models					
	Feb	Mar	Apr	Feb		Mar		Apr	
Variable	Variance (%)			Variance (%)	*p*-value	Variance (%)	*p*-value	Variance (%)	*p*-value
SST	26.5	5.4	10.3	5	***			1	*
T200	4.6	10.4	16.1			11	***	17	**
SSS	9	6.6	9.3					5	***
UWI	28.9	10.3	3.7	3	***	3	*	2	*
VWI	8.3	9.7	13.5	2	***			5	***
Chla	16	9.8	9.07						
Depth	2.7	6.2	7.27						
Slope	0.3	6.5	9.25			1			
DtC	8.1	12.2	6.02					1.1	
Coord	38	34.9	26	15	***	19	***	13	***
Full models				54		56		56.4	

Note: Contribution of the smooth terms to the variance of each full model and significance level of environmental variables ($P < 0.1$., $P < 0.05$*, $P < 0.01$**, $P < 0.001$***) for February (prespawning), March (peak of spawning), and April (postspawning). Significance levels of univariate models are all significant ($p < 0.05$).

Abbreviations: Chla, Chlorophyll *a*; Coord, Interaction between the coordinates longitude and latitude; Depth and slope of the seafloor; DtC, distance to coast; SSS, sea surface salinity; SST, sea surface temperature; T200, temperature at 200 m depth; UWI, east–west wind component velocity; VWI, north–south wind component velocity.

*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.

February, March, and April. Consequently, the interaction between longitude and latitude was included as a smoothed term to avoid the spatial autocorrelation in the final models. Finally, for the fitting of the final full models of each month, the data were divided randomly, leaving 70% of the data for the training test and the remaining 30% for validation.

The mackerel CPUEs were predicted backwards and forwards in time for the period 1992–2018 for which predictors data were available. The predicted CPUEs were standardized to values between 0 and 1 and finally split in two different periods with an equivalent number of years (1992–2005 and 2006–2018) and mapped in order to show the change produced between these periods for each month. The tendency that mackerel is experiencing in migration timing between 1992 and 2018 was estimated using the CoG (Center of Gravity) of the monthly predicted CPUEs of this species through the years, calculated through the R package SDMTools (VanDerWal et al., 2014). For a clearer representation of the analyzed trends, the 5-year period unweighted moving average of each month trend was calculated. A 5-year period is recommended to smooth out inter-annual variability while maintaining long-term fluctuations (Hamilton, 1994).

3 | RESULTS

The univariate models show the importance of environmental variables during the period February–April, such as SST, Chla, and eastwards (UWI) and northwards (VWI) wind components (Table 2). SST and UWI are the predictors with highest variance explained in February (prespawning migration), explaining 26.5% and 28.9% of the variance, respectively, followed by Chl*a*, with a value of 16%. In March, when most of the spawning occurs, there is not such importance for any of these variables, although wind stress and temperature, both SST and temperature at 200 m depth (T200), are still relevant, being slightly behind the distance to coast (DtC) in the variance explained. In April, it is highly significant the importance of T200, which increases since February, while SST relevance decreases.

The response curves of February full model show a clear tendency for the most important predictors: SST and both components of the wind stress (Figure 4). In the case of SST, maximum CPUEs can be observed at temperatures below 13.1° and starts to decline as temperature elevates at a maximum of near 13.6°. As for wind components, it is observed a preference by low or very high west–east wind and positive values of VWI; that is, northwards wind favors the appearance of mackerel during this month. For the models of March, DtC, the most explanatory predictor with 12.2% of the variance explained in univariate models, with maximum at less than 20 nm, was discarded for the full model because of its poor contribution. Finally, regarding wind components, UWI, the most relevant variable in February apart from coordinates interaction and SST, shows that all values are positive (eastwards wind), with high CPUEs in soft winds from 1.5 to 2.5 ($m \cdot s^{-1}$), while VWI appears to be the most relevant wind component for April, according to the variance explained, showing the maximum CPUEs in negative values (southwards wind), and decreasing as the southerly wind increases.

