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## Characterization of the pelagic fish community of the north-western and northern Spanish shelf waters<sup>a</sup>

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This study demonstrates the utility of trawl data, collected during acoustic surveys of pelagic fish stocks as a way of confirming fish identification, to characterize the pelagic community, as well as allowing description and prediction of fish distribution patterns, based on data from Spanish Atlantic Ocean shelf surveys during spring 2005–2011. The composition of the pelagic community is described, as well as spatial and temporal patterns of variation in both the community composition and the presence and importance of two of the main exploited pelagic species, sardine *Sardina pilchardus* and anchovy *Engraulis encrasicolus*. The most important species in terms of both frequency of occurrence and standardized mass in hauls were mackerel *Scomber scombrus*, hake *Merluccius merluccius*, horse mackerel *Trachurus trachurus*, *S. pilchardus* and bogue *Boops boops*. Multivariate analysis indicated significant effects of depth, geographical area and year on haul composition. Descriptive generalized additive models (GAM), with latitude, longitude and depth as predictors, identified clear spatial patterns in the occurrence and abundance of both *S. pilchardus* and *E. encrasicolus*, with abundance being highest closer to the coast and, in the case of *E. encrasicolus*, higher near the French and Portuguese borders. Further GAM analysis, using environmental variables to explain spatial patterns, revealed significant effects of depth and sea surface temperature (SST) gradient and depth on *S. pilchardus* importance, while *E. encrasicolus* importance was related to SST. The importance of both species in hauls was higher in the years of higher spawning stock biomass (SSB) and *E. encrasicolus* also appeared to expand its range when SSB was higher.

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Key words: Cantabrian Sea; *Engraulis encrasicolus*; Iberian Peninsula; *Sardina pilchardus*.

### INTRODUCTION

Northern and north-western Iberian shelf waters have been exploited for their marine resources over many centuries. From whaling to fishing, and lately aquaculture and shellfish exploitation, these waters have provided the livelihood for the largest fishing

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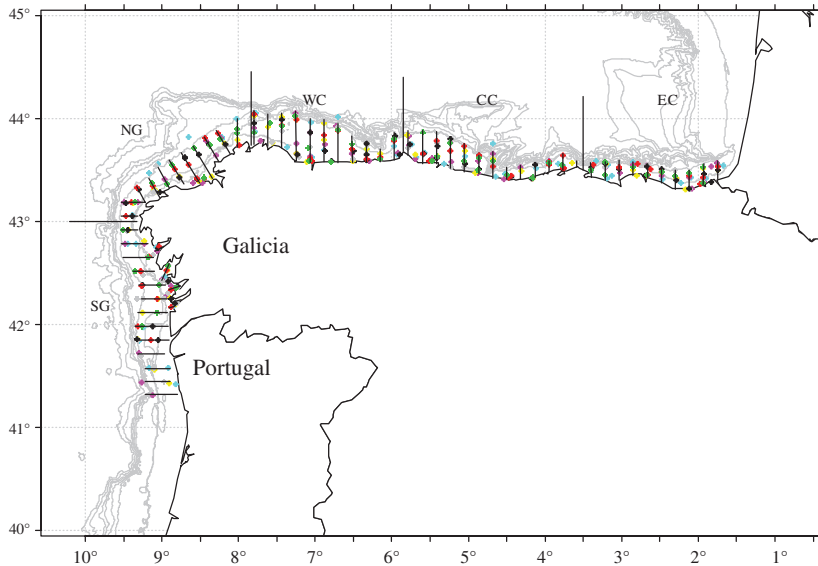


FIG. 1. Map of the study area showing location of pelagic hauls used in the present analysis. The study area was subdivided into south Galicia (SG), north Galicia (NG), western Cantabria (WC), central Cantabria (CC) and eastern Cantabria (EC) for the purposes of multivariate analysis. ■, 2005; ■, 2006; ■, 2007; ■, 2008; ■, 2009; ■, 2010; ■, 2011.

fleet in the EU as well as supporting a wide range of associated jobs related to the processing of fishes and shellfish (Vázquez Seijas, 1998).

The orientation of the coastline, north–south along western Iberia up to Cape Finisterre, then turning north–eastwards towards Cape Estaca de Bares and finally running west–east in the Cantabrian Sea, has a great influence on the oceanography and general ecosystem dynamics of the area (Fig. 1). Although the continental shelf is relatively narrow (*c.* 30–40 km in Galicia and even narrower in the Cantabrian Sea, as little as 12 km in some areas; OSPAR, 2000), the Galician Atlantic Ocean coast (west of Cape Estaca de Bares) is the northern edge of the eastern North Atlantic upwelling system, which ensures elevated primary production and high ecosystem productivity (Figueiras *et al.*, 2002). An additional characteristic of the southern Galicia coast is the presence of the rías, river valleys that the sea has flooded and that can extend 20–35 km inland. The intensity of the upwelling decreases towards the inner Bay of Biscay and the temperature difference across the study area can be  $>10^{\circ}\text{C}$  when intense upwelling occurs in Galician waters. This conspicuous gradient has consequences for the overall dynamics of the ecosystem and the distribution of marine communities (*e.g.* macroalgae; Fernández, 2011).

The Spanish Institute of Oceanography (IEO) began its spring acoustic surveys in 1984 with the original aim of obtaining the necessary fishery-independent information to carry out the analytical assessment of the Iberian sardine *Sardina pilchardus* (Walbaum 1792) stock by acoustic methods combined with the information provided by pelagic trawls. The annual (with some interruptions) survey series has undergone some methodological changes over the years and a shift in its main aim, with the survey gradually evolving into a platform for the monitoring of the pelagic ecosystem of the northern and north–western shelf. The survey now produces biomass estimates

for a wider range of pelagic fish species and collects information on other components of the ecosystem.

In this paper, the information provided by the pelagic trawls, which are routinely carried out to identify the species producing echo traces detected during the annual surveys, is used to characterize the pelagic community. In the past, most studies of fish assemblages or communities have used information provided by demersal surveys focused on bottom-living fishes (Fariña *et al.*, 1997; Serrano *et al.*, 2006) and there is a lack of similar studies on the pelagic environment. This study concentrated on the period 2005–2011, firstly because the data collection methodology has been consistent over this period, and secondly because it provides a time series in which the stocks of two of the most economically important species [*S. pilchardus* and anchovy *Engraulis encrasicolus* (L. 1758)] have shown important changes in abundance (ICES, 2011a). The spawning stock biomass (SSB) of the Iberian *S. pilchardus* stock is considered to be currently far below the long-term average (ICES, 2011b) owing to the lack of strong recruitments since 2004, which has caused the SSB to decline (since 2006) to the lowest values in the series. For *E. encrasicolus*, the fishery on the Bay of Biscay stock was closed in 2006 but re-opened in 2010. The *E. encrasicolus* stock is now considered to be at full reproductive capacity with the SSB estimated in 2011 being one of the highest in the time series (ICES, 2011b).

The aims of this paper are (1) to summarize the overall composition of the pelagic community in the Galician and Cantabrian continental shelf area during 2005–2011 and identify the environmental factors [*e.g.* depth, geographic location, sea surface temperature (SST) and chlorophyll-*a*] that may contribute to its variability; (2) to describe spatial and temporal patterns of variation in presence and importance in the hauls of *S. pilchardus* and *E. encrasicolus* and to determine which part of this variation can be ascribed to environmental factors that are generally considered to be important determinants of fish distribution, such as depth, SST and primary production (proxied by chlorophyll-*a* concentration); (3) to determine if there has been significant interannual variation in the presence and importance of *S. pilchardus* and *E. encrasicolus* in the trawls and if this variability is related to changes in stock abundance.

## MATERIALS AND METHODS

### DATA COLLECTION

PELACUS surveys take place annually in spring (March to April). The sampling grid consists of parallel transects, separated by 8 nautical miles (14.8 km), perpendicular to the coastline, and is surveyed during daylight hours over a period of 30 days. The area of the continental shelf covered each year extends from 30 to 200 m depth and the survey always runs from the Portuguese border to the French border. In some years, when time allows, additional transects are carried out in Portuguese and French waters (at the start and at the end of the survey, respectively). During the surveys, the acoustic energy reflected by marine organisms is measured continuously and pelagic trawls are carried out to help identify the species that are reflecting the acoustic energy. In addition, data are also routinely collected on the hydrography and hydrodynamics of the water masses (with rosettes and conductivity, temperature and depth sensors), on the composition, distribution and biomass of phytoplankton and zooplankton, on the composition of the ichthyoplankton (using a continuous underwater fish egg sampler) and marine mammal and seabird presence (using trained observers). An outline of the sampled area is shown in Fig. 1.

