



## Temperature and food-mediated variability of European Atlantic sardine recruitment



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### ABSTRACT

The influence of the environmental conditions during larval development on the resulting recruitment strength was investigated for European sardine (*Sardina pilchardus*) at Atlanto-Iberian waters. Satellite-derived Sea Surface Temperature (SST) and Chlorophyll-*a* concentration (Chla) data from the previous spawning seasons (January to March/April and October to December of the previous year) were related to recruitment success data in the main recruitment hotspots. Recruitment data was taken from yearly acoustic scientific cruises and from the ICES recruitment index estimated by an age-structured model for the entire stock. A linear discriminant analysis model using SST, Chla, and the abundance of spawners during the spawning season identified years of high and low recruitment for all the recruitment hotspots with an accuracy of  $\geq 79\%$ . In general, high recruitment years were associated with high Chla and low SST, although the most important variables to discriminate between the groups were area-specific. High recruitment years were mostly related to high food availability (Chla), particularly during the last quarter of the previous year. In Western Iberia and in the Gulf of Cadiz, high recruitment years were also associated to lower SST, whereas in the Bay of Biscay, where SST during the winter was generally below the optimal range  $\approx 11\text{--}12\text{ }^{\circ}\text{C}$  for sardine larval development, higher recruitment was associated with high SST. For ICES data of the southern European sardine stock, lower SST and higher Chla during the last quarter of the previous year were associated with high recruitment years and SST alone was able to discriminate between the two recruitment groups with 73% accuracy. Although the time-series of available data are still small, these significant relationships are consistent with field and laboratory studies relating larval growth and mortality with main environmental drivers. These relationships should be further investigated in the following years to evaluate if they can be used to construct reliable indicators to predict the level of recruitment and abundance with sufficient advance to help in the management of this important fishing resource.

### 1. Introduction

Small pelagic fish are key species in the most productive regions of the world's oceans, particularly in upwelling regions, where they occupy a fundamental intermediate trophic level (Bakun, 2006). The dominant pelagic fish in the Western Iberian Upwelling Ecosystem is the European sardine (*Sardina pilchardus*; hereafter called sardine). This species is distributed from the North Sea to Mauritania (Culley, 1971), off the Madeira, Azores and Canary Archipelagos and in the Mediterranean and adjacent waters (Andreu, 1969; Suau, 1959). Sardine fishery in the northern areas to the Iberian stock (from the Bay of Biscay

up to the North Sea), are currently unregulated (regulation is currently limited to Portugal and Spain). However, there is an increasing fishery being developed in the northern areas ( $> 35\%$  increase in the last decade compared to the 90's, ICES, 2015) where sardine population dynamics is still poorly studied. Off the Iberian Peninsula, sardines are the most landed fish, representing approximately 40% of the total capture (DGRM, 2016). The Atlanto-Iberian sardine stock has been declining since 2006, and sardine abundance is now at an historical minimum, with severe socio-economic consequences for Portuguese and Spanish fishing communities. Although fishing mortality estimates were particularly high in some of the recent years, environmental

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parameters are hypothesized as the main causes for the decline of sardine abundance (ICES, 2015).

Fish recruitment strength is considered to be strongly related to environment conditions (Houde, 2008). The impact of environmental conditions is particularly important for short lived small pelagics, whose stocks can potentially recover with one year of good recruitment or collapse with a short series of low recruitment years (Katara, 2014). In these situations, the recovery of the stock is highly dependent on a high pulse of recruitment. Since the work by Hjort (1914) it is recognized that the mortality occurring during the early life stages is particularly relevant in shaping the strength of the recruitment. Larval survival is affected by both abiotic and biotic factors; temperature and hydrography, predation and food availability, respectively, being considered the most relevant ones (Houde, 2008). Temperature and food availability are known to affect both year-to-year fluctuations and long-term trends in fish populations (e.g. Loeng, 1989). Water temperature affects the rate of metabolic processes and therefore shapes the distribution and abundance of poikilothermic organisms such as sardines (e.g. Blaxter, 1991). The recent expansion of sardine distribution further north, to the North and Baltic Seas, after 40 years of absence in those areas (Alheit et al., 2012), can be associated with increased water temperature registered for the north Atlantic (e.g. Levitus et al., 2005). At the Iberian Peninsula, higher temperatures have been associated to lower landings (Solari et al., 2010; Santos et al., 2012; Leitão et al., 2014; Gamito et al., 2015; Teixeira et al., 2016; Malta et al., 2016), although no clear mechanism by which temperature negatively affects recruitment has been identified yet.

Temperature influences the seasonality of sardine reproduction (Stratoudakis et al., 2007) and the subsequent survival of the developing larvae (Garrido et al., 2016). These two biological processes can significantly affect the inter-annual strength of sardine recruitment, as shown for other fish species, including clupeoids (Ottersen et al., 2013). Increased temperature is likely to have an impact on the timing and density of plankton blooms, and by that indirectly affect the recruitment. Interannual and geographic variations of plankton productivity can affect the reproductive potential of the indeterminate serial spawning sardines (Zwolinski et al., 2001; Garrido et al., 2007) but food concentration can also have a massive impact in larvae survival (Caldeira et al., 2014). Massive stocks of pelagic fishes are only possible in the most productive regions of the world oceans, such as the Eastern Boundary Upwelling Ecosystems (Fréon et al., 2009), supporting the notion that food availability plays a critical role in their dynamics.

Recent laboratory experiments have shown that the optimal temperature for larval sardine development varies between 13 and 17 °C and that survival outside these boundaries is reduced, particularly during the first weeks of life (Garrido et al., 2016). These results were in accordance with a previous analysis of field samples, showing that sardine spawning activity is linked to SST, with an optimum at 14–15 °C and avoidance below 12 °C and above 16 °C (Stratoudakis et al., 2007). During the protracted spawning season off Iberian waters, sardines might experience temperatures that are higher than tolerable during the first months of reproduction (autumn), and experience temperatures lower than optimal during the last months of the spawning season (winter and spring), which can have important consequences for larval survival. On the other hand, recent laboratory experiments have also shown that sardine larvae depend of large food concentrations to be able to survive (Caldeira et al., 2014) and only from ≈20 days-post-hatching are able to swim effectively and maximize foraging efficiency (Silva et al., 2014). Therefore low larval survival linked with sub-optimal temperature and low food availability may result in low recruitment strength.