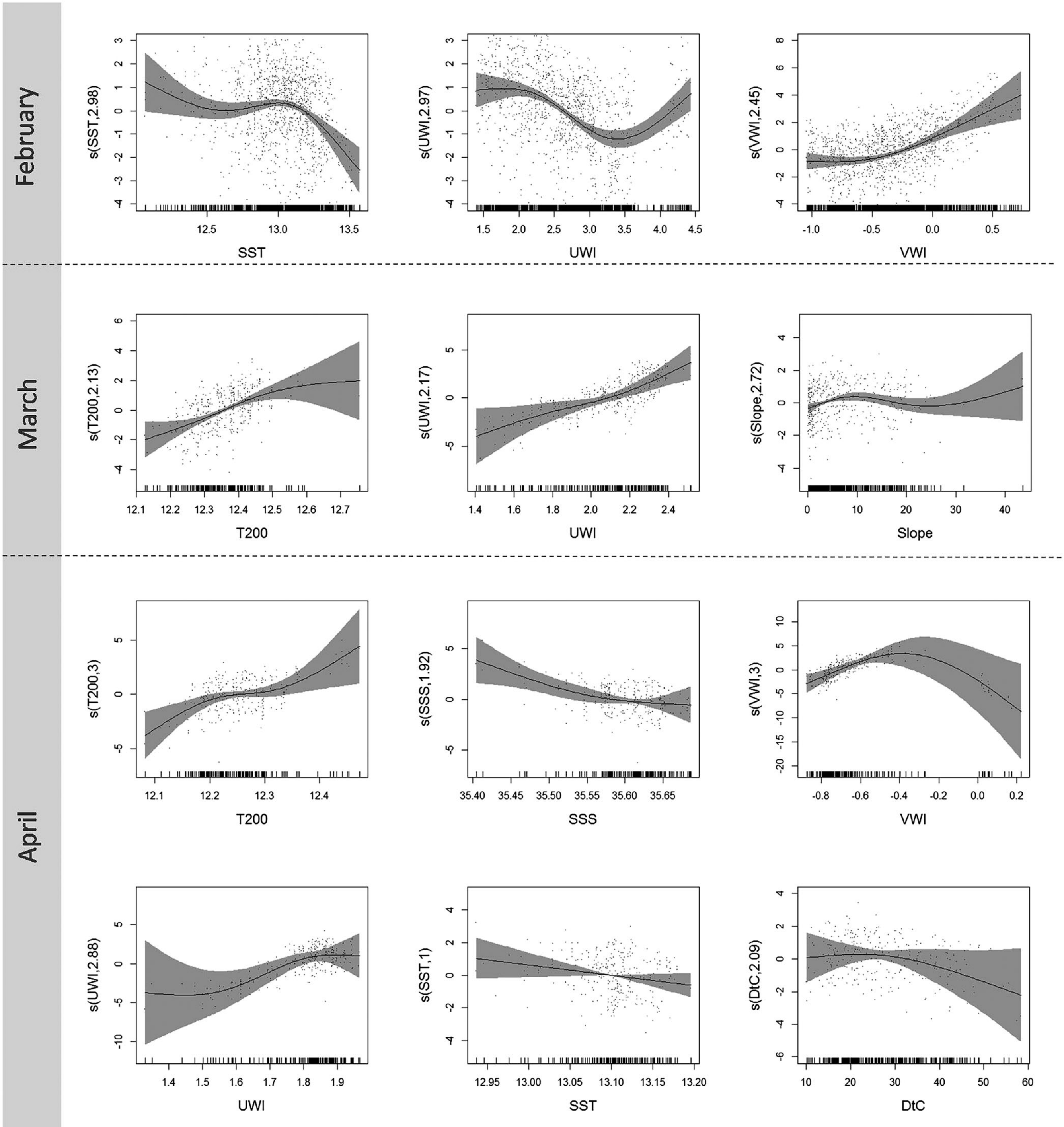

FIGURE 4 Response curves of the full models for the mackerel migration along the northwestern Iberian Peninsula and Cantabrian Sea during February (prespawning), March (spawning), and April (postspawning). SST: sea surface temperature; UWI: west–east wind component velocity; VWI: south–north wind component velocity; T200: temperature at 200 m depth; SSS: sea surface salinity; DtC: distance to coast; and slope

Table 2 also shows the *p*-values and the amount of variance that each variable contributes to the full model. Both temperatures and wind stress were finally key predictors for the migratory patterns and the distribution of mackerel. The deviances explained of the full models were all greater than 50%. Figure 5 shows the least squares lines of the predicted versus observed CPUE values of the test data set. In all the cases, the predicted values of the models were equivalent to the observed ones, presenting a slope with a ratio close to 1:1 and an adjusted *r*-squared of 0.43, 0.59, and 0.56 for the months of February, March, and April, respectively.

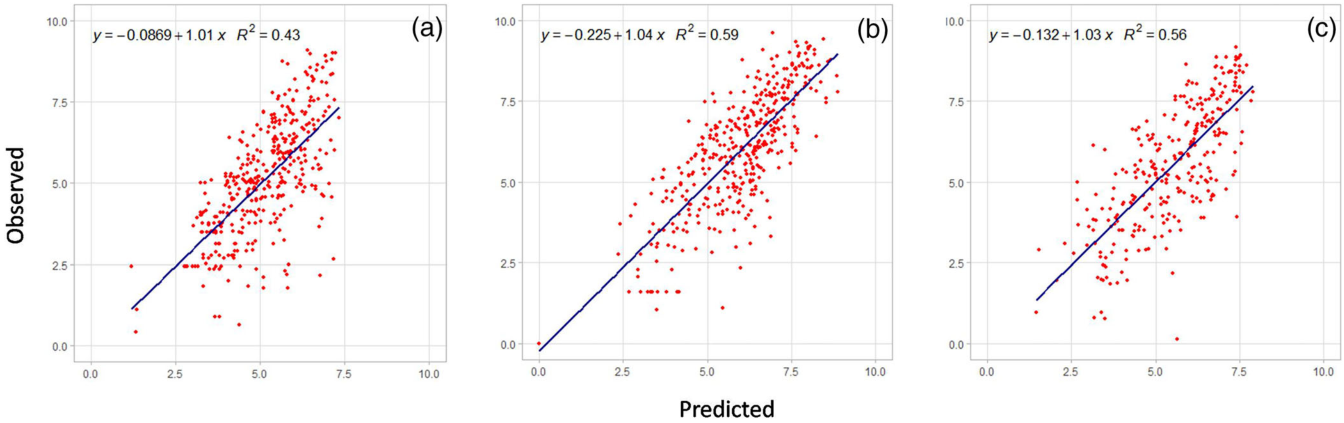

FIGURE 5 Comparison of the predicted versus observed catch per unit of effort (CPUE) values for the full models of February (a), March (B), and April (C) and least-square lines of fit

TABLE 3 Final terms of the GAMs full models (SST: sea surface temperature; SSS: sea surface salinity; UWI: west wind component velocity; VWI: south wind component velocity; DtC: distance to coast; lon,lat: geographic position; T200: temperature at 200 m depth; slope of the seafloor) obtained as predictors of the response variable CPUE (catch per unit of effort) of mackerel for the months of February (prespawning), March (spawning), and April (postspawning)

Month	Models
February	Log (CPUE) ~ s (SST, $k = 4$) + s (UWI, $k = 4$) + s (VWI, $k = 4$) + s (lon,lat)
March	Log (CPUE) ~ s(T200, $k = 4$) + s (UWI, $k = 4$) + s (slope, $k = 4$) + s (lon,lat)
April	Log (CPUE) ~ s (SST, $k = 4$) + s(T200, $k = 4$) + s (SSS, $k = 4$) + s (UWI, $k = 4$) + s (VWI, $k = 4$) + s (DtC, $k = 4$) + s (lon,lat)

Abbreviation: CPUE, catch per unit of effort.