To identify the species and size classes responsible for the acoustic energy detected, pelagic trawls are carried out with one of the two nets: a 76/70 pelagic trawl with a 20 m vertical opening and a 10 mm mesh cod end or a 57/52 pelagic trawl with a 10 m vertical opening and the same mesh size in the cod end. The nomenclature refers to the lengths of the footrope and headline (76 or 57 m, respectively) and the length of the lateral ropes (70 or 52 m, respectively). The choice of one or the other net depends on the topography and the substratum where fishing is going to take place, in particular the availability of enough unobstructed ground for the net to be deployed and recovered and for effective fishing to occur. Fishing generally takes place close to the bottom to ensure that fishes enter the net and do not escape below the footrope.

From 2005 to 2011, a total of 403 valid hauls was carried out during daylight hours. Some of these were further south in Portuguese waters or on the French shelf and, because these areas were not sampled every year, these data were removed from subsequent analysis leaving a new total of 384 hauls.

Individuals of 117 taxa were found in the hauls. Many of these, however, were rare: 46 taxa were recorded only once (*i.e.* a few individuals in a single haul) and several others occurred in a very small number of hauls. To avoid giving undue importance to very rare species in subsequent analysis of community composition, all taxa that were present in <10 hauls were excluded. Also, any species that were not sampled consistently over the time series, *e.g.* jellyfish, and species which regularly enter the net while at the surface (*e.g.* Henslow's swimming crab *Polybius henslowii*) were removed from the analysis. The final number of taxa considered was 25.

For overall description of the pelagic community, relative importance of the different species was estimated as: (1) percentage frequency of occurrence in hauls and (2) proportion of the total (standardized) mass. The duration of a haul is variable and ultimately depends on the number of fishes that enters the net and the conditions where fishing takes place. Because of this variability and the fact that two nets with different swept areas were routinely used, the importance by mass of each species in each haul was standardized as the sum mass (kg) of the individuals of that species divided by the sum mass of all individuals of all species in the haul (kg). This procedure was used to avoid trawls with higher catches contributing relatively more to the estimated overall composition of the pelagic community. Nevertheless, and because the frequency of occurrence cannot be standardized in the same way, haul duration was also included as an explanatory variable in subsequent analyses.

Confidence limits on the proportion of the total mass represented by each species in the hauls were calculated taking into account (between-haul) sampling error. The process involved resampling with replacement (*i.e.* bootstrapping), with the addition of all species mass from a haul to the overall value each time a haul was selected. Medians and 95% C.L. from 1000 bootstrap runs were derived using the package boot (Canty & Ripley, 2011) from R ([www.r-project.org](http://www.r-project.org)).

Oceanographic variables were extracted from databases held by the Environmental Research Division, Southwest Fisheries Science Centre and U.S. National Marine Fisheries Service (<http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp/>). Dynamic oceanographic variables [SST ( $^{\circ}$  C) and chlorophyll-*a* concentration ( $\text{mg m}^{-3}$ )] were extracted for each week from the Moderate Resolution Imaging Spectroradiometer (MODIS)/Aqua satellite (available at *c.*  $0.05^{\circ}$  spatial resolution). Additionally, the spatial variability (range) of environmental variables for a given cell was estimated by calculating proportional change ( $C_P$ ) within a surrounding  $3 \times 3$  cell grid using a moving window as follows:  $C_P = [100 (x_{\max} - x_{\min})] x_{\max}^{-1}$ , where  $x_{\max}$  is the maximum value and  $x_{\min}$  is the minimum value. This dimensionless metric expresses the magnitude of the range of variation in each habitat variable, scaled to the maximum value.

## GENERAL PATTERNS IN SPECIES COMPOSITION: MULTIVARIATE ANALYSIS

Two approaches were used, ANOSIM + SIMPER analyses (Clarke & Warwick, 1994) and redundancy analysis (RDA). Specifically, this study investigated which species contributed most to patterns in community composition, and which environmental variables might be

responsible. While PRIMER is widely used for this kind of analysis, RDA offers the possibility to simultaneously test the effects of a larger number of explanatory variables. Therefore, RDA was applied to both presence and abundance datasets but included an analysis of presence data using PRIMER for comparison.

In PRIMER, a non-parametric two-way ANOSIM test was used to investigate the presence of significant differences in species presence between groups of hauls. The analysis was performed on a between-sample similarity matrix based on the Bray–Curtis index derived from presence or absence data. The groups analysed were defined based on (1) area and depth and (2) area and year. Hauls were therefore grouped into five geographical areas (south Galicia, SG: from Portugal to Cape Finisterre; north Galicia, NG: from Cape Finisterre to Cape Estaca de Bares; western Cantabria, WC: from Cape Estaca de Bares to Cape Peñas; central Cantabria, CC: from Cape Peñas to Cape Ajo; and eastern Cantabria, EC: from Cape Ajo to the border between Spanish and French waters). Trawl depth was divided into three categories (shallow: <50 m, medium: 50–120 m and deep: >120 m).

SIMPER analysis was used to determine the contribution of each species to the average Bray–Curtis dissimilarity between hauls. SIMPER allows the identification of those species that contribute more to the differences between areas, years and depths. Both ANOSIM and SIMPER were run using PRIMER 6.1.6.

RDA, a multivariate technique that explicitly models the patterns in a set of response variables as a function of a series of explanatory variables (Zuur *et al.*, 2007), was used to summarize general patterns in species presence and in species importance (by standardized mass) in individual pelagic trawls and to determine relationships with a series of putative explanatory variables (year, depth, area where the haul took place, SST, SST range, chlorophyll-*a*, chlorophyll-*a* range and haul duration). Based on ecological niche theory, relationships between the presence (or abundance) of a species (or a group of species) in a haul and variables such as those analysed are likely to be non-linear. Therefore, because RDA assumes linear relationships between response and explanatory variables, all explanatory variables were transformed into categorical variables and these were then converted to dummy variables (0, 1), thus ensuring that relationships would be linear. Groups for trawl location and depth were the same as used for the ANOSIM and SIMPER tests. Trawl duration was divided into three categories (short: <15 min; medium: 15–40 min; long: >40 min). The remaining explanatory variables (SST, SST range, chlorophyll-*a* and chlorophyll-*a* range) were all divided into two categories each. Response variables were centred but not standardized. Because of the presence of substantial numbers of double zeros or multiple zeros (arising from joint absences of two or more species; Zuur *et al.*, 2007) in the response variables (Fig. 3), a Chord transformation was applied to all response variables selected (Zuur *et al.*, 2007). Bi-plots and tri-plots were used to visualize correlations between species presence and standardized species mass (response variables), explanatory variables and individual hauls (samples). Numerical output included eigenvalues for the RDA axes, weightings showing the contribution of each species to each axis and significance test values for each explanatory variable (based on 9999 permutations of the data).

## UNIVARIATE ANALYSIS : *S. PILCHARDUS* AND *E. ENCRASICOLUS* DISTRIBUTION AND IMPORTANCE

Following exploratory analysis, *e.g.* identification of outliers, investigation of collinearity, simple exploratory generalized additive models (GAM) using three-dimensional (3-D) smoothers were fitted to the response variable series to reveal possible interactions between pairs of continuous explanatory variables. Interactions for pairings, such as latitude and SST, were not considered as they were not included in the same models. Although the survey design provides adequate coverage to visualize the latitude  $\times$  longitude interaction, for other pairs of variables (*e.g.* chlorophyll-*a* and SST) data were available for only a small proportion of parameter space, *e.g.* at low SSTs there were only low chlorophyll-*a* values, making it difficult to visualize interactions. Finally, therefore, and considering that this study is essentially building hypotheses about factors affecting species distribution rather than developing definitive models, the results reported here concentrate only on interactions between pairs of variables remaining in the final models. Higher-level (three or four-way) interactions could

not be tested in this manner and indeed could only have been tested by reducing some of the variables to categories. GAMs were then used to model the spatio-temporal patterns of distribution and local abundance of *S. pilchardus* and *E. encrasicolus* in three ways: (1) to describe the spatio-temporal variability in species presence or absence and importance in the hauls, (2) to determine the extent to which the previously modelled spatial component of variation in species presence or absence and importance in the hauls could be explained by a suite of environmental variables (*e.g.* depth, SST and chlorophyll-*a*) and (3) to determine whether significant interannual variation identified could be related to annual indices of species abundance.