Previous works have studied the relationships between environmental factors and sardine abundance/recruitment/catches in the Atlanto-Iberian ecosystem (e.g. Borges et al., 2003; Solari et al., 2010; Santos et al., 2012; Leitão et al., 2014; Gamito et al., 2015; Teixeira et al., 2016). Most of these studies focus on the effect of environmental

factors causing the transport of eggs and larvae offshore (e.g. upwelling index) on the survival of early life stages of sardine, while other direct effects, such as the effect of food availability and water temperature on larval growth and condition received less attention (Solari et al., 2010). The great majority of these studies used data of landings to compare with environmental data and analyse pooled data of the entire Atlanto-Iberian region, finding significant relationships of total sardine landings with several environmental factors, mainly SST followed by wind strength and NAO. Few studies have addressed the regional variability of environmental factors. Leitão et al. (2014) analysed the relationship between landings and environmental variables separately according to different sub-stocks, corresponding to ICES sub-divisions, identifying different environmental drivers of sardine landings according to the regions, and showing that the study of the effect of environmental drivers on sardine populations should be area-specific. In fact, *Sardina pilchardus* like other small pelagic fish species, has a large distribution, inhabiting permanent and seasonal upwelling regions, gulfs, bays and coastal waters surrounding islands. The predominant environmental factors of larval survival (e.g. prey availability and water temperature) differ significantly throughout the vast latitudinal range of the distribution of the species. Therefore, relationships between the inter-annual variability of environmental drivers and recruitment strength is likely to be area-specific. Within each area, sardines have recruitment hotspots which are defined as the main spawning grounds where environmental conditions are important for the survival of larvae, and thus contributing to the success of recruitment (Checkley et al., 2009; ICES, 2015). The aim of this study is to evaluate if temperature and food availability at the time of sardine larvae development can be used as proxies to estimate the subsequent recruitment strength at the main recruitment hotspots off Atlanto-Iberian waters (Northwestern Iberian coast, Gulf of Cadiz, and Bay of Biscay, Silva et al., 2009). Ultimately, the goal is to predict sardine recruitment with sufficient advance to help in the management of the Atlanto-Iberian stocks, using satellite-derived SST and Chla.

## 2. Materials and methods

### 2.1. Study area

The relation between environmental data and sardine recruitment was investigated for the areas that are considered to be recruitment “hotspots” for sardine in the Iberian-Biscay region, particularly the northwestern Iberia, the Gulf of Cadiz and the Bay of Biscay (Checkley et al., 2009; ICES, 2015, Fig. 1). The western Iberia area is influenced by freshwater outflow (e.g. Douro and Minho rivers) and has a summer seasonal upwelling regime while the Bay of Biscay and Gulf of Cadiz are sheltered areas which also have an important input of freshwater from rivers (e.g., Adour and Gironde, and Guadalquivir respectively) and are not propitious for upwelling (Aristegui et al., 2009).

### 2.2. Recruitment index and abundance of sardine

Sardine recruitment data were derived from spring acoustic cruises carried out annually by IPMA (Portuguese Institute for the Ocean and the Atmosphere) off the Western Portuguese coast from 1986 to 2014 with gaps in 1987, between 1989 and 1994, 1996, 2004 and 2012 (ICES, 2015). As of 1996 the area covered was extended southward to the Gulf of Cadiz and from 2000 in the Bay of Biscay (by IFREMER, L'Institut Français de Recherche pour l'Exploitation de la Mer, cruises). The acoustic surveys are carried out along predefined parallel transects, perpendicular to bathymetry from 20 to 200 m depth with 8 nautical miles (nm) inter-transect distance. Surveying was limited to daylight and echo-integration was performed from 20 cm above the seabed (prior, echogram bottom was manually corrected) to 3 m below the transducer, along 1 nm elementary distance sampling units (ESDU). Fish samples were collected with pelagic and bottom trawls. Trawl