The predicted CPUEs were finally projected according to the full models (Table 3). For the maps that represent the full models comparison in the periods 1992–2005 and 2006–2018, the average of the predicted CPUE values of the 3 months was calculated and represented in Figure 6, which shows different trends from the first period to the second depending on the month considered. In February, it can be observed a gradual increase in the prediction of the species captures in the easternmost zone of the study area, moving westwards from the French coast to the Basque Country, while during the months after, the trend revealed a general increase in the CPUEs prediction for the entire area in March and a slight decrease in April. These trends can also be observed in the temporal evolution of the CoG of mackerel CPUEs by month during the period 1992–2018 (Figure 7), in which positive trends are shown in February and March, and a slight negative trend can be observed in April, although the last one is not significant (p-value > 0.1).

4 | DISCUSSION

The present study, in line with previous works based on fisheries data to model the abundance of mackerel (Brunel et al., 2017), confirms that the use of CPUEs as a proxy of abundance can be of great help in contributing to the knowledge of the migratory cycle of this species. Our results show that northeastern Atlantic migration patterns seem to be mainly influenced by environmental factors. Wind component and SST have appeared to be the environmental drivers with greater influence on the prespawning migration patterns of mackerel along the northwestern Iberian Peninsula and Cantabrian Sea. VMS processing and analysis for LHM have revealed a very high sensitivity and specificity to this fishery (Ducharme-Barth & Ahrens, 2016; Punzón et al., 2003), providing a very valuable information to study the distribution and phenology of migratory species of fisheries interest, such as mackerel. On the one hand, they have the great advantage of supplying a large amount of data, which allows us to avoid the use of information that a priori may be inconclusive or even generate noise. On the other hand, they cover the entire period of activity of the species in a given study area, while fisheries-independent data show too often a more limited temporal and spatial information. According to Pennino et al. (2016), fishery-dependent data respond better to environmental variables more related to hydrodynamics, while fisheries-independent data respond better to environmental variables more related to seafloor geomorphology. This may have influenced the poor contribution of the bathymetric variables or even DtC in the models developed by the present study, especially those for March and April.

Therefore, it is necessary to take into account the multiple factors that can affect the configuration and conduct of fisheries to try to make the process of disentangling these data as transparent and efficient as possible. If this process is carried out efficiently, it has been

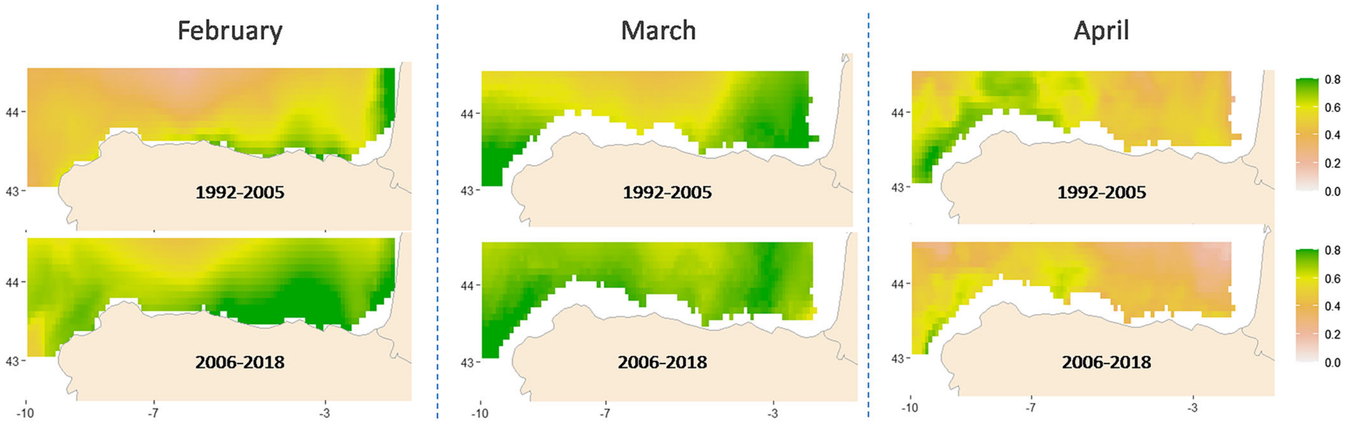

FIGURE 6 Distribution of the predicted catch per unit of effort (CPUE) of mackerel in the northwestern Iberian Peninsula and Cantabrian Sea during February–April between 1992 and 2018. It has been divided into two different periods: in the upper row, it is shown the average between the years 1992–2005, and in the lower row, those of the period 2006–2018. Predicted CPUEs have been rescaled to values from 0 to 1. The areas without data for the months of March and April are due to the inclusion of T200 in the models. Grid size has a resolution of 0.08° × 0.08°

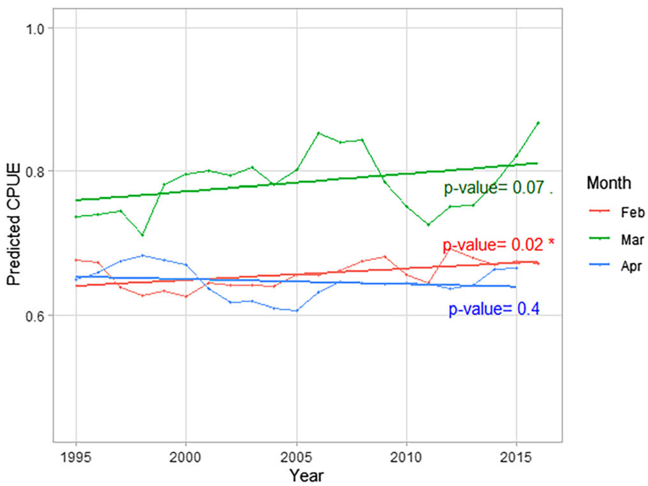

FIGURE 7 Five-year moving average of the centers of gravity (CoG) of the mackerel predicted catch per unit of effort (CPUE) in the northwestern Iberian Peninsula and the Cantabrian Sea during February, March, and April. It is also shown the regression lines and the significance values

shown that it is possible to contribute significantly to the knowledge of the phenology of marine species in the pelagic environment, both in the identification of drivers explaining the migrations of these species (Pennino et al., 2016) and the detection of changes that can occur in their migratory regimes (Dufour et al., 2010).