Models with only latitude, longitude, year and duration of haul were run to describe the distribution of the species (step 1 above), with and without interaction between latitude and longitude effects, while for the second type of models, latitude and longitude were substituted by environmental variables. For both types of analyses, continuous explanatory variables were fitted as smoothers. Chlorophyll-*a* and SST range were cube-root transformed to reduce the effect of a few high values. The interaction of latitude and longitude effects may be captured by fitting a 3-D smoother to both variables simultaneously (using  $k = 4 \times 4 = 16$ ). The smooth surface contains both individual effects and interactions, with the latter evident as complexities on the surface.

Poisson GAMs with a log link were used for *S. pilchardus* mass data while for *E. encrasicolus* mass, negative binomial GAMs with a log link were used because no satisfactory fits could be obtained assuming a Poisson distribution. Binomial GAMs with a logit link were used for the presence or absence data. In all cases, the maximum number of d.f. for smoothers was restricted to 3 ( $k = 4$ ) to avoid over-fitting. Backward selection was used and, at each step, the least important non-significant variable remaining in the model was dropped. The consequence of removing these variables was tested using an *F*-test; they were retained if their presence significantly improved the model fit. Once final models were obtained, residuals were checked for patterns and autocorrelation, and the absence of influential data points was confirmed by examining a plot of hat values.

To determine if the (significant) interannual variation found in the abundance and presence of *S. pilchardus* and *E. encrasicolus* could be related to changes in stock abundance (step 3 above), the final models for these species were re-run, substituting the relevant SSB for year. SSB figures were obtained from the latest ICES analytical assessments (ICES, 2011*b*).

## RESULTS

### HAUL CHARACTERISTICS

Between 50 and 60 hauls were carried out each year in spring in the main area of the survey (Spanish northern and north-western waters) (Table I). North Galicia is the area where the least valid hauls were obtained, and none in very shallow depths (<50 m) owing to the presence of a very rocky sea floor along with widespread presence of fixed fishing gear (Table I). In all the other areas, except south Galicia, most hauls took place in deeper waters. Almost 70% of the trawls lasted between 15 and 40 min, with shorter hauls only taking place on 32 occasions (8.3%) and longer hauls ( $n = 84$ ) occurring mainly in the 2011 survey ( $n = 27$ ) and in Galicia ( $n = 48$ ). Shorter hauls were relatively more frequent in shallower waters while the opposite was true for deeper waters.

### GENERAL DESCRIPTION OF THE PELAGIC COMMUNITY

In general, most hauls caught few species, with the number of taxa per haul ranging from one to 12 and a mean value at slightly below six taxa. Fishes (21

TABLE I. Summary of number ( $n$ ) of hauls sampled in each year, by area, depth range and duration class. The table also shows hauls sampled in each area by depth range and duration class. Areas are as shown in Fig. 1: south Galicia (SG), north Galicia (NG), western Cantabria (WC), central Cantabria (CC) and eastern Cantabria (EC). Depth ranges are <50 m (shallow), 50–120 m (medium) and >120 m (deep). Duration classes are <15 min (S), 15–40 min (R) and >40 min (L)

Year	$n$	By area					By depth			By duration		
		SG	NG	WC	CC	EC	Shallow	Medium	Deep	S	R	L
2005	53	12	8	10	12	11	9	24	20	7	39	7
2006	55	9	8	13	13	12	6	21	28	5	43	7
2007	50	10	8	13	10	9	6	21	23	4	30	16
2008	57	20	6	11	10	10	5	27	25	11	41	5
2009	58	11	11	13	12	11	11	18	29	3	45	10
2010	60	12	11	11	15	11	1	24	35	2	46	12
2011	51	8	10	11	12	10	3	16	32	0	24	27
Total	384	82	62	82	84	74	41	151	192	32	268	84

Area	By depth			By duration		
	Shallow	Medium	Deep	S	M	L
SG	20	32	30	7	51	24
NG		19	43	6	32	24
WC	4	30	48	8	60	14
CC	12	35	37	4	69	11
EC	5	35	34	7	56	11
Total	41	151	192	32	268	84

By depth	By duration		
	S	M	L
Shallow	8	29	4
Medium	11	114	26
Deep	13	125	54
Total	32	268	84

taxa) dominated the hauls, with cephalopods (four taxa) being present in less than one-third of hauls and representing <0.2% of the standardized mass.

The most important species in terms of both frequency of occurrence and standardized mass was mackerel *Scomber scombrus* L. 1758, which was present in over three quarters of the hauls and represented >27% of the standardized mass (Table II). Other common species were hake *Merluccius merluccius* (L. 1758), also present in more than three quarters of the hauls, although representing <8% of the standardized mass, and horse mackerel *Trachurus trachurus* (L. 1758), *S. pilchardus* and bogue *Boops boops* (L. 1758), each constituting around 15% of the standardized mass, although *T. trachurus* was found in many more hauls than *S. pilchardus* or *B. boops*.

TABLE II. Overall importance of species identified in the hauls carried out during the PELLAGUS acoustic surveys (2005–2011) ( $n = 384$ ). The first estimate ( $E$ ) indicates the number of hauls containing each prey category,  $\%E$  is the same estimate expressed as percentage while  $\%W$  is the total (standardized) per cent mass (adjusted taking account of the total catch mass for the haul). Values in parentheses are 95% C.L.

Taxa	$E$	$\%E$	$\%W$
Fishes	384	100	99.82 (99.690–99.910)
<i>Sardina pilchardus</i>	196	51.0	14.48 (11.850–17.450)
<i>Engraulis encrasicolus</i>	86	22.4	0.96 (0.504–1.503)
<i>Mauroliscus muelleri</i>	29	7.6	0.28 (0.013–0.798)
<i>Micromesistius poutassou</i>	140	36.5	5.91 (4.156–7.859)
<i>Merluccius merluccius</i>	305	79.4	7.95 (6.131–9.991)
<i>Capros aper</i>	66	17.2	5.12 (3.520–6.888)
<i>Belone belone</i>	17	4.4	0.57 (0.020–1.35)
<i>Trachurus trachurus</i>	283	73.7	14.80 (12.370–17.210)
<i>Trachurus picturatus</i>	84	21.9	0.88 (0.362–1.543)
<i>Trachurus mediterraneus</i>	74	19.3	2.27 (1.508–3.193)
<i>Boops boops</i>	232	60.4	12.94 (10.700–15.640)
<i>Diplodus sargus</i>	16	4.8	0.27 (0.082–0.525)
<i>Pagellus acarne</i>	16	4.8	0.04 (0.011–0.072)
<i>Pagellus bogaraveo</i>	12	3.1	0.00 (0.001–0.006)
<i>Petromyzon marinus</i>	14	3.7	0.00 (0.000–0.001)
<i>Spondylisoma cantharus</i>	44	11.5	0.24 (0.107–0.422)
<i>Ammodytes</i> spp.	10	2.6	0.46 (0.021–1.040)
<i>Aphia minuta</i>	10	2.6	0.08 (0.002–0.247)
<i>Scomber scombrus</i>	321	83.6	27.28 (23.870–30.450)
<i>Scomber colias</i>	175	45.6	3.23 (2.110–4.536)
<i>Mola mola</i>	23	6.0	2.06 (0.995–3.430)
Cephalopods	106	27.6	0.18 (0.088–0.304)
<i>Loligo forbesi</i>	11	2.9	0.01 (0.002–0.023)
<i>Loligo vulgaris</i>	23	6.0	0.05 (0.012–0.110)
<i>Alloteuthis</i> spp.	50	13.0	0.10 (0.034–0.212)
<i>Todaropsis eblanae</i>	34	8.9	0.01 (0.006–0.025)

Other species that appeared frequently in the hauls included Spanish mackerel *Scomber colias* Gmelin 1789, blue jack mackerel *Trachurus picturatus* (Bowdich 1825) and Mediterranean horse mackerel *Trachurus mediterraneus* (Steindachner 1868), each contributing <4% to the overall standardized mass. *Engraulis encrasicolus* was present in slightly over one-fifth of the hauls but constituted <1% of the overall standardized mass.

The 95% C.L. for the percentage mass estimates, based on sampling error at the level of the combined surveys, are in general, and for most species, relatively narrow (Fig. 2 and Table II).