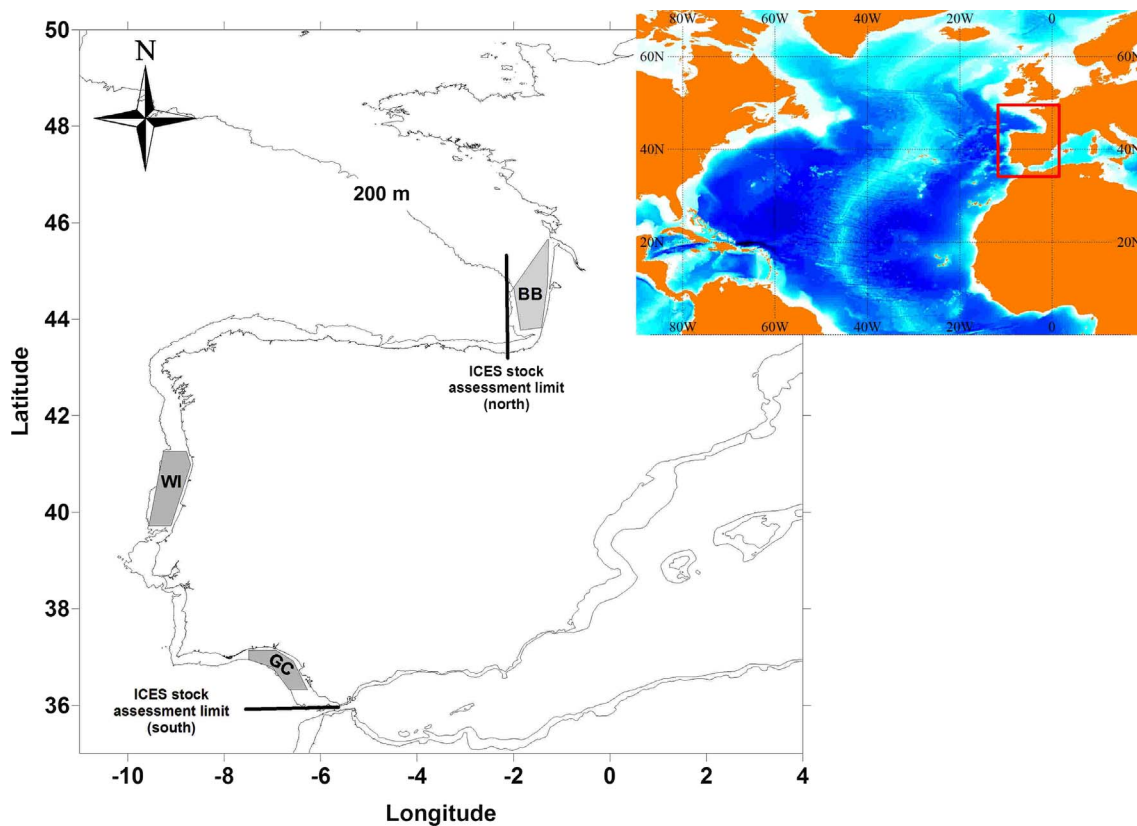


Fig. 1. Location of the recruitment “hotspots” of Iberian sardine *Sardina pilchardus* corresponding to the areas where satellite-derived SST and Chla data were extracted. WI-Western Iberia, GC- Gulf of Cadiz and BB- Bay of Biscay. The limits (horizontal and vertical lines) of the Atlanto-Iberian sardine stock (ICES recruitment data) and the 200 m bathymetry are also presented.

samples were used to assist in species identification to split the acoustic energy within species and by length. For each trawl, a sample of approximately 100 kg of fish was taken and sorted by species. For sardine, a sub-sample of 100 individuals was taken and their total length (TL) and weight (W) were measured. In this study, juveniles were considered to be individuals with  $TL \leq 16.0$  cm (Silva et al., 2009). Sardine age-at-length show that individuals with  $TL \leq 16.0$  cm broadly represent the recruiting year-class in spring surveys (age-1 individuals). Therefore, for the present purposes, recruits were considered specimens with total length smaller than length of first maturity ( $\sim 16$  cm, Silva et al., 2006). The index of recruitment corresponds to the estimate of abundance of recruits and was estimated for northwestern Iberia, the Gulf of Cadiz and the Bay of Biscay (Fig. 1). Spawning stock indices were estimated as the abundance of sardines  $> 16$  cm obtained at the acoustic research cruise held in each region, respectively, in the previous year.

Annual recruitment and spawning stock biomass estimates for the Atlanto-Iberian sardine stock (herewith called ICES Data) were also available since 1978 from the ICES Working Group on the Assessment of Sardine. These estimates are outputs of a statistical age-structured fisheries stock assessment model, Stock Synthesis (Methot and Wetzel, 2013; ICES, 2015) applied to sardine fisheries and population data in the Iberian Peninsula. Input data for the model are biomass and age composition of catches and indices of population abundance and age composition from two scientific surveys, the annual spring acoustic cruises and a triennial cruise that evaluates spawning biomass. The model integrates sub-models for the main demographic processes: birth, natural and fishing death, growth and maturation. Parameters (e.g. fishery and survey catchabilities) and output quantities (recruitment, fishing mortality and stock abundance) are estimated minimizing a log likelihood function which combines components for the various sets of data. For a detailed description of the assessment methodology, see ICES (2015).

### 2.3. Satellite derived sea surface temperature and Chlorophyll *a*

In this work we test the hypothesis that recruitment is influenced by temperature and food availability experienced by the larvae during early development. For this reason, only the conditions occurring during the spawning of the previous year were taken into account. We have assumed that satellite-derived SST is a good proxy of the temperature experienced by sardine larvae during early ontogeny, when they occur mostly in the surface layers of the water column (Santos et al., 2006). We have also assumed that satellite-derived Chla is a good proxy for the food availability for sardine larvae given that they depend mostly of phytoplankton and small herbivorous or omnivorous copepods (Garrido and van der Lingen, 2014 and references herein) whose biomass is generally correlated to Chla concentration (Uitz et al., 2006). For adult sardines, depending of phyto- and zooplankton species, feeding intensity was also shown to be correlated to satellite-derived Chla in the studied area (Garrido et al., 2008a). Satellite-derived data used were monthly averages of Sea Surface Temperature (SST), from daily PATHFINDER V5.2 products (Casey et al., 2010), and monthly averages of Chlorophyll-*a* concentration (Chla) from GlobColour products (all details on input data and algorithms used are described in the GlobColour Product User Guide 2014) for each of the sardine recruitment hotspots (Fig. 1). The polygons defining the recruitment areas were based on the information described in Checkley et al. (2009) and ICES (2015), comprising in those areas the continental shelf (from the coast to the 200 m isobath).

In this study, AVHRR Pathfinder Version 5.2 (PFV5.2) data were used, obtained from the US National Oceanographic Data Center and GHRSSST (<http://pathfinder.nodc.noaa.gov>). PATHFINDER V5.2 product (Casey et al., 2010) is a skin temperature estimate of the ocean temperature (first mm of the surface layer). The nightly data was collected to avoid most of the sub-daily variations of temperature in this

thin layer very sensitive to the sun irradiance. Those products, impacted by cloud coverage, are global and available from 1981 to 2012 with a spatial resolution of  $\sim 4$  km.

For Chlorophyll-*a*, the daily products of GlobColour 2nd processing (2014) were used, generated from GSM algorithm (Maritorena and Siegel, 2005) in the frame of OSS2015 project (EU-FP7), using ESA ENVISAT MERIS RR and NASA SeaWiFS, MODIS and VIIRS data. Products and statistics are processed by ACRI-ST and distributed through the Hermes portal (hermes.acri.fr). Those products have the advantage of offering better coverage than single sensor products.