The water temperature has been described as the main environmental driver of the spawning migration of mackerel in the northeastern Atlantic (Hughes et al., 2014; Jansen, 2014; Jansen & Gislason, 2011; Jansen et al., 2016; Mendiola et al., 2006; Punzón et al., 2009). The present study confirms the importance of both SST and T200. Our models show a great relevance of SST during February, when the arrival of reproductive individuals to the coasts of the Cantabrian Sea begins, as well as a great importance of T200 in April, when mainly develops the trophic migration. Thus, the contribution of the SST to the variance of the full model of March is far less significant than that obtained in February, and the same happens if we compare the T200 of March with that of April, as the former is less significant. This is consistent with the fact that precisely in March is when mackerel preferably spawns in the area. In this month, the geographical variables could be more important than temperature or wind stress which can be deduced from the DtC univariate model importance according to the variance and *r*-squared or for the coordinates contribution to the full model of March. These results suggest a possible geographical attachment for spawning, likely due to long-term stable environmental conditions present in spawning areas, similar to what Reglero et al. (2012) inferred in their study on the spawning strategy of bullet tuna.

Another important aspect is that the relevance of the T200 increases from February to April, both in the univariate models and in its contribution to the full model, which makes us to infer that the trophic migration develops preferentially at a greater depth than the spawning migration. Besides, the maximum values of the response curves of DtC in the univariate models, estimated at 12, 17, and 20 nm for February, March, and April, respectively, also support the idea that mackerel develops its trophic migration along the Cantabrian Sea in shallower waters and near the coast and return back to the feeding areas in deeper waters and at a greater distance from the coast.

In the February model, it is highly remarkable that, in addition to the widely studied temperature dependence (Hughes et al., 2014; Jansen, 2014; Jansen & Gislason, 2011; Jansen et al., 2016; Mendiola et al., 2006; Punzón et al., 2009), the west wind component is also a very relevant environmental driver of the mackerel migration along the Cantabrian Sea and the northwestern Iberian Peninsula. This relevance may be due to its direct relationship with upwelling and turbulence, which can directly affect both migratory behavior and spawning itself (Borja et al., 2002; Villamor, Gonzalez-Pola, et al., 2011). In fact, eastwards transport is directly related to the intensity of upwelling/downwelling and directly affects the circulation pattern of the Bay of

Biscay (Cabanas & Alvarez, 2005; Lavín, 1991). Besides, the impact of turbulence could affect the prey of mackerel, increasing the dispersal of zooplankton and reducing their availability (Borja et al., 2008).

According to the response curves of the models, there is a change in trend in the direction and speed of the winds between February and April, as well as in the preference of the mackerel. Thus, in the month of February, we found a greater affinity for mild winds from southwest, which is the dominant one during winter, and in the month of April, we found more affinity for northerly winds. The work developed by Borja et al. (2008) has been related the success in the recruitment of anchovy with an increase in upwelling favored by winds from the northeast direction, especially in the month of April. This relationship has been evidenced in the present work by the high level of correlation between the variables related to the wind and the upwelling indices, and it also becomes more relevant in the month of April, in which there is an increase in upwelling due to the predominance of northeast winds. Furthermore, in the same study, Borja et al. (2008) detected an increase in downwelling between the years 1998 and 2005, especially in April, consistent with the period in which CPUE predictions are lowest in our study, which specifically is from 2001 to 2005. These interdependent relationships between winds and upwelling also favor the dependence of the predicted CPUEs with other variables, such as the Chla, which is favored by the increase in upwelling (Botas et al., 1990).

In 2009, Punzón and Villamor concluded that an advance in the timing migration of the south spawning component of NEAM had occurred, which also led to an advance in the timing of fisheries targeted to this species. The most noticeable change occurred in 1999–2000, where the shift went from obtaining 50% of the catch in April to obtaining it in March. Likewise, the predictive CPUEs developed in the present study for April have shown important difference by comparing these years with the later period. According to the models representing this month, the prediction of the CPUEs suffers a significant decrease throughout the study period, especially important in the aforementioned years. This concordance in the results of both studies makes us rely on the validity of the results relative to the analyzed environmental predictors.

The maps that show the probability of occurrence of this species in February, during which the fisheries targeting mackerel starts their activity in the area, shows a slight tendency to increase the predictive CPUEs in the east side, between meridians 2°W and 5°W, in front of the Cantabrian and Basque Country coasts. This area is where the LHM and PS fisheries mainly develop their activity, as can be seen in Figure 2, and generally start fishing earlier than the trawl gears. The model developed for this month has SST and UWI as the two predominant environmental factors. The joint action of both factors seems to favor the prespawning migration of the species to the study area as we move through the year. The relationship between these two factors with pelagic fisheries was already analyzed by Reid et al. (2001), who concluded that positive NAO (North Atlantic Oscillation) anomalies affect the distribution of winds favoring the intensity of westerly winds and higher temperatures, which assisted the migration of horse mackerel.

Temporal trends can be seen more clearly when smoothing analysis are carried out by using moving averages. Thus, the trend of the CPUEs of mackerel in February does seem to be favored in the eastern side of the study area, and in March, there is also a clear positive trend. Conversely, the predicted CPUEs of the model developed for April is slightly negative, although did not showed a significant trend.

This study confirms the usefulness of fisheries data to increase the knowledge of the distribution and spatial–temporal patterns of pelagic species of interest to fisheries (Abad-Uribarren et al., 2020) and the phenology of the species and make predictions in the short and medium terms in a climate change context (Peer & Miller, 2014). In these predictions, temperature should be taken into account, especially to determine the arrival of the mackerel to the spawning areas, but the interaction with other variables is also decisive, such as the winds during the entire migratory period and their effect on upwelling episodes, which may influence the species behavior by modulating the beginning of trophic migration and adapting it according to productivity. On the other hand, the possibility of making long-term predictions of prespawning migration is highly reliable, but it is different in terms of trophic migration, which can be influenced by other variables that may be more likely related to periods of productivity.