## MULTIVARIATE ANALYSIS

The two-way ANOSIM with area and depth as factors revealed significant differences in the presence of species between areas across depth categories ( $R = 0.208$ ,



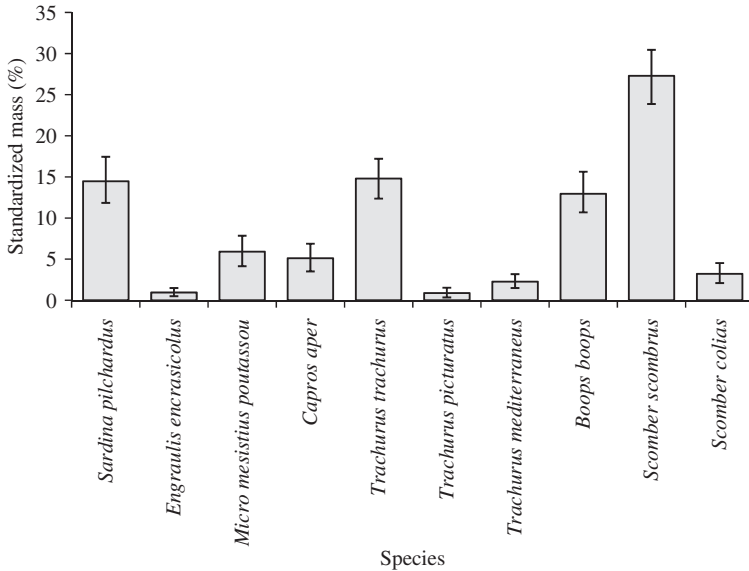


FIG. 2. Standardized percentage mass estimates ( $\pm 95\%$  C.L.), based on between-haul sampling error for the main species found in the hauls carried out during the PELACUS surveys (2005–2011).

$P < 0.001$ ) and between depths across areas ( $R = 0.295$ ,  $P < 0.001$ ). Pair-wise differences between depth categories were all significant ( $P < 0.001$ ) as were most pair-wise differences between areas. The difference between south Galicia and north Galicia was not significant.

Likewise, the ANOSIM with area and year showed significant differences between areas across years ( $R = 0.187$ ,  $P < 0.001$ ) and between years across areas ( $R = 0.099$ ,  $P < 0.001$ ). There were significant differences between all pairs of areas ( $P < 0.05$ ). Pair-wise differences between year categories were mostly significant, although differences between 2007 and 2009, 2008 and 2010 and 2009 and 2010 were not significant ( $P > 0.05$ ).

A group of *c.* 10 species, the species with higher frequency of presence, in general, contributed most to dissimilarities between areas (Table III). Several species (*B. boops*, *T. mediterraneus*, *T. trachurus* and *S. colias*) showed increased frequency of presence from south Galicia towards the eastern Cantabria, with *B. boops* showing the most conspicuous pattern with an average frequency of  $< 0.2$  in south Galicia and  $> 0.8$  in eastern Cantabria. The opposite pattern was observed only in sunfish *Mola mola* (L. 1758), which had low overall frequencies of presence. Some species showed maximal average frequencies of presence at the edges of the study area (*e.g.* *M. merluccius* and *S. pilchardus*), whereas others showed maximum frequencies in the central part of the study area (between north Galicia and the central Cantabria) and were less frequent in south Galicia and the eastern Cantabria (*e.g.* *T. picturatus*).

This group of *c.* 10 species also accounted for much of the dissimilarity between depth categories (Table IV). Again, there was high variability in the rank of contribution to dissimilarities between depth categories and in the pattern of average frequency of presence of the species across depths. For instance, blue whiting *Micromesistius poutassou* (Risso 1827) was clearly linked to the deep category and

TABLE III. Average frequency of presence for each taxon in each area [south Galicia (SG), north Galicia (NG), western Cantabria (WC), central Cantabria (CC) and eastern Cantabria (EC)] and its contribution to dissimilarity (%) between geographically contiguous areas. Only species that contribute to 90% of cumulative dissimilarity in any of the pairs of areas considered are included

Species	Frequency of presence					% Contribution to dissimilarity			
	SG	NG	WC	CC	EC	SG-NG	NG-WC	WC-CC	CC-EC
<i>Alloteuthis</i> spp.	0.49	0.06	0.04	0.01	0.03	7.59	–	–	–
<i>Belone belone</i>	0.01	0.05	0.06	0.08	0.01	–	2.08	2.11	–
<i>Boops boops</i>	0.33	0.34	0.57	0.94	0.78	6.74	9.36	9.84	6.55
<i>Capros aper</i>	0.02	0.19	0.26	0.23	0.16	–	7.39	7.22	6.04
<i>Diplodus sargus</i>	0.01	0.00	0.06	0.05	0.08	–	–	–	2.07
<i>Engraulis encrasicolus</i>	0.21	0.08	0.13	0.20	0.49	3.38	4.20	5.52	10.43
<i>Loligo vulgaris</i>	0.09	0.00	0.04	0.08	0.08	–	–	1.97	2.89
<i>Merluccius merluccius</i>	0.85	0.85	0.73	0.73	0.82	5.17	6.81	6.11	6.67
<i>Mola mola</i>	0.12	0.06	0.06	0.02	0.03	4.38	2.42	–	–
<i>Mauroliticus muelleri</i>	0.09	0.18	0.01	0.04	0.09	6.07	4.02	–	2.48
<i>Micromesistius poutassou</i>	0.41	0.56	0.32	0.20	0.38	8.46	9.44	6.62	7.91
<i>Pagellus acarne</i>	0.02	0.05	0.02	0.06	0.05	–	–	–	2.07
<i>Spondyliosoma cantharus</i>	0.12	0.10	0.07	0.13	0.15	–	–	2.55	4.05
<i>Scomber colias</i>	0.16	0.21	0.37	0.68	0.84	4.61	7.59	11.11	8.25
<i>Sardina pilchardus</i>	0.46	0.16	0.33	0.71	0.82	5.46	6.35	11.64	8.00
<i>Scomber scombrus</i>	0.77	0.81	0.88	0.87	0.85	8.22	6.53	4.08	4.59
<i>Todaropsis eblanae</i>	0.06	0.18	0.06	0.08	0.08	5.10	4.55	2.65	2.95
<i>Trachurus mediterraneus</i>	0.06	0.03	0.12	0.32	0.41	–	–	4.78	6.75
<i>Trachurus picturatus</i>	0.15	0.31	0.35	0.18	0.12	8.56	9.33	7.11	5.11
<i>Trachurus trachurus</i>	0.63	0.58	0.70	0.81	0.95	11.56	10.28	7.08	5.15

had the highest contribution to the dissimilarity between deep and medium depths. *Merluccius merluccius* showed increased average frequency with greater depth but contributed most to dissimilarity between shallow and medium depths. Other species with a general pattern of increase with increasing depth were *S. scombrus* and *T. picturatus*. Several other species were more frequent at shallow and medium depths, e.g. *S. pilchardus*, *B. boops* and *T. mediterraneus*, whereas *S. colias* occurred with higher frequency at medium depths.

In the RDA of data on species presence in hauls, the sum of all canonical eigenvalues was 0.24 indicating that all the explanatory variables used in the analysis together explained 24% of the variation in the response variables. Axes 1 and 2 accounted for 12.60 and 0.04% of the variation, respectively. For species importance (by standardized mass) in hauls, the sum of all canonical eigenvalues was 0.21, with axes 1 and 2 accounting for 10.30 and 0.05% of the variation, respectively. In both analyses, there were significant effects of depth, area and year (Table V), consistent with the PRIMER analysis of presence or absence data. Importantly, RDA results revealed no effect of haul duration, suggesting that the standardization of species mass was effective and that presence was insensitive to haul duration. In general, the main species (*S. scombrus*, *T. trachurus*, *S. pilchardus*, *B. boops* and *M. poutassou*) contributed the most to variation in the sample set. Based on visual examination of

TABLE IV. Average frequency of presence for each taxon in each depth category [ $<50$  m (shallow), 50–120 m (medium) and  $> 120$  m (deep)] and its contribution to dissimilarity (%) between depths. Only species that contribute to 90% of cumulative dissimilarity in any of the pairs of depth categories are included