Sardines mainly spawn from October to March in western and southern Iberia, where two peaks generally occur, a primary one in November/December and a secondary in March/April, whereas in the Bay of Biscay the spawning seasonality is similar although the main peak occurs in spring months and a secondary one occurs during the autumn (Stratoudakis et al., 2007 and references herein). Recruitment data was related to satellite-derived SST and Chla, averages computed for the three recruitment hotspots during two periods of the previous year; 1) one from January to March (referred as SST1 and Chla1) for the Western Iberia and Gulf of Cadiz, whereas in the Bay of Biscay SST1 and Chla1 correspond to the period from January to April, to account for the spawning season extending further into the spring; 2) a second period was considered from October to December (referred as SST2 and Chla2). As an example, the periods of January to March/April 2009 and October to December 2009 were related to the recruitment strength estimated in the acoustic survey carried out during the spring of 2010. These periods correspond to sardine spawning season months that would generate fish with lengths ranging from 10 to 16 cm (Silva et al., 2006). Due to cloud coverage during winter, a large portion of the years failed to have SST and Chla data during the month of December for the western Iberian coast. To overcome this deficiency, we have decided to use mean data from October and November to characterise this spawning period for this area, since these months had the highest inter annual variability and highest potential to explain differences in the recruitment.

SST data, available since 1981 and Chla data, available since 1998 were investigated in the three recruitment hotspots identified off the Iberia. In the case of the ICES data, which estimates the recruitment for the whole Atlanto-Iberian sardine stock, as explained before, recruitment was related to the conditions of the main spawning area of the Atlanto-Iberian sardine stock, which is the western (upwelling) coast. Therefore, satellite data from the western Iberia was used to study the relationship with ICES data.

#### 2.4. Data analysis

Linear Discriminant Analysis (LDA), a data classification and dimensionality reduction technique, was applied to investigate the ability of satellite-derived SST and Chla, and the abundance of spawners in discriminating between high and low recruitment years. The cut-off level to separate high and low recruitments was determined by the mean, where years when recruitment was above the mean were classified as “high” and those lower than the mean classified as “low” for each of the recruitment hotspots. In a first approach, five explanatory variables were used to try to predict recruitment: spawning stock abundance, SST1, Chla1, SST2, Chla2. Given that years with missing data in any of the explanatory variables were excluded from the analysis, this significantly reduced the number of years available to test this relationship. To increase the number of years with available data, two additional types of LDA per area were done; one only using satellite-derived SST and Chla data and a third one only using SST (SST database is significantly larger than that of Chla).

Non-normal predictor variables (abundance of adults and Chla data) were log-transformed. T-tests were used to compare the differences between individual explanatory variables between the recruitment groups.

Main LDA assumptions were tested using the Shapiro-Wilk normality test and the Box's M test of homogeneity of covariance matrices based on the chi-square approximation. A backward stepwise selection procedure was adopted in the LDA to select, by cross-validation, the variables that mostly contribute to the separation of recruitment between groups, using the stepclass function of R package “Klar”. Variables that contribute most to the prediction of group membership were considered those with the largest absolute values of the standardised regression coefficients (Worth and Cronin, 2003). The overall significance of the discriminant function analysis was evaluated by using Wilk's Lambda test, which is used in multivariate analysis of variance evaluating the significance of differences between the means of identified groups based on a combination of dependent variables.

Cross-validation by jackknife technique (Rencher, 2002) was used to evaluate the accuracy of the classifications for the different groups of recruitment. With this method, one observation at a time is eliminated from the sample, then the remaining observations are used to construct a discriminant function which is used to classify the eliminated observation. Classification rates are obtained by cumulative rates of classifying all the available observations and the overall accuracy was evaluated by quantifying the ratio of correctly classified years with high or low recruitments to the total number of years. Statistical analyses were performed using the open source software R version 2.9.2 of R Development Core Team.

### 3. Results

ICES recruitment estimates of the Atlanto-Iberian sardine stock varied between 5.2 and 48.4 billion fish in the time range from 1978 to 2012 and showed a decreasing trend in recent years (Fig. 2, panel A). A similar trend is also observed for the spawning stock biomass estimates (Fig. 2, panel A). In both cases the lowest values were registered in recent years.

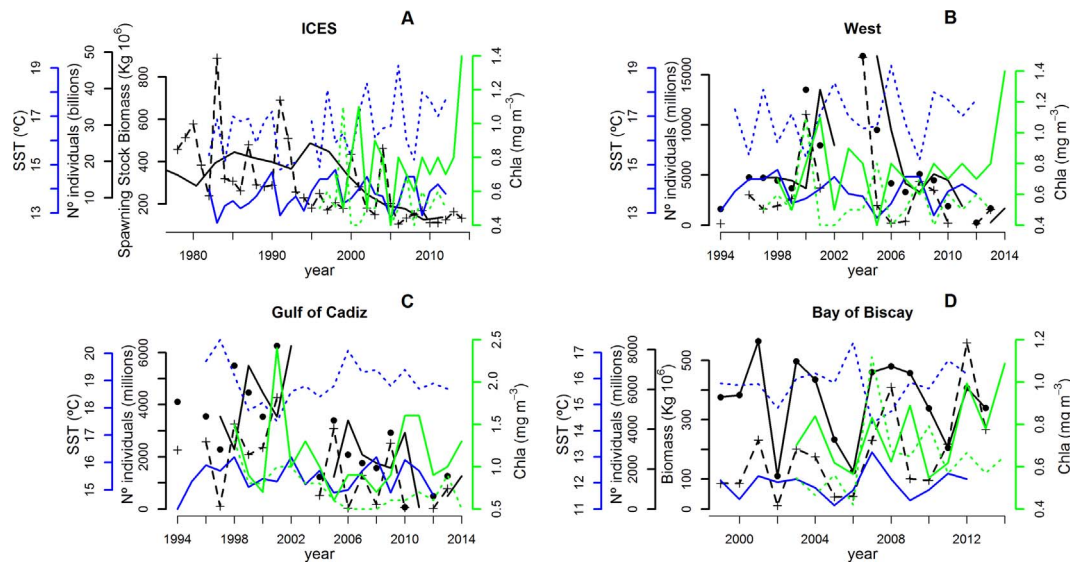
Acoustic survey data indicate that the proportion of recruits in relation to the entire stock has increased in the last decade. In recent years both in Western Iberia and in the Gulf of Cadiz this proportion represents more than 80% (Fig. 2, panels B and C). In the surveys, recruits were mostly concentrated at the western Iberian coast, followed by the Bay of Biscay and the Gulf of Cadiz ( $3326 \pm 976$ ,  $2740 \pm 222$ ,  $1587 \pm 302$ ; mean  $n^\circ$  recruits  $\times 10^6 \pm$  SE, respectively) (Fig. 2, panel D).