LHM is just one of the four main fisheries in the study area with mackerel as the main target species. It has been the fishery on which our study has been based because the classification techniques performed in PS, PTB, and OTB from VMS and logbooks have shown lower specificity. However, once the predictors affecting Atlantic mackerel migration in the southern spawning component have been reviewed, it would be important to complete the full picture in future studies, as there is a clear spatial segregation with OTB, which mainly operates in the western Cantabrian and could provide essential information on the importance of the T200 as a fishery that operates at greater depths. In addition, as shown in Figure 2, PS is a very important fishery in the eastern region, as evidenced by the study conducted by Ramos et al. (2011) on life cycle assessment (LCA).

In addition, it is important to analyze the consequences that certain types of rules and regulations have on the behavior of the fleet, since the penalization of the Spanish mackerel fisheries caused that fishing pressure was placed in the period immediately before the spawning between 2010 and 2014 by producing competition between the different fisheries for the reduced quota. Thus, studies on the phenology of species are especially important to support advice on fisheries in relation to TACs and quotas, as well as for possible recommendations to the different actors involved in the sector, so that catches are focused on those moments that cause less damage to the reproductive success of the species and thus ensure the long-term sustainability of the resource.

ACKNOWLEDGMENTS

This study was funded by CLIFISH (CTM2015-66400-C3-1-R and CTM2015-66400-C3-2-RMINECO/FEDER).

AUTHOR CONTRIBUTIONS

A.R-B., E.C-R., and A.P. conceived the ideas and designed the study. A.R-B, G.J., and J.M.G-I. developed the models and analyzed the data. E.M. supervised and coordinated the study. All the authors discussed the results and wrote the paper. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ORCID

Augusto Rodríguez-Basalo https://orcid.org/0000-0002-4626-3194
Antonio Punzón https://orcid.org/0000-0001-6703-7690
Gabriel Jordà https://orcid.org/0000-0002-2782-8727
José Manuel González-Irusta https://orcid.org/0000-0002-3948-604X

REFERENCES

Abad-Uribarren, A., Ortega-García, S., March, D., Brahms, C. Q., Magaña, F. G., & Díaz, G. P. (2020). Exploring spatio-temporal patterns of the mexican longline tuna fishery in the gulf of Mexico: A comparative analysis between yellowfin and bluefin tuna distribution. *Turkish Journal of Fisheries and Aquatic Sciences*, *20*(2), 113–125. https://doi.org/10.4194/1303-2712-v20_2_04

Anderson, J. J., Gurarie, E., Bracis, C., Burke, B. J., & Laidre, K. L. (2013). Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecological Modelling*, *264*, 83–97. https://doi.org/10.1016/j.ecolmodel.2013.03.009

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., & Óskarsson, G. J. (2012). Climate-related variations in the occurrence and distribution of mackerel (Scomber scombrus) in Icelandic waters. *ICES Journal of Marine Science*, *69*(7), 1289–1297. https://doi.org/10.1093/icesjms/fss084

Borja, A., Fontán, A., Sáenz, J., & Valencia, V. (2008). Climate, oceanography, and recruitment: The case of the Bay of Biscay anchovy (Engraulis encrasicolus). *Fisheries Oceanography*, *17*(6), 477–493. https://doi.org/10.1111/j.1365-2419.2008.00494.x

Borja, A., Uriarte, A., & Egaña, J. (2002). Environmental factors and recruitment of mackerel, Scomber scombrus L. 1758, along the north-east Atlantic coasts of Europe. *Fisheries Oceanography*, *11*(2), 116–127. https://doi.org/10.1046/j.1365-2419.2002.00190.x

Botas, J. A., Fernández, E., Bode, E., & Anadón, R. (1990). A persistent upwelling off the central Cantabrian coast (Bay of Biscay). *Estuarine, Coastal and Shelf Science*, *30*(2), 185–199. https://doi.org/10.1016/0272-7714(90)90063-W

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling*, *157*(2–3), 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Bruge, A., Alvarez, P., Fontán, A., Cotano, U., & Chust, G. (2016). Thermal niche tracking and future distribution of Atlantic mackerel spawning in response to ocean warming. *Frontiers in Marine Science*, *3(June*, 1–13. https://doi.org/10.3389/fmars.2016.00086

Brunel, T., Damme, C. J. G. Van, Samson, M., & Dickey-collas, M. (2017). Quantifying the influence of geography and environment on the northeast Atlantic mackerel spawning distribution, (December 2016), 1–15. https://doi.org/10.1111/fog.12242

Cabanas, J. M., & Alvarez, I. (2005). Ekman transport patterns in the area close to the Galician coast (NW, Spain). *Journal of Atmospheric & Ocean Science*, *10*(4), 325–341. https://doi.org/10.1080/17417530601127548

Casabella, N., Lorenzo, M. N., & Taboada, J. J. (2014). Trends of the Galician upwelling in the context of climate change. *Journal of Sea Research*, *93*, 23–27. https://doi.org/10.1016/j.seares.2014.01.013

Castro, J., Punzón, A., Pierce, G. J., Marín, M., & Abad, E. (2010). Identification of métiers of the northern Spanish coastal bottom pair trawl fleet by using the partitioning method CLARA. *Fisheries Research*, *102*(1–2), 184–190. https://doi.org/10.1016/j.fishres.2009.11.011

Cheung, W. W. L., Reygondeau, G., & Frölicher, T. L. (2016). Large benefits to marine fisheries of meeting the 1.5°C global warming target. *Science*, *354*(6319), 1591–1594. https://doi.org/10.1126/science.aag2331

Cheung, W. W. L., Watson, R., & Pauly, D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, *497*(7449), 365–368. https://doi.org/10.1038/nature12156