Species	Frequency of presence			% Contribution to dissimilarity	
	Shallow	Medium	Deep	Shallow-medium	Medium-deep
<i>Aphia minuta</i>	0.10	0.03	0.00	2.21	–
<i>Alloteuthis</i> spp.	0.32	0.17	0.06	4.40	3.15
Ammodytidae	0.17	0.02	0.00	3.25	–
<i>Boops boops</i>	0.76	0.74	0.46	7.02	7.93
<i>Capros aper</i>	0.02	0.01	0.26	–	5.60
<i>Diplodus sargus</i>	0.10	0.08	0.00	2.11	–
<i>Engraulis encrasicolus</i>	0.22	0.26	0.20	6.17	5.30
<i>Loligo vulgaris</i>	0.12	0.09	0.02	3.18	–
<i>Merluccius merluccius</i>	0.49	0.72	0.92	9.29	6.80
<i>Mola mola</i>	0.05	0.07	0.05	3.24	2.08
<i>Mauroliticus muelleri</i>	0.00	0.00	0.15	–	2.53
<i>Micromesistius poutassou</i>	0.02	0.16	0.60	3.01	10.13
<i>Spondyliosoma cantharus</i>	0.22	0.23	0.00	5.36	3.54
<i>Scomber colias</i>	0.39	0.59	0.36	6.79	7.01
<i>Sardina pilchardus</i>	0.61	0.66	0.37	9.27	8.13
<i>Scomber scombrus</i>	0.61	0.81	0.9	9.26	5.58
<i>Todaropsis eblanae</i>	0.00	0.03	0.15	–	2.76
<i>Trachurus mediterraneus</i>	0.44	0.34	0.02	6.81	5.56
<i>Trachurus picturatus</i>	0.02	0.14	0.32	–	6.56
<i>Trachurus trachurus</i>	0.71	0.68	0.79	9.28	7.98

the plots for the analysis of standardized mass, depth was strongly correlated with the importance of *B. boops* (shallow waters) and *M. poutassou* (deeper waters) in the hauls. The area effect was most strongly correlated with importance of *S. scombrus* in the hauls. *Trachurus trachurus* importance was related to explanatory variable 2007, reflecting the high importance of this species in hauls in 2007. For presence or absence analysis, depth was correlated with the presence of several species, *Alloteuthis* spp. (shallow waters) and *M. poutassou*, *S. scombrus* and *T. picturatus* (deeper waters) while the area effect was most strongly correlated with the presence of *Alloteuthis* spp. (south Galicia), boarfish *Capros aper* (L. 1758) and *T. picturatus* (west Cantabria), *M. merluccius* and *M. poutassou* (north Galicia) and *S. colias* and *B. boops* (central Cantabria).

#### UNIVARIATE ANALYSIS: *S. PILCHARDUS* AND *E. ENCRASICOLUS* DISTRIBUTION AND IMPORTANCE

Considering firstly models with latitude and longitude as separate smoothers (no interaction), the final model for *S. pilchardus* presence in the hauls explained 24.3% of the deviance (Table VI) and indicated the existence of significant spatial variability but no significant temporal (interannual) variability in *S. pilchardus* presence in the hauls. For *E. encrasicolus*, both spatial and temporal variability were

TABLE V. Results of the redundancy analysis carried out for data on species presence and species importance (by standardized mass) in pelagic trawls performed as part of the PELACUS surveys (2005–2011)

Variable	<i>F</i> -statistic	<i>P</i>	Variable	<i>F</i> -statistic	<i>P</i>
Medium depth	16.271	<0.001	Medium depth	14.117	<0.001
Shallow depth	17.200	<0.001	Shallow depth	17.196	<0.001
South Galicia	17.579	<0.001	West Cantabria	12.384	<0.001
North Galicia	10.701	<0.001	South Galicia	6.308	<0.001
West Cantabrian	7.091	<0.001	North Galicia	8.341	<0.001
2007	4.634	<0.001	Central Cantabrian	3.147	<0.01
2008	3.801	<0.001	2007	2.501	<0.05
2006	3.06	<0.001	Short duration	1.716	>0.05
2005	3.417	<0.001	Regular duration	1.378	>0.05
2010	2.479	<0.01	SST range	1.635	>0.05
2009	2.234	<0.01	SST	1.579	>0.05
Central Cantabria	1.972	<0.05	2010	1.966	>0.05
Regular duration	1.494	>0.05	Chlorophyll- <i>a</i>	1.343	>0.05
Short duration	1.512	>0.05	2006	1.062	>0.05
Chlorophyll- <i>a</i>	1.226	>0.05	2008	1.250	>0.05
Chlorophyll- <i>a</i> range	0.999	>0.05	2005	1.169	>0.05
SST range	0.819	>0.05	2009	0.820	>0.05
SST	0.422	>0.05	Chlorophyll- <i>a</i> range	0.914	>0.05

SST, sea surface temperature.

significant. In addition, inclusion of haul duration significantly improved the overall fit of the *S. pilchardus* model (*F*-test,  $P < 0.05$ ), although its individual effect was not significant. The final model for *S. pilchardus* importance (standardized mass) in the hauls explained a lower percentage (20.8%) of the deviance (Table VI), but this time both temporal and spatial variability were significant. Similar results were obtained for *E. encrasicolus* importance in the hauls, with the model explaining 18% of deviance. In both cases, inclusion of haul duration significantly improved the overall model fit (*F*-test,  $P < 0.05$ ), although its individual effect was not significant.

Models that included the interaction between effects of latitude and longitude on presence and importance of *S. pilchardus* and *E. encrasicolus* in the hauls generally explained a greater percentage of deviance (31.8% of the deviance in *S. pilchardus* presence and 33.8% in *S. pilchardus* importance). For *E. encrasicolus*, these models explained 27.4 and 16.7% of the deviance in presence and importance, respectively. The 3-D smoothers obtained showed apparent interactions, as indicated by the complexity of the smooth surface, between-effects of latitude and longitude for the presence and importance of *S. pilchardus* and for the presence of *E. encrasicolus*. In particular, it is apparent that there were stronger longitudinal trends along the west coast than along the north coast, presumably because longitude is a proxy for depth on the west coast. No interaction was evident for *E. encrasicolus* importance and, indeed, deviance explained was slightly reduced in the model with a 3-d smoother (Fig. 3).

TABLE VI. Results of the generalized additive models for *Sardina pilchardus* and *Engraulis encrasicolus* found in the pelagic trawls carried out as part of the PELACUS acoustic surveys (2005–2011)

Species	Type of model	Type of data	Variable	P	Deviance explained (%)
<i>Sardina pilchardus</i>	Descriptive	Presence or absence	Latitude	<0.001	24.3
			Longitude	<0.001	
			Duration	>0.05	
			Latitude × longitude	<0.001	
			Year	>0.05	
		Importance	Year	<0.001	20.8
			Latitude	<0.001	
			Longitude	<0.001	
			Duration	>0.05	
			Latitude × longitude	<0.001	
	Explanatory with year	Presence or absence	Depth	<0.001	17.7
			Duration	<0.01	
			SST	<0.05	
			Chlorophyll- <i>a</i>	>0.05	
			SST range	>0.05	
		Importance	Year	>0.05	28.2
			Year	<0.001	
			Depth	<0.001	
			SST range	<0.001	
			SST range	<0.001	
Explanatory with SSB	Presence or absence	Depth	<0.001	14.6	
		Duration	<0.01		
		SST range	<0.05		
		Chlorophyll- <i>a</i>	>0.05		
		SSB	<0.001		
	Importance	Depth	<0.001	26.8	
		SST range	<0.001		
		SST range	<0.001		
		SST range	<0.001		
		SST range	<0.001		
<i>Engraulis encrasicolus</i>	Descriptive	Presence or absence	Latitude	<0.05	21.0
			Longitude	<0.001	
			Year	<0.001	
		Importance	Latitude × longitude	<0.001	27.4
			Year	<0.001	
			Year	<0.001	
	Descriptive	Presence or absence	Year	<0.001	18.0
			Longitude	<0.001	
			Latitude	<0.05	
		Importance	Duration	>0.05	16.7
			Latitude × longitude	<0.001	
			Year	<0.001	
			Duration	>0.05	

TABLE VI. Continued

Species	Type of model	Type of data	Variable	<i>P</i>	Deviance explained (%)
	Explanatory with year	Presence or absence	SST	<0.001	18.5
Year			<0.001		
Depth			<0.05		
	Explanatory with SSB	Presence or absence	Importance	<0.001	14.1
SST			<0.001		
Year			<0.001		
	Explanatory with SSB	Presence or absence	SSB	<0.001	17.4
SST			<0.05		
Depth			<0.05		
	Explanatory with SSB	Importance	SSB	<0.001	14.4
SST			<0.001		
SST			<0.001		

SST, sea surface temperature; SSB, spawning stock biomass.

#### UNIVARIATE ANALYSIS: EXPLAINING *S. PILCHARDUS* AND *E. ENCRASICOLUS* DISTRIBUTION AND IMPORTANCE

The final environmental model for presence of *S. pilchardus* in the hauls explained 17.7% of the deviance (Table VI) and showed that *S. pilchardus* presence was negatively related to depth and positively related to SST (Fig. 4). Haul duration had a negative linear effect on *S. pilchardus* presence in the hauls. In addition, inclusion of three individually non-significant variables, namely chlorophyll-*a*, SST gradient and year, significantly improved the model fit (*F*-tests,  $P < 0.05$ ). For presence or absence of *E. encrasicolus*, the final model explained 18.5% of deviance (Table VI) and indicated that *E. encrasicolus* presence was positively related to SST and year but negatively related to depth (Fig. 5).