During the spawning season the environmental variables, SST and Chla, differ both within and between these regions. As expected, SST varied meridionally, being higher at the Gulf of Cadiz ( $13.7 \pm 0.09$  and  $18.8 \pm 0.10$  °C; mean SST  $\pm$  SE during the first and last quarters of the year, respectively), intermediate in the Western Iberia ( $13.8 \pm 0.10$  and  $17.0 \pm 0.20$  °C) and significantly lower in the Bay of Biscay, particularly during the first quarter of the year ( $11.7 \pm 0.10$  and  $15.7 \pm 0.10$  °C). Chla concentration was higher in the Gulf of Cadiz in the first and last quarters of the year ( $1.12 \pm 0.09$  and  $0.73 \pm 0.04$  mg m<sup>-3</sup>) followed by the Bay of Biscay ( $0.78 \pm 0.04$  and  $0.63 \pm 0.04$  mg m<sup>-3</sup>) and the Western Iberian coast ( $0.76 \pm 0.05$  and  $0.58 \pm 0.04$  mg m<sup>-3</sup>).

Following the criteria mentioned before the thresholds to separate high and low recruitments were set at 1.93, 2, and 2 billion fish (recruits) for the western Iberia, southern Iberia (Gulf of Cadiz) and Bay of Biscay, respectively, and 7.92 billion recruits for ICES data.

High and low recruitment groups were characterized by significant differences of different predictor variables for the different recruitment areas (Fig. 3). The spawning stock size was similar for years classified as high and low recruitment in the case of the Western Iberia and the Gulf of Cadiz (Table 1). Contrarily, years classified as having high recruitment had a significantly higher number of spawners than years of low recruitment in the case of the Bay of Biscay and for the ICES data (Table 1).

During the spawning season, the mean SST between January and



**Fig. 2.** Time series of the number or biomass of age 1 sardines (black dashed line) vs the number of age 2+ (adults) sardines or the Spawning stock biomass (SSB) (black solid line), mean satellite-derived SST and Chla during the previous spawning season (solid lines during the first quarter and dashed lines during the last quarter of the previous year) for A) ICES B) Western Iberia, C) Gulf of Cadiz, D) Bay of Biscay datasets.

March of the previous year was generally lower than 12 °C in the Bay of Biscay, while in the other areas was generally higher than 13 °C. Mean SST did not differ significantly between high and low recruitment for the Western Iberia, Gulf of Cadiz and ICES data but in the Bay of Biscay was significantly higher in recruitment years (Table 1). The mean SST between October and December of the previous year was significantly lower in high recruitment years for the Gulf of Cadiz and ICES data, while in the Western Iberia and the Bay of Biscay no differences were detected (Table 1). Mean Chla concentration for the two spawning periods of the previous year was similar for high and low recruitment years for all the areas tested (Fig. 3).

The LDA was able to separate years of high and low recruitment based on the abundance of spawners and mean satellite-derived SST and Chla determined for the first and last quarters of the previous year in the three recruitment hotspots tested and also for the ICES recruitment index (Table 2).

The cross-validation test indicated that the LDA correctly classified  $\geq 79\%$  of the observations. For all areas, the most important variable for the discrimination of high and low recruitment years, as shown by the standardized coefficients, was Chla, followed by SST (Table 2). The abundance of spawners was the least important variable for the discrimination between groups.

By initially excluding the abundance of spawners as explanatory variable, and in that way using a larger dataset, Chla was identified as the main variable to significantly separate the groups for all. In the case of the Western Iberia region the correct classification of recruitment based on SST and Chla increased to 100% of correct classification by cross-validation, contrary to the Gulf of Cadiz, where the discriminatory power decreased significantly from 80% to 67% (Table 2). In the case of the Bay of Biscay and the ICES data, discarding the spawning stock biomass as an initial variable did not decrease the discriminatory power of the function, which correctly classified 80% and 79% of the years as high or low recruitment, respectively (Table 2).

When just considering SST to discriminate between the groups the sample size available increased, but the success to discriminate years of good and bad recruitment was not significant for the Western Iberia and Gulf of Cadiz. For the Bay of Biscay and ICES data the discriminant function was still able to significantly separate years of high and low recruitment with a correct classification of 78 and 73%, respectively (Table 2).

#### 4. Discussion

This study shows that SST and Chla during periods of sardine larvae development can be used to predict years of high and low recruitment for the main recruitment hotspots of the species in Atlanto-Iberian waters, with a correctness of  $\geq 79\%$ . The underlying hypothesis of this study focused on environmental forcing acting upon the egg and larval stages, as it is generally recognized that early life stages are particularly vulnerable to environmental variability and that factors affecting the early life history stages are the major contributors of recruitment variability. The most important factors affecting recruitment strength were area-specific, due to differences of the prevailing environmental conditions. Chla was the most important variable separating the groups of high and low recruitment for all recruitment areas and for the ICES data. This agrees with recent laboratory experiments showing that European sardine larvae depend on high food concentrations to survive, particularly during the first weeks of life, when swimming and foraging abilities are very limited (Caldeira et al., 2014; Silva et al., 2014; Garrido et al., 2016).

The diet composition of sardine larvae has been described as mainly composed of copepod eggs and nauplii as well as copepodites of smaller-sized species, although some phytoplankton is occasionally present (revision in Garrido and van der Lingen, 2014). This could have resulted in Chla being a poor proxy of food availability for the larvae. However, significant relationships to recruitment were found for several areas investigated in this work and, when found, were consistently positive. For the mainly zooplanktivorous adult sardines in western and southern Iberia, Chla was found to be a good proxy of feeding intensity (Garrido et al., 2008a), revealing that for these areas, Chla seems to be a good indicator of zooplankton prey availability. Given the variability of the feeding apparatus and diet composition of sardine populations living in contrasting environments such as the Atlantic and Mediterranean Sea (Costalago et al., 2015), the use of Chla as a proxy of food availability in other areas characterized by different trophic webs should be done with caution.