Curtin, R., & Prellezo, R. (2010). Understanding marine ecosystem based management: A literature review. *Marine Policy*, *34*(5), 821–830. https://doi.org/10.1016/j.marpol.2010.01.003

Ducharme-Barth, N. D., & Ahrens, R. N. M. (2016). Classification and analysis of VMS data in vertical line fisheries: Incorporating uncertainty into spatial distributions. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(11), 1749–1764. https://doi.org/10.1139/cjfas-2016-0181

Dufour, F., Arrizabalaga, H., Irigoien, X., & Santiago, J. (2010). Climate impacts on albacore and bluefin tunas migrations phenology and spatial distribution. *Progress in Oceanography*, *86*(1–2), 283–290. https://doi.org/10.1016/j.pocean.2010.04.007

EC. (2009). Council regulation (EC) no 43/2009 of 16 January 2009 fixing for 2009 the fishing opportunities and associated conditions for certain fish stocks and groups of fish stocks, applicable in community waters and, for community vessels, in waters where catch l. *Official Journal of the European Union*, *22*, 1–205.

Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, *430*(7002), 881–884. https://doi.org/10.1038/nature02808

European Commission. (2009). Council regulation (EC) no 1224/2009. Establishing a community control system for ensuring compliance with the rules of the common fisheries policy. *Official Journal of the European Union*, *L343*, 1–47.

FAO. (2016). The state of world fisheries and aquaculture 2016. Contributing to food security and nutrition for all. Rome. Retrieved from http://www.fao.org/3/a-i5555e.pdf

Fraga, F. (1981). Upwelling off the Galician coast, Northwest Spain. *Coastal and Estuarine Sciences*, *1*, 176–182. https://doi.org/10.1029/CO001p0176

Gaertner, D., & Dreyfus-Leon, M. (2004). Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purse-seine fishery simulated with artificial neural networks. *ICES Journal of Marine Science*, *61*(5), 812–820. https://doi.org/10.1016/j.icesjms.2004.05.002

Gelaro, R., McCarty, W., Suárez, M. J., Todling, R., Molod, A., Takacs, L., Randles, C. A., Darmenov, A., Bosilovich, M. G., Reichle, R., Wargan, K., Coy, L., Cullather, R., Draper, C., Akella, S., Buchard, V., Conaty, A., da Silva, A. M., Gu, W., … Zhao, B. (2017). The modern-era retrospective analysis for research and applications, version 2 (MERRA-2). *Journal of Climate*, *30*(14), 5419–5454. https://doi.org/10.1175/JCLI-D-16-0758.1

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Hamilton, J. (1994). *Time Series Analysis*. Princeton University Press. https://doi.org/10.1515/9780691218632

Hannesson, R. (2013). Sharing the Northeast Atlantic mackerel. *ICES Journal of Marine Science*, *70*(2), 259–269. https://doi.org/10.1093/icesjms/fss134

Hastie, T., & Tibshirani, R. (1987). Generalized additive models: Some applications. *Journal of the American Statistical Association*, *82*(398), 371–386. https://doi.org/10.1080/01621459.1987.10478440

Hintzen, N. T., Bastardie, F., Beare, D., Piet, G. J., Ulrich, C., Deporte, N., Egekvist, J., & Degel, H. (2012). VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fisheries Research*, *115-116*, 31–43. https://doi.org/10.1016/j.fishres.2011.11.007

Hughes, K. M., Dransfeld, L., & Johnson, M. P. (2014). Changes in the spatial distribution of spawning activity by north-east Atlantic mackerel in warming seas: 1977 – 2010. *Marine Biology*, *161*(11), 2563–2576. https://doi.org/10.1007/s00227-014-2528-1

ICES. (2015). Report of the working group on widely distributed stocks (WGWIDE). 25 August - 31 August 2015, Pasaia, Spain., 646 pp. https://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2015/WGWIDE/01%20WGWIDE%20Report.pdf

ICES. (2019a). Working group on widely distributed stocks (WGWIDE). *Ices Scientific Reports*, *1*.

ICES. (2019b). Workshop on a research roadmap for mackerel (WKRRMAC). *Ices Scientific Reports*, *1*. https://doi.org/10.17895/ices.pub.5541

Iversen, S. A. (2002). Changes in the perception of the migration pattern of Northeast Atlantic mackerel during the last 100 years. *ICES Marine Science Symposia*, *215*, 382–390. Retrieved from http://prep.ices.dk/sites/pub/Publication Reports/Marine Science Symposia/Phase 2/-ICES Marine Science Symposia - Volume 215–2002 - Part 46 of 70.pdf

Jansen, T. (2014). Pseudocollapse and rebuilding of North Sea mackerel (Scomber scombrus). *ICES Journal of Marine Science*, *71*(2), 299–307. https://doi.org/10.1038/278097a0

Jansen, T., & Gislason, H. (2011). Temperature affects the timing of spawning and migration of North Sea mackerel. *Continental Shelf Research*, *31*(1), 64–72. https://doi.org/10.1016/j.csr.2010.11.003

Jansen, T., & Gislason, H. (2013). Population structure of Atlantic mackerel (Scomber scombrus). *PLoS ONE*, *8*(5), e64744. https://doi.org/10.1371/journal.pone.0064744

Jansen, T., Post, S. L., Kristiansen, T., Oskarsson, G. J., Boje, J., MacKenzie, B. R., Broberg, M., & Siegstad, H. (2016). Ocean warming expands habitat of a rich natural resource and benefits a national economy. *Ecological Applications*, *26*(7), 2021–2032. https://doi.org/10.1002/eap.1384

Kaufman, L., & Rousseuw, P. J. (1986). Clustering large sets (with discussion). *Pattern Recognition in Practice*, *II*, 405–416. https://doi.org/10.2307/2532178

Lambert, C., Pettex, E., Dorémus, G., Laran, S., Stéphan, E., Canneyt, O. V., & Ridoux, V. (2017). How does ocean seasonality drive habitat preferences of highly mobile top predators? Part II: The eastern North-Atlantic. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *141*, 133–154. https://doi.org/10.1016/j.dsr2.2016.06.011

Langan, J., Puggioni, G., Oviatt, C., Henderson, M., & Collie, J. (2021). Climate alters the migration phenology of coastal marine species. *Marine Ecology Progress Series*, *660*, 1–18. https://doi.org/10.3354/meps13612

Lavín, A. (1991). Afloramiento en el noroeste de la Pensinsula Iberica; indices de afloramiento en el punto 43° N11° W: Periodo 1966-1989. *Inf. Téc. Inst. Esp. Oceanog*, *91*, 1–39.