The final environmental model for *S. pilchardus* importance in the hauls showed negative relationships with both year and depth and a positive relationship with SST gradient (Fig. 6). The model explained 28.2% of deviance (Table VI).

For *E. encrasicolus* importance, the final model indicated that more *E. encrasicolus* were found in more recent years and in warmer waters (Fig. 7). The model explained 14.1% of the deviance. For all these environmental models, repeat runs fitting depth and SST effects together as 3-D smoothers indicated no substantial interaction.

#### UNIVARIATE ANALYSIS: SPECIES IMPORTANCE AND SPECIES PRESENCE OR ABSENCE AND THEIR RELATIONSHIP WITH STOCK ABUNDANCE

Inclusion of the Iberian *S. pilchardus* stock SSB (substituting year) in the final environmental model for *S. pilchardus* presence in the hauls did not improve the model fit and it was dropped from the final model (Table VI).

For *S. pilchardus* importance (standardized mass), SSB was retained in the final model, which showed that *S. pilchardus* importance in the hauls increased with SSB [Fig. 8(a)].

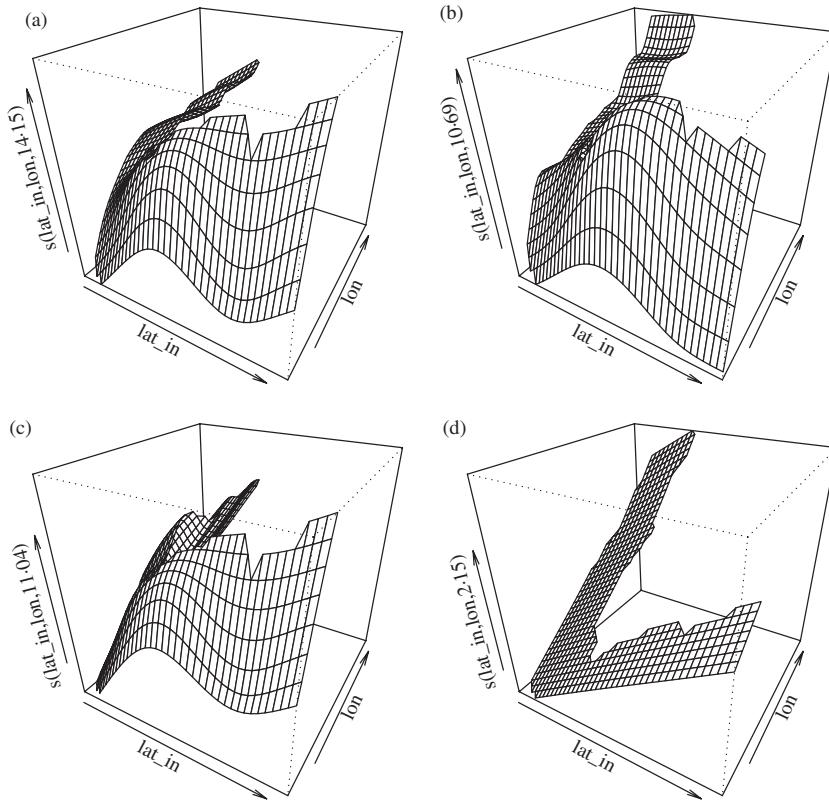


FIG. 3. Three-dimensional smoothers for the effects of latitude (lat) and longitude (lon) on: (a) *Sardina pilchardus* presence, (b) *Engraulis encrasicolus* presence, (c) *S. pilchardus* importance (standardized mass) and (d) *E. encrasicolus* importance (standardized mass). These surfaces capture the individual effects of both variables and their interactions: interactions are evident from irregularities in the form of the surface, here evident in all cases but (d). Latitude values have been flipped to obtain a figure that follows the coastline from the border with Portugal (closest corner) to French waters (farthest corner).

Model results showed that *E. encrasicolus* presence in the hauls was significantly related to Bay of Biscay *E. encrasicolus* SSB (Table VI), increasing linearly with *E. encrasicolus* SSB [Fig. 8(b)]. The final model for *E. encrasicolus* importance in the hauls also showed that importance increased linearly with *E. encrasicolus* SSB [Fig. 8(c)].

## DISCUSSION

### GENERAL VALIDITY OF THE THEORETICAL AND ANALYTICAL FRAMEWORK

Pelagic ecosystems are fluid systems where fish abundance, distribution and life history are related to physical (*e.g.* currents and temperature) and biological variables (*e.g.* abundance and food availability). Community composition would be the result

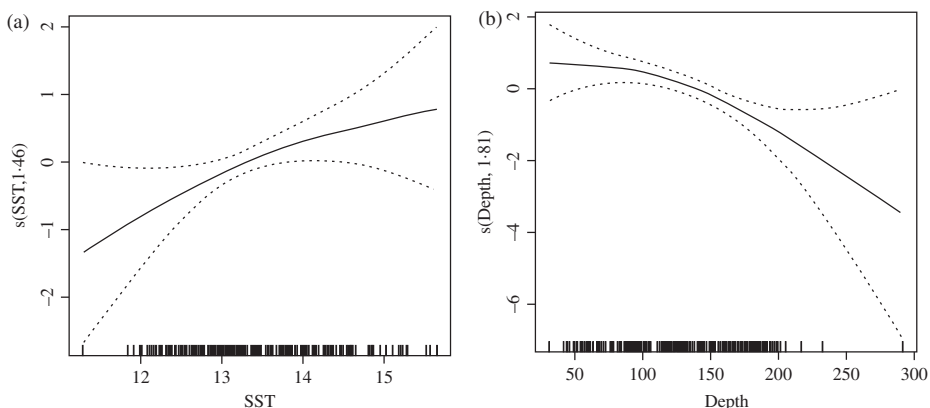


FIG. 4. Final generalized additive model for presence or absence of *Sardina pilchardus* in hauls in relation to environmental variables: smoothers (—) for significant effects of (a) sea surface temperature (SST) and (b) depth (....., 95% C.I.).

of the different niches and habitat preferences of individual species and how they exploit the differences in the oceanography and the general ecosystem dynamics across the area. Because of the lack of defined boundaries in pelagic habitats, however, identifying areas within the distribution of a species that are essential for its survival, the rationale behind essential fish habitat (EFH) studies (Valavanis *et al.*, 2008), becomes difficult and indeed the validity of the approach could be questioned. Nevertheless, information on the realized habitat of a species can provide a useful basis to infer its potential habitat even if it should be taken into account that the environment in which fishes live is intrinsically multidimensional and reducing this complexity to a small number of processes (environmental tolerance or preference and population size) to explain a species distribution may give an incomplete picture.

Some further issues relate to the methodological approach used here. First, this study has not explicitly defined hypotheses about environmental relationships, rather selecting environmental variables that meet two criteria: (1) they are generally thought to be important in determining fish distribution (based on theoretical considerations and empirical evidence) and (2) they are readily available at appropriate spatial and temporal resolutions. The analysis is therefore, to a certain extent, data driven but it should be emphasized that there is an explicit general hypothesis underlying the work, namely, that species distributions (and the distribution of abundance) are, at least in part, determined by environmental tolerance and preferences, and will also be influenced by abundance. Furthermore, it can be expected that some spatio-temporal patterns in the distribution can be described and even predicted but that not all of this variation will be captured by environmental variables that are available for inclusion in the analysis.

In terms of details of the model-fitting process, interactions have not routinely been included in these models. Exploratory analysis suggested that there was little or no evidence of interactions in the case of the majority of combinations of explanatory variables.