In areas where temperature tends to be below or above the optimal range for larval development, temperature could be one of the main limiting factors for the success of recruitment. The Bay of Biscay was the only area where SST fell below the optimal temperature range for the species, particularly during the winter months. For this area, SST was identified as one of the main factors discriminating between years

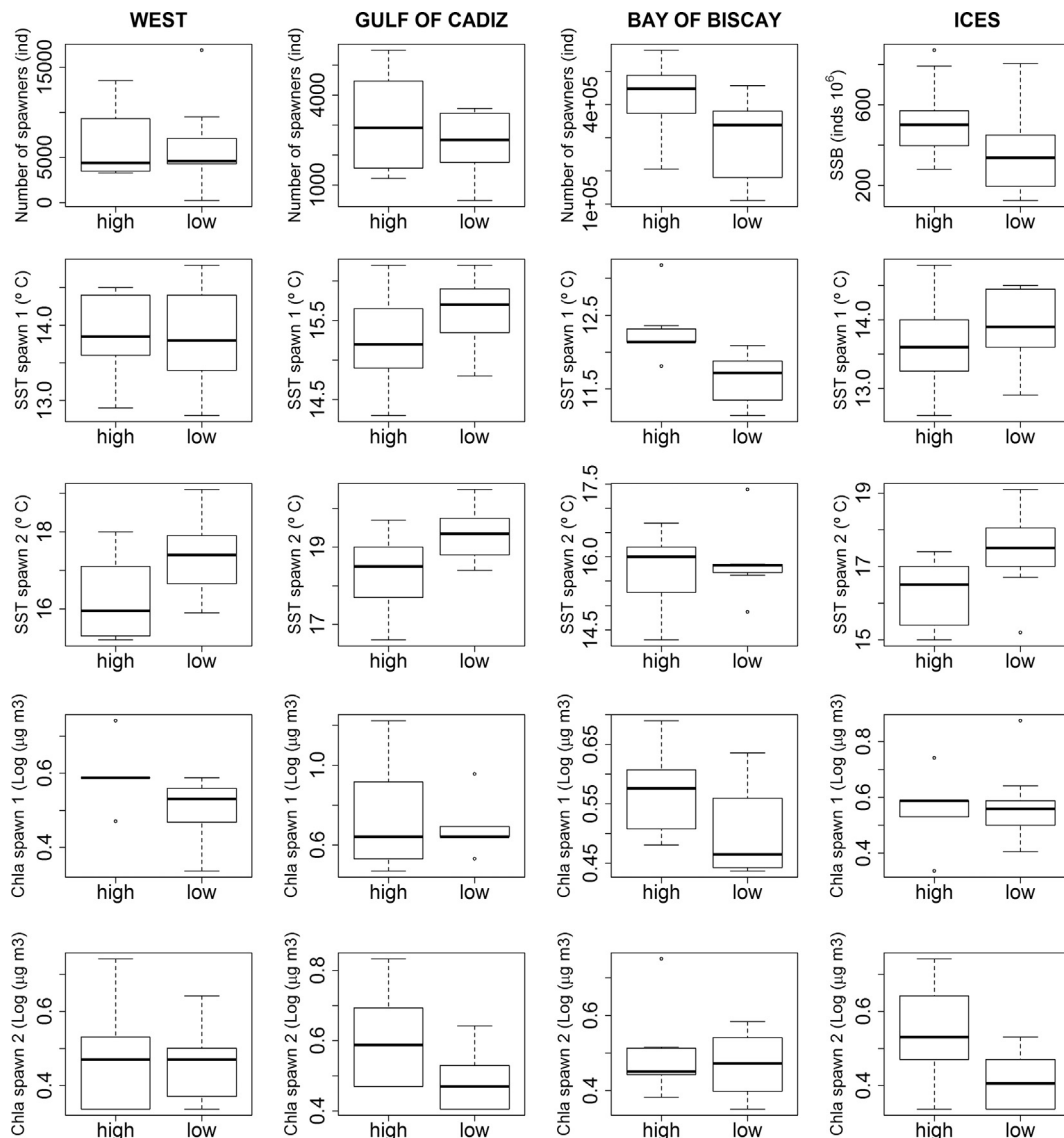


Fig. 3. Boxplots of the abundance of sardines (number of fish of age 2+ for Western Iberia, Gulf of Cadiz and Bay of Biscay, and spawning stock biomass for ICES data), SST and Chla during the first (SST1 and Chla1) and last (SST2 and Chla2) quarter of the year before for years classified as having high and low recruitment for A) Western Iberia, B) Gulf of Cadiz, C) Bay of Biscay and D) ICES data. All data available for each area were included.

of high and low recruitment, especially during the first quarter of the year, and this variable alone was able to discriminate recruitment groups with 78% accuracy. In contrast, in the Western Iberia and Gulf of Cadiz recruitment hotspots, the mean SST during spawning occurring during the first quarter of the year fell within the optimal range for most years where data is available. Despite the higher importance of Chla to discriminate between high and low recruitment years in the Gulf of Cadiz, mean SST during the last quarter of the year for this area was on several years higher than the optimal range, and associated with low recruitment years. Therefore, SST seems to be an important factor determining the strength of the recruitment in the coldest and warmest regions of the Biscay and Gulf of Cadiz waters, respectively.

With the increasing water temperature observed in recent years in the Northern Canary Upwelling Ecosystem (Western Iberian) ranging from 0.02 to 0.03 °C yr<sup>-1</sup> since 1985 (Relvas et al., 2009), recruitment off the Gulf of Cadiz might be expected to be negatively influenced by temperature, considering the reduced optimal temperature window for sardine larvae to develop. On the other hand, an increase of SST in the Bay of Biscay could be potentially beneficial in simplistic terms, but higher temperature could also favour the direct competitors of sardines which are abundant in that area, such as the European anchovy