Lehtonen, H. (1996). Potential effects of global warming on northern European freshwater fish and fisheries. *Fisheries Management and Ecology*, *3*(1), 59–71. https://doi.org/10.1111/j.1365-2400.1996.tb00130.x

Lemos, V. M., Ávila Troca, D. F., Castello, J. P., & Vieira, J. P. (2016). Tracking the southern Brazilian schools of Mugil liza during reproductive migration using VMS of purse seiners. *Latin American Journal of Aquatic Research*, *44*(2), 238–246. https://doi.org/10.3856/vol44-issue2-fulltext-5

Lengyel, A., & Botta-Dukát, Z. (2018). Silhouette width using generalized mean—A flexible method for assessing clustering efficiency. *BioRxiv*, 1–27. https://doi.org/10.1101/434100

Levin, P. S., Fogarty, M. J., Murawski, S. A., & Fluharty, D. (2009). Integrated ecosystem assessments: Developing the Scientific basis for ecosystem-based Management of the Ocean. *PLoS Biology*, *7*(1), e14. https://doi.org/10.1371/journal.pbio.1000014

Martin, T. G., Chadès, I., Arcese, P., Marra, P. P., Possingham, H. P., & Norris, D. R. (2007). Optimal Conservation of Migratory Species. *PLoS ONE*, *2*(8). https://doi.org/10.1371/journal.pone.0000751

Mendiola, D., Alvarez, P., Cotano, U., Etxebeste, E., & de Murguia, A. M. (2006). Effects of temperature on development and mortality of Atlantic mackerel fish eggs. *Fisheries Research*, *80*(2–3), 158–168. https://doi.org/10.1016/j.fishres.2006.05.004

Mills, C. M., Townsend, S. E., Jennings, S., Eastwood, P. D., & Houghton, C. A. (2007). Estimating high resolution trawl fishing effort from satellite-based vessel monitoring system data. *ICES Journal of Marine Science*, *64*(2), 248–255. https://doi.org/10.1093/icesjms/fsl026

Nikolioudakis, N., Skaug, H. J., Olafsdottir, A. H., Jansen, T., Jacobsen, J. A., & Enberg, K. (2019). Original article drivers of the summer-distribution of Northeast Atlantic mackerel (Scomber scombrus) in The Nordic Seas from 2011 to 2017; a Bayesian hierarchical modelling approach. *ICES Journal of Marine Science*, *76*, 530–548. https://doi.org/10.1093/icesjms/fsy085

Nøttestad, L., Utne, K. R., Óskarsson, G. J., Jónsson, S. P., Jacobsen, J. A., Tangen, Ø., Anthonypillai, V., Aanes, S., Vølstad, J. H., Bernasconi, M., Debes, H., Smith, L., Sveinbjörnsson, S., Holst, J. C., Jansen, T., & Slotte, A. (2015). Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (Scomber scombrus) in The Nordic Seas from 2007 to 2014. *ICES Journal of Marine Science*, *73*, 359–373. https://doi.org/10.1093/icesjms/fsv218 Original

Olafsdottir, A. H., Rong, K., Arge, J., Jansen, T., Óskarsson, G. J., Nøttestad, L., Elvarsson, B. P., Broms, C., & Slotte, A. (2019). Geographical expansion of Northeast Atlantic mackerel (Scomber scombrus) in the Nordic seas from 2007 to 2016 was primarily driven by stock size and constrained by low temperatures. *Deep-Sea Research Part*, *II*, *159*, 152–168. https://doi.org/10.1016/j.dsr2.2018.05.023

Peer, A. C., & Miller, T. J. (2014). Climate change, migration phenology, and fisheries management interact with unanticipated consequences. *North American Journal of Fisheries Management*, *34*(1), 94–110. https://doi.org/10.1080/02755947.2013.847877

Pennino, M. G., Conesa, D., López-Quílez, A., Muñoz, F., Fernández, A., & Bellido, J. M. (2016). Fishery-dependent and -independent data lead to consistent estimations of essential habitats. *ICES Journal of Marine Science*, *73*(9), 2302–2310. https://doi.org/10.1093/icesjms/fsw062

Prego, R., Varela, M., DeCastro, M., Ospina-Alvarez, N., Garcia-Soto, C., & Gómez-Gesteira, M. (2012). The influence of summer upwelling at the western boundary of the Cantabrian coast. *Estuarine, Coastal and Shelf Science*, *98*, 138–144. https://doi.org/10.1016/j.ecss.2011.12.009

Punzón, A., Serrano, A., Sánchez, F., Velasco, F., Preciado, I., González-Irusta, J. M., & López-López, L. (2016). Response of a temperate demersal fish community to global warming. *Journal of Marine Systems*, *161*, 1–10. https://doi.org/10.1016/j.jmarsys.2016.05.001

Punzón, A., & Villamor, B. (2009). Does the timing of the spawning migration change for the southern component of the Northeast Atlantic mackerel (Scomber scombrus, L. 1758)? An approximation using fishery analyses. *Continental Shelf Research*, *29*(8), 1195–1204. https://doi.org/10.1016/j.csr.2008.12.024

Punzón, A., Villamor, B., Carrera, P., & González-quirós, R. (2003). Spawning migration change in the southern component of the Northeast Atlantic Mackerel (*Scomber scombrus*).

Punzón, A., Villamor, B., Gonzalez-Quiros, R., Abaunza, P., Costas, G., & Gancedo, R. (2009). El Flujo Migratorio de la Caballa del Atlántico Nordeste (*Scomber scombrus*) en el Mar Cantábrico.