The trawl sampling did not follow a specific sampling design, as its primary aim was to provide ground-truthing for acoustic data. As such, data are only available



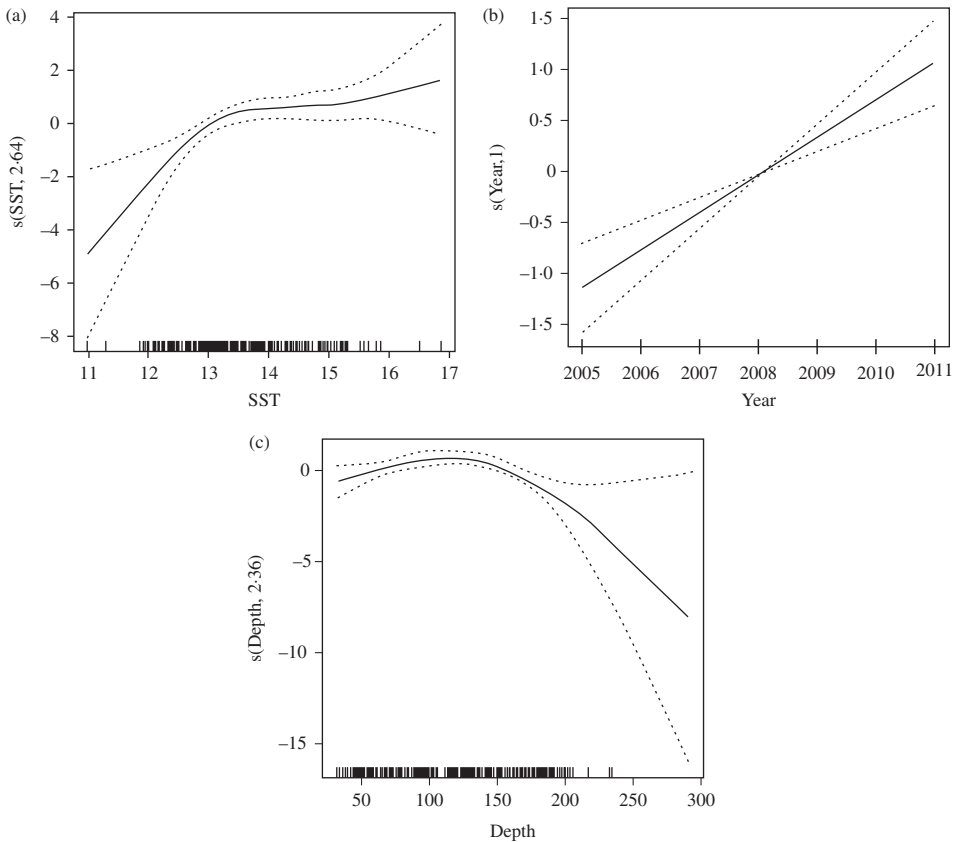


FIG. 5. Final generalized additive model for presence or absence of *Engraulis encrasicolus* in hauls in relation to environmental variables: smoothers (—) for significant effects of (a) sea surface temperature (SST), (b) year and (c) depth (....., 95% C.I.).

in areas where fishes were detected by the echosounder. This study, however, used statistical methods (GAMs) that do not assume random sampling and for which good coverage is more important. Satellite-derived environmental data were used, for which there is only information on the characteristics of the water surface when it is more likely that the whole water column would play a role in determining a species distribution. The main advantages are that (1) using surface data potentially allows model predictions to be extrapolated to adjacent areas (or time periods) that were not surveyed and for which no sub-surface data are therefore available and (2) because satellite data are available across a wide area at high resolution, it is possible to derive average values for a user-defined buffer zone around each sampling point; indeed an investigation of effects of scale would be a useful future analysis.

## COMPOSITION OF THE PELAGIC COMMUNITY

The results indicate that the community is dominated by a relatively small number of species. The variability in community composition (in terms of species presence

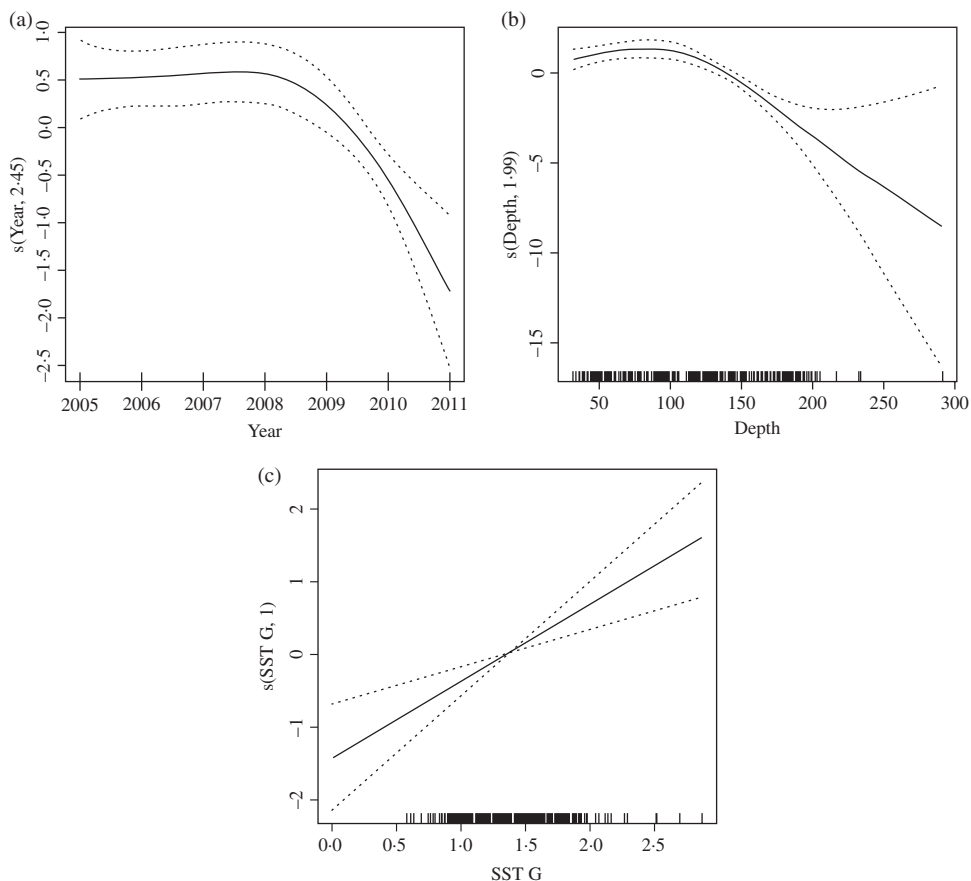


FIG. 6. Final generalized additive models for importance (standardized mass) of *Sardina pilchardus* in hauls in relation to environmental variables: smoothers (—) for significant effects of (a) year, (b) depth and (c) sea surface temperature (SST) range (....., 95% C.L.).

and importance) was at least partly geographical, as shown by the significant effect of sub-area in the RDA. Depth was also shown to significantly influence community composition and there was also significant between-year variation. The ANOSIM analysis on species presence carried out using PRIMER can consider only two explanatory variables simultaneously but this analysis also confirmed significant effects of geographical area, depth and year.

#### DESCRIPTIVE MODELS OF *S. PILCHARDUS* AND *E. ENCRASICOLUS* DISTRIBUTION

For *S. pilchardus*, the final models explained over 20% of the variation in presence and importance, and it is interesting to note that no interannual variation was apparent in presence data while year was a significant variable in the final model for *S. pilchardus* importance, a finding supported in subsequent analyses. For *E. encrasicolus*, significant interannual variation was found both for presence and importance in

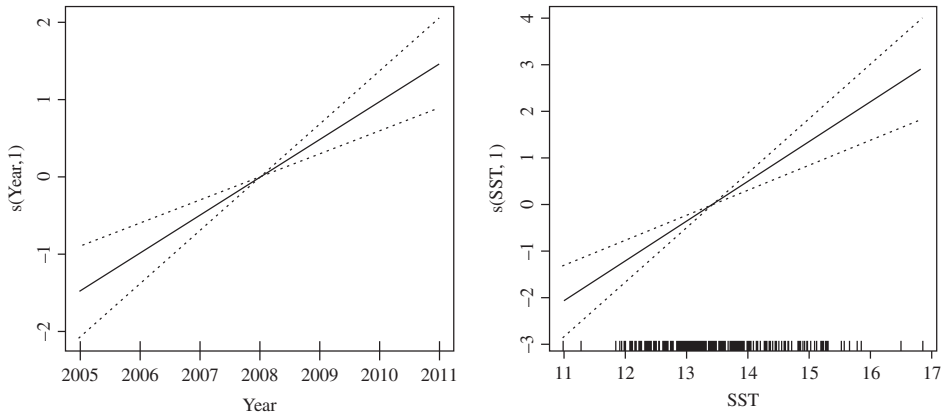


FIG. 7. Final generalized additive models for importance (standardized mass) of *Engraulis encrasicolus* in hauls in relation to environmental variables: smoothers (—) for significant effects of (a) year and (b) sea surface temperature (SST) (....., 95% C.L.).

the hauls, with geographical variables also explaining around 20% of the variability in the distribution of this species.

As expected, these models were generally improved by allowing an interaction between latitude and longitude and thus capturing the overall nature of spatial variation. The model for *S. pilchardus* importance explained almost 34% of deviance. It was decided to restrict the complexity of the fitted surfaces (using  $k = 4 \times 4 = 16$ ) to avoid simply re-describing the observed data, and the total deviance explained by the models is therefore, as noted above, to a certain extent arbitrary.