(*Engraulis encrasicolus*), or even allow the northward distribution of more tropical species, such as chub mackerel (*Scomber colias*), which are competitors and predators of this species (Garrido et al., 2015). In future scenarios of ocean temperature rise predicted by climate change models (IPCC, 2014), not only the direct effect of temperature on larval growth and survival should be considered but also the interplay between food availability and temperature. Larval daily ration needs increase with increasing temperature because of the positive relationship between temperature and metabolism but also because larvae need to spend more energy swimming to be able to capture more prey (Houde et al., 1993). Laboratory experiments have shown that at good feeding conditions, sardine larvae growth increased with increasing temperature, within the optimal temperature range (13–17 °C), but this was achieved at the expense of a significant increase of foraging events (Garrido et al., 2016), suggesting that larvae would depend on high food densities to survive at higher temperatures. Food availability using Chla as a proxy was the most relevant variable for the success of sardine recruitment in the Western Iberia and Gulf of Cadiz, probably because of the high daily ration needed to support a faster growth associated with higher temperatures. The Bay of Biscay was the only area where high temperatures were associated to high recruitment years because,

**Table 1**

Results of the *t*-test comparing the abundance of spawners, Sea Surface Temperature (SST) and Chlorophyll *a* estimated during the previous spawning season (first –SST1 and Chla1 and last quarters – SST2 and Chla2) between high and low recruitment groups for the Western Iberia, Gulf of Cadiz, Bay of Biscay and ICES data. Significant differences at  $p \leq 0.005$  are represented by “\*”.

Area	Variable	N	t	p-value
Western Iberia	Log (abundance spawners)	12	–0.51	0.61
Gulf of Cadiz		12	–0.76	0.40
Bay of Biscay		15	–1.91	0.05*
ICES		36	–2.47	0.02*
Western Iberia	SST spawn 1	15	–0.18	0.85
Gulf of Cadiz		15	1.20	0.24
Bay of Biscay		14	–3.12	0.009*
ICES		31	1.47	0.15
Western Iberia	SST spawn 2	15	1.89	0.08
Gulf of Cadiz		15	2.32	0.03*
Bay of Biscay		14	0.39	0.70
ICES		31	4.74	< 0.001***
Western Iberia	Log (Chla spawn 1)	13	–1.68	0.12
Gulf of Cadiz		13	–0.41	0.69
Bay of Biscay		11	–1.21	0.27
ICES		17	0.06	0.95
Western Iberia	Log (Chla spawn 2)	13	–0.30	0.76
Gulf of Cadiz		13	–1.83	0.10
Bay of Biscay		11	–0.44	0.66
ICES		16	–1.85	0.12

as explained above, spawning takes place below the temperature optimum for this species. For the Gulf of Cadiz and the Western Iberia areas, high recruitment years were associated with mean Chla  $> 0.45 \text{ mg m}^{-3}$  and low recruitment years with concentrations below this value.

Besides testing the power of the discriminating functions in the main recruitment areas of Atlanto-Iberian waters, this study has also applied the same rationale with the ICES recruitment index. Although the ICES database is fishery-dependent and therefore has some limitations compared with the data from acoustic surveys (although it is also calibrated using acoustic data in recent years), it is a longer database than the others and therefore more robust to assess the difference between the groups and the predictive power. The high correlation between environmental conditions in northwestern Iberia and the southern stock recruitment (ICES data) support the conclusions of Silva et al. (2009) and Correia et al. (2014), suggesting that at least for some cohorts, this area is largely responsible for the overall recruitment and, possibly, that adult fish originating from this area migrate to southern areas of Iberia. On the other hand, spawning stock biomass was not correlated with or, at most, weakly related to recruitment strength in the recruitment hotspots. This result is in accordance with those of Santos et al. (2012), suggesting that stock size is not the main driver of sardine recruitment strength.

A significant relationship was found between the extent of the potential sardine habitat and larval food availability (defined by depth and satellite-derived SST and Chla) and sardine recruitment off Morocco (Machu et al., 2009). That study suggested that years of low recruitment occurred when the optimal spawning period in terms of temperature and salinity did not coincide with periods of high food availability. Salinity was not included as an explanatory variable in our simple hypothesis because our previous laboratory experiments have shown that temperature variability had a significantly larger effect on sardine larval survival than did salinity (Garrido, unpublished), which is in accordance with previous experiments showing a large tolerance of sardine larvae to variations of water salinity (Blaxter, 1969).

Our working hypothesis investigates a direct and simplistic mechanism in which temperature and food availability for sardine larvae during spawning can be used to explain the regional recruitment strength of Atlanto-Iberian sardine populations. However, these indicators might fail to explain the recruitment strength for sardine

populations living in different areas, such as in the Mediterranean Sea. Recent works found that the recent decrease in abundance of small pelagic fishes in that area was not related to a decrease in the recruitment strength but to slower growth and the disappearance of older individuals (Van Beveren et al., 2014). This suggests that, for the Mediterranean sardines, bottom-up processes affecting the juvenile and adult populations might be affecting the dynamics of the populations more than the recruitment variability.

Other indirect effects correlated to temperature may play a role in explaining sardine recruitment strength, most importantly those associated with dispersal, particularly in upwelling areas. In fact, temperature could be a proxy of other variables, namely of coastal upwelling strength, and therefore larval dispersal. Analysis of the relationship between sardine recruitment and several abiotic factors suggested that SST was arguably a better candidate for a causal role in determining recruitment success than sunspots, NAO, and wind strength (Solari et al., 2010 and references herein). Temperature and food availability can also affect the intensity of the reproduction and quality of the eggs produced (Garrido and van der Lingen, 2014). In fact, the spatial differences of the feeding ecology of adult sardines were shown to affect their lipid composition, and also the fatty acid reserves transferred to their progeny (Garrido et al., 2007, 2008b) but the role of maternal effects on recruitment variability is currently unknown. Predation is considered one of the main biotic factors explaining the inter-annual fluctuations of small pelagic fish abundance (Houde, 2008). However, the inter-annual variability of predator biomass is difficult to assess, varies with growth rate and ontogeny and no complete dataset is available. Recent studies have shown that sardine eggs are a main prey for chub mackerel (*Scomber colias*) juveniles (Garrido et al., 2015) and in fact sardines were shown to have an opposite recruitment trend to chub mackerel in southern waters (Martins et al., 2013). A negative relationship was found between sardine landings and SST (Teixeira et al., 2016) while a positive relationship was found between chub mackerel landings per unit effort and SST, which mean that, to some degree, mean SST might be an indirect proxy of other important factors.