Punzón, A., Villamor, B., & Preciado, I. (2004). Analysis of the handline fishery targeting mackerel (Scomber scombrus, L.) in the north of Spain (ICES division VIIIbc). *Fisheries Research*, *69*(2), 189–204. https://doi.org/10.1016/j.fishres.2004.05.002

Ramos, S., Vázquez-Rowe, I., Artetxe, I., Moreira, M. T., Feijoo, G., & Zufía, J. (2011). Environmental assessment of the Atlantic mackerel (Scomber scombrus) season in the Basque Country. Increasing the timeline delimitation in fishery LCA studies. *The International Journal of Life Cycle Assessment*, *16*(7), 599–610. https://doi.org/10.1007/s11367-011-0304-8

Reglero, P., Ciannelli, L., Alvarez-Berastegui, D., Balbín, R., López-Jurado, J. L., & Alemany, F. (2012). Geographically and environmentally driven spawning distributions of tuna species in the western Mediterranean Sea. *Marine Ecology Progress Series*, *463*, 273–284. https://doi.org/10.3354/meps09800

Reid, P. C., De Fatima Borges, M., & Svendsen, E. (2001). A regime shift in the north sea circa 1988 linked to changes in the north sea horse mackerel fishery. *Fisheries Research*, *50*(1–2), 163–171. https://doi.org/10.1016/S0165-7836(00)00249-6

Robinson, C., & Schumacker, R. (2009). Interaction effects: Centering, variance inflation factor, and interpretation issues. *Multiple Linear Regression Viewpoints*, *35*(1), 6–11.

Robinson, R. A., Crick, H. Q. P., Learmonth, J. A., Maclean, I. M. D., Thomas, C. D., Bairlein, F., Forchhammer, M. C., Francis, C. M., Gill, J. A., Godley, B. J., Harwood, J., Hays, G. C., Huntley, B., Hutson, A. M., Pierce, G. J., Rehfisch, M. M., Sims, D. W., Santos, M. B., Sparks, T. H., … Visser, M. E. (2009). Travelling through a warming world: Climate change and migratory species. *Endangered Species Research*, *7*, 87–99. https://doi.org/10.3354/esr00095

Rousseeuw, P. J., & Kaufman, L. (2009). *Finding Groups in Data: An Introduction to Cluster Analysis*. John Wiley & Sons.

Russo, T., Carpentieri, P., DAndrea, L., De Angelis, P., Fiorentino, F., Franceschini, S., Garofalo, G., Labanchi, L., Parisi, A., Scardi, M., & Cataudella, S. (2019). Trends in effort and yield of trawl fisheries: A case study from the Mediterranean Sea. *Frontiers in Marine Science*, *6 (APR*, 1–19. https://doi.org/10.3389/fmars.2019.00153

Semmens, D. J., Diffendorfer, J. E., López-Hoffman, L., & Shapiro, C. D. (2011). Accounting for the ecosystem services of migratory species: Quantifying migration support and spatial subsidies. *Ecological Economics*, *70*(12), 2236–2242. https://doi.org/10.1016/j.ecolecon.2011.07.002

Sotillo, M. G., Cailleau, S., Lorente, P., Levier, B., Aznar, R., Reffray, G., Amo-Baladrón, A., Chanut, J., Benkiran, M., & Alvarez-Fanjul, E. (2015). The MyOcean IBI Ocean forecast and reanalysis systems: Operational products and roadmap to the future Copernicus service. *Journal of Operational Oceanography*, *8*(1), 63–79. https://doi.org/10.1080/1755876X.2015.1014663

Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D., & Herrick, S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change*, *1*(9), 449–456. https://doi.org/10.1038/nclimate1301

Trenkel, V. M., Huse, G., MacKenzie, B. R., Alvarez, P., Arrizabalaga, H., Castonguay, M., Goñi, N., Grégoire, F., Hátún, H., Jansen, T., Jacobsen, J. A., Lehodeyh, P., Lutcavage, M., Mariani, P., Melvin, G. D., Neilson, J. D., Nøttestad, L., Óskarsson, G. J., Payne, M. R., … Speirs, D. C. (2014). Comparative ecology of widely distributed pelagic fish species in the North Atlantic: Implications for modelling climate and fisheries impacts. *Progress in Oceanography*, *129(PB*, 219–243. https://doi.org/10.1016/j.pocean.2014.04.030

VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L., & Storlie, C. (2014). Package 'SDMTools'. R package (R Foundation for Statistical Computing, 2014).

Villamor, B., Gonzalez-Pola, C., Lavín, A., Valdés, L., Lago De Lanzós, A., Franco, C., Cabanas, J. M., Bernal, M., Hernandez, C., Iglesias, M., Carrera, P., & Porteiro, C. (2011). Environmental control of Northeast Atlantic mackerel (Scomber scombrus) recruitment in the southern Bay of Biscay: Case study of failure in the year 2000. *Fisheries Oceanography*, *20*(5), 397–414. https://doi.org/10.1111/j.1365-2419.2011.00592.x

Villamor, B., Lanzós, A. L. De, Pérez, J. R., Franco, C., Garabana, D., Cubero, P., Navarro, M. R., Solla, A., Álvarez, I., & Antolinez, A. (2011). Temporal variability of the spawning season for the southern component of the Northeast Atlantic Mackerel (*Scomber scombrus*).

Witt, M. J., & Godley, B. J. (2007). A step towards seascape scale conservation: Using vessel monitoring systems (VMS) to map fishing activity. *PLoS ONE*, *2*(10), e1111. https://doi.org/10.1371/journal.pone.0001111

How to cite this article: Rodríguez-Basalo, A., Punzón, A., Ceballos-Roa, E., Jordà, G., González-Irusta, J. M., & Massutí, E. (2022). Fisheries-based approach to disentangle mackerel (*Scomber scombrus*) migration in the Cantabrian Sea. *Fisheries Oceanography*, 1–13. https://doi.org/10.1111/fog.12594