Although 20–30% deviance explained is quite typical for ecological analysis (Zuur *et al.*, 2007), it is worth noting, however, that 70–80% of variation in presence and importance of these species in the hauls thus remains unexplained. This is likely to be, at least partly, a sampling issue. Although C.L. on importance estimates, based on between-haul variability, were relatively narrow, there is a need to quantify within-haul sampling error and to fully disentangle effects of haul duration and net dimensions, which may not have been fully controlled for in the present analysis.

Although species importance was standardized against total catch in the haul, the variable haul duration appeared in some of the models (as might be expected, especially for species presence). Surprisingly, however, the relationships with haul duration were negative for both presence and importance, for both *S. pilchardus* and *E. encrasicolus*. This is counter-intuitive and may indicate a sampling bias, *e.g.* the net was left in the water for a longer time when fewer fish were present (or acoustic density was lower).

It was necessarily assumed that catchability or net selectivity for each species is constant (even if it differs between species), whereas in reality it may depend on a range of factors, *e.g.* the size of the fish.

Finally, seasonal or diurnal variation in distribution was not considered in this study. Although the surveys are always in spring, sampling takes place over a 30 day period. Variation over this time scale, however, is virtually impossible to detect as it cannot be distinguished from spatial variation (since the surveys always follow

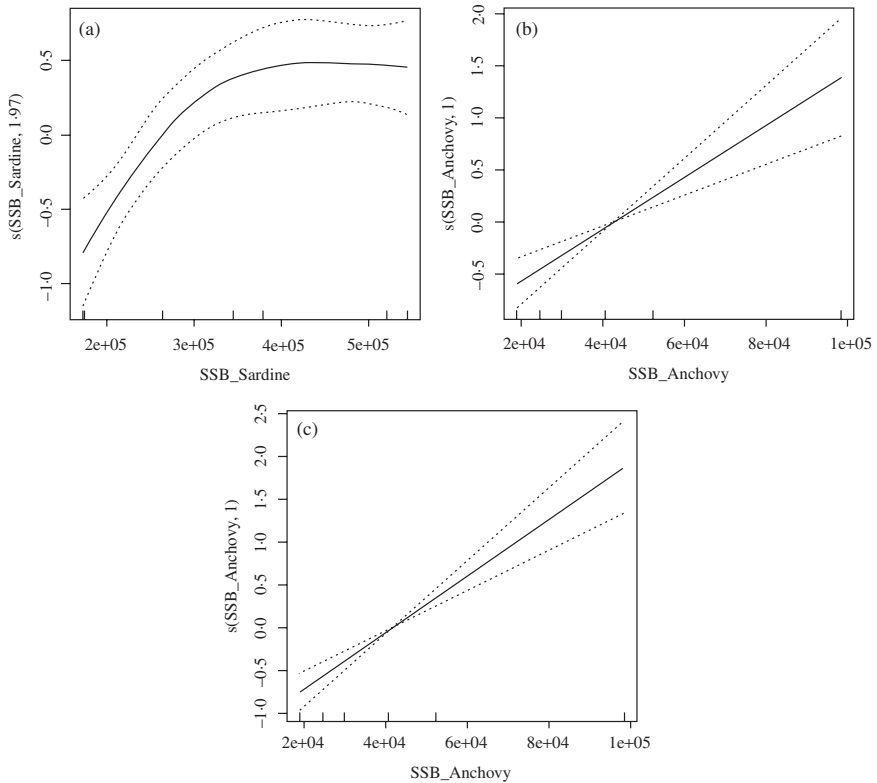


FIG. 8. Smoothers (—) for significant effects of spawning stock biomass (SSB) in final generalized additive models relating *Sardina pilchardus* and *Engraulis encrasicolus* presence and importance to SSB and environmental variables: (a) effect of *S. pilchardus* SSB on *S. pilchardus* importance, (b) effect of *E. encrasicolus* SSB on *E. encrasicolus* presence, (c) effect of *E. encrasicolus* SSB on *E. encrasicolus* importance (....., 95% C.I.).

a standard route from Portugal to France). Future work will also need to examine diurnal variation.

## PREDICTIVE MODELS OF *S. PILCHARDUS* AND *E. ENCRASICOLUS* DISTRIBUTION

The study aimed at explaining species distribution, in particular, in terms of environmental preferences, as this is likely to provide a better basis for prediction, thus offering prospects of fishery forecasting and modelling future effects of climate change.

Depth appeared in the final models for the presence and importance of *S. pilchardus* and for the presence of *E. encrasicolus* in the hauls, while year appeared in every model except for *S. pilchardus* presence. As depth increases, the presence of *S. pilchardus* and *E. encrasicolus* both decrease in the hauls, and also the importance of *S. pilchardus*, confirming its general association with more coastal waters. Among the other variables considered, SST was related to *S. pilchardus* and *E. encrasicolus* presence and importance and SST range related to the presence and

importance of *S. pilchardus*. Similar results were obtained by Tugores *et al.* (2011) in the Mediterranean Sea, who also found depth and SST to be the main variables explaining *S. pilchardus* presence or absence, using a modelling approach similar to the one used in this study. Bellido *et al.* (2008) also found depth to be the main environment variable explaining *S. pilchardus* presence or absence in their study in the western Mediterranean Sea. Their final models explained a similar percentage of deviance (20–30%) to this study and included SST and chlorophyll-*a*.

Although the environmental models of species presence explained a smaller proportion of deviance than the original descriptive spatio-temporal models, the majority of the deviance explained by those models was captured by the environmental variables used. Essentially, these models define limits of distribution but do not indicate anything about variation in abundance within these limits.

The environmental model of *S. pilchardus* importance performed better than the original descriptive spatio-temporal model (without the interaction) but less well than the descriptive model that allowed an interaction between latitude and longitude. This implies, firstly, that the environmental variables selected were important in determining *S. pilchardus* local abundance and, secondly, that they varied spatially in a relatively complex way. This suggests that simple spatio-temporal distribution models may be less useful when modelling patterns of abundance than for modelling the limits to species range.

## EFFECTS OF SPECIES ABUNDANCE

When the effect of SSB was added to the environmental models of species abundance, it was retained and, for both *S. pilchardus* and *E. encrasicolus*, had a significant positive effect, suggesting that local density generally increases as broad-scale abundance increases, as might be expected. For the models of species presence, *E. encrasicolus* SSB had a significant effect on *E. encrasicolus* presence but *S. pilchardus* SSB had no effect on *S. pilchardus* presence. Thus, *E. encrasicolus* appears to extend its range in high abundance years, which is consistent with the understanding of *E. encrasicolus* on the Spanish Atlantic Ocean coast, namely that it mainly comprises fish from a stock whose core distribution lies outside the surveyed area (in the Bay of Biscay). In the case of *S. pilchardus*, distribution range appears to remain relatively stable (because year did not have a significant effect on the models), even though local importance varies in proportion to stock size.

In conclusion, the results indicated that the pelagic fish community of north-western and northern Spanish shelf waters is dominated by a relative small number of species and that the relative importance of the different species has remained stable during the 7 year study period considered in spite of wide year-to-year variation in abundance of individual species. The exception seems to have been 2007, the only year that was found to be significantly different in the analysis of species importance. Species presence or absence showed wider interannual variation with minor species contributing, in this case, to differences between years. The fact remains, however, that this study used a relatively short time series (with the survey basically covering one season).

This study has shown how descriptive statistical models may be used to capture the nature of spatio-temporal variation in a species distribution. These models identified clear spatial patterns in the occurrence and abundance of both *S. pilchardus*

and *E. encrasicolus*, with abundance highest closer to the coast and, in the case of *E. encrasicolus*, clearly higher near the French and Portuguese borders. Because the predictive power of such models is limited, however, it is of interest to determine what part of the observed variation is related to environmental preferences. This modelling approach can, as a by-product, provide information on EFH as well as reveal the proportion of the distribution pattern that cannot be so explained. Significant effects of SST gradient and depth were seen for *S. pilchardus* importance while *E. encrasicolus* importance was related to SST.

One additional factor that needs to be included when modelling a species distribution is species abundance, with the expectation that the realized niche expands in years of high abundance. The results show that importance of both *S. pilchardus* and *E. encrasicolus* in hauls was higher in years of higher SSB, but interannual variation was not apparent for the *S. pilchardus* presence model. This suggests that the range of *S. pilchardus* has not changed as a result of declining abundance since 2008, but its importance in survey catches has decreased.

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