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ORIGINAL ARTICLE

Effect of environmental conditions on the seasonal and inter-annual variability of small pelagic fish abundance off North-West Africa: The case of both Senegalese sardinella

Modou Thiaw¹ | Pierre-Amaël Auger^{2,3} | Fambaye Ngom¹ | Timothée Brochier^{1,4,5} | Saliou Faye¹ | Ousmane Diankha⁶ | Patrice Brehmer^{1,4}

¹Centre de Recherches Océanographiques de Dakar-Thiaroye (CRODT), Institut Sénégalais de Recherches agricoles (ISRA), Dakar, Sénégal

²Laboratoire de l'Environnement Marin (UMR 195 Lemar), Technopôle Brest Iroise, Institut de Recherche pour le Développement (IRD), Plouzané, France

³Instituto Milenio de Oceanografía and Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile

⁴Laboratoire de l'Environnement Marin (UMR 195 Lemar), Institut de Recherche pour le Développement (IRD), Hann, Dakar, Sénégal

⁵Institut de Recherche pour le Développement (IRD), UMI 209 UMMISCO, Univ. Paris 06, Sorbonne Universités, Bondy, France

⁶Laboratoire de Physique de l'Atmosphère et de l'Océan Siméon Fongang (LPAO-SF/ESP), Université Cheikh Anta Diop de Dakar (UCAD), Dakar, Fann, Sénégal

Correspondence

Modou Thiaw

Email: modouth@hotmail.fr

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Abstract

The objective of this study was to assess the effect of environmental variations on the abundance of *Sardinella aurita* and *Sardinella maderensis* in Senegalese waters in the upwelling system. Monthly data indicating the abundance of sardinella were first estimated from commercial statistics, using Generalized Linear Model from 1966 to 2011. Abundance indices (AIs) were then compared with environmental indices, at the local scale, a Coastal Upwelling Index (CUI) and a coastal Sea Surface Temperature (SST) index, and on a large scale, the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO) and the Multivariate El Niño Southern Oscillation Index (MEI), using correlations and times series analyses. The results showed that the abundance of sardinella is determined by a strong seasonal pattern and inter-annual fluctuations. The abundance of *S. aurita* peaked in spring and in autumn, whereas that of *S. maderensis* peaked in the warm season (July–September). The trend of the sardinella abundance was significantly correlated with the CUI, especially in autumn and spring. Interannual fluctuations of *S. maderensis* and *S. aurita* abundance are, respectively, driven by the precocity and the duration of the upwelling season that is attributed to distinct migration patterns. Both sardinella species also respond with a delay of around 4 years to the winter NAO index and the autumn CUI, and the AMO index, respectively, both related to migration patterns. The wide variations in sardinella biomass are caused by variations in environmental conditions, which should be considered in the implementation of an ecosystem-based approach in sardinella stocks management.

KEYWORDS

Climatic change, oceanography, *Sardinella aurita*, *Sardinella maderensis*, small pelagic, small-scale fisheries

1 | INTRODUCTION

The North-West (NW) African coast, being one of the four major eastern boundary upwelling systems (EBUS), is characterized by an important biological productivity owing to its upwelled nutrients, which help to sustain large fish populations. Small pelagic fish constitute a resource of primary importance, which is heavily exploited in Senegal, Mauritania and Morocco. In Senegal, small pelagic fish mainly include, by order of importance in the average landings: sardinella (*Sardinella aurita* or round sardinella, and *Sardinella maderensis* or flat sardinella), mackerel (*Scomber scombrus*), anchovy (*Engraulis encrasicolus*), ethmalosa (*Ethmalosa fimbriata*), horse mackerel (*Trachurus* spp.) and sardines (*Sardina pilchardus*); they are all aggregative species occurring in a fish school (Brehmer et al., 2007). The sardinella accounts for more than 70% of the total landings that is mainly provided by the small-scale fishery (CRODT, 2009). On average, the yearly landings of sardinella, within e.g., the years 2002–2006, were estimated at 284,000 tons/year (FAO, 2007).

The size of the sardinella populations is highly variable within and over the years, in connection with the environmental control on growth and recruitment processes (for example, Cury et al., 2000). These variations might be accentuated by the constant increase in fishing pressure (Sharp & Csirke, 1983). The sardinella stocks have been considered to be overexploited since 2006 (FAO, 2006) by small-scale fisheries, foreign industrial fishing vessels which operate within the framework of the bilateral agreements and the illegal non-reported fisheries (Belhabib, Koutob, Sall, Lam, & Pauly, 2014).

Sardinella species possess a relatively short life span of approximately 7 years (Chesheva, 1998, 2006) and a high natural mortality rate (Camarena-Luhers, 1986; Fréon, 1988). The *S. aurita* reproduction is continuous with two annual reproductive peaks, the first one in May–June and the second between September and November (Fréon, 1988; Ndiaye, 2013). Because of the spatial variability and strong seasonality of the coastal upwelling, *S. aurita* spawning is not uniform along the coast but occurs preferentially over the Arguin Bank (Mauritania), the south of Cap-Vert (Senegal) (Boëly, Chabanne, & Fréon, 1978; Boëly, Chabanne, Fréon, & Stéquent, 1982; Conand, 1977) and, to a lesser extent, in between the two regions (Fréon, 1988). For *S. maderensis*, two spawning periods of *S. maderensis* were determined (Ba et al., 2016). The first spawning period was from April to October, with two spawning peaks, one in June–August and the other in October. The second spawning period occurred from early January to the end of February, with a single intense spawning peak. *Sardinella maderensis* almost spawned all year round, with spawning peaks at these periods.

Sardinella are widely spread along the NW African coasts. Boëly (1980) described the large migrations of *S. aurita