A recent and comprehensive revision of stock management (Skern-Mauritzen et al., 2016) showed that, of the 1250 stocks analysed throughout the world, only 2% have incorporated environmental drivers into tactical management measures, 37.5% of which are dedicated to small pelagic fishes. Two of them relate to *Sardina pilchardus* stocks, one in the Mediterranean Sea and the other off Morocco, and use a Chla index as influencing the system carrying capacity and growth rate, and an unspecified environmental index, respectively. For Iberian waters, we tested the discriminatory power of our model for 3 different areas and one independent fishery-based estimate, and the high accuracy achieved suggests that the combined and significant role of SST and Chla for larval survival might be a good predictor of recruitment strength. Although the environmental variables developed in this study just predict a binary indicator (due to data availability constraints impeding e.g. to predict recruitment as a continuous variable or identifying more groups of recruitment strength), it can be useful to decrease the error of stock predictions and lead to more reliable catch advice. However, these are still small datasets (1–3 decades) and larger time-series are needed to confirm the reliability of the forecast that can be incorporated into sardine stock assessment and management. Due to satellite operability and observations in adequate scales, using satellite-derived SST and Chla to predict high or low recruitment conditions with several months in advance and with a high percentage of correctness ( $\approx 80\%$  of the cases) could provide valuable support to fisheries management.

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**Table 2**

Results of the Linear Discriminant Analysis (LDA) differentiating high and low number of sardine recruits based on adult's abundance (in millions of fish for the Western Iberian-West and Gulf of Cadiz-Cadiz, and in thousand tons for the Bay of Biscay and ICES spawning stock biomass), sea surface temperature (SST in °C) and Chlorophyll-a concentration (Chla in mg m<sup>-3</sup>) from the previous spawning season. (–) represents variables excluded from the model by backward variable selection. (x) represents variables not included in the initial model. Jack-knife (leave-one out) cross-validation classification success matrices are represented by group and total for each LDA (% Correct). (ˆ) refers to logarithmic transformation to achieve a normal distribution.

Area	Group	N	Group means					% Correct	Wilk's lambda
			Adults year before	SST 1	SST 2	CHLA 1	CHLA 2		
<b>A. Abundance of adult sardines and satellite-derived SST and Chla combined</b>									
WEST	HIGH	5	–	13.53	16.55	–	0.50 <sup>ˆ</sup>	100	Wilks = 0.27 9 F = 5.167 p = 0.004
	LOW	5	–	14.15	17.35	–	0.45 <sup>ˆ</sup>	100	
	Coefficients	–	6.89	5.36	–	28.91	TOTAL: 100		
CADIZ	HIGH	6	3097	15.30	18.61	0.73 <sup>ˆ</sup>	0.60 <sup>ˆ</sup>	83	Wilks = 0.03 F = 21.256 p = 0.005
	LOW	4	2541	15.75	19.55	0.69 <sup>ˆ</sup>	0.42 <sup>ˆ</sup>	75	
	Coefficients	0.001	3.74	2.16	8.05	–35.9	TOTAL:80		
BISCAY	HIGH	6	414	12.29	–	–	0.50 <sup>ˆ</sup>	86	Wilks = 0.17 F = 5.944 p = 0.038
	LOW	4	288	11.48	–	–	0.46 <sup>ˆ</sup>	100	
	Coefficients	–9.28 × 10 <sup>-6</sup>	–4.48	–	–	14.70	TOTAL: 90		
ICES	HIGH	5	364	–	16.28	–	0.54 <sup>ˆ</sup>	67	Wilks = 0.455 F = 3.983 p = 0.041
	LOW	9	320	–	17.23	–	0.40 <sup>ˆ</sup>	88	
	Coefficients	–0.004	–	1.04	–	–3.54	TOTAL:79		
<b>B. Satellite-derived SST and Chla only</b>									
WEST	HIGH	5	X	13.55	16.55	–	0.50 <sup>ˆ</sup>	100	Wilks = 0.138 F = 10.847 p = 0.004
	LOW	7	X	14.08	17.42	–	0.46 <sup>ˆ</sup>	100	
	Coefficients	X	3.33	3.09	–18.88	12.61	TOTAL:100		
CADIZ	HIGH	6	X	–	18.40	–	0.60 <sup>ˆ</sup>	75	Wilks = 0.521 F = 4.135 p = 0.05
	LOW	6	X	–	19.25	–	0.45 <sup>ˆ</sup>	63	
	Coefficients	X	–	–1.07	–	–5.57	TOTAL:67		
BISCAY	HIGH	6	X	12.30	15.68	0.77	0.77 <sup>ˆ</sup>	86	Wilks = 0.113 F = 9.774 p = 0.013
	LOW	4	X	11.48	16.17	0.65	0.65 <sup>ˆ</sup>	100	
	Coefficients	X	–5.47	2.231	–5.74	28.77	TOTAL:90		
ICES	HIGH	5	X	–	16.28	–	0.54 <sup>ˆ</sup>	75	Wilks = 0.527 F = 4.933 p = 0.02
	LOW	9	X	–	17.63	–	0.40 <sup>ˆ</sup>	80	
	Coefficients	X	–	1.12	–	–2.19	TOTAL:79		
<b>C. Satellite-derived SST only</b>									
WEST	HIGH	6	X	13.56	16.54	X	X	57	Wilks = 0.708 F = 2.262 p = 0.150
	LOW	8	X	14.08	17.42	X	X	71	
	Coefficients	X	0.86	1.05	X	X	TOTAL:64		
CADIZ	HIGH	8	X	15.25	18.50	X	X	60	Wilks = 0.879 F = 0.823 p = 0.462
	LOW	7	X	15.60	19.10	X	X	60	
	Coefficients	X	1.07	0.52	X	X	TOTAL:60		
BISCAY	HIGH	7	X	12.29	–	X	X	75	ANOVA F = 9.76 p = 0.008
	LOW	7	X	11.63	–	X	X	83	
	Coefficients	X	2.52	–	X	X	TOTAL:78		
ICES	HIGH	18	X	13.63	16.25	X	X	75	Wilks = 0.644 F = 7.455 p = 0.002
	LOW	11	X	13.93	17.44	X	X	70	
	Coefficients	X	0.75	1.06	X	X	TOTAL:73		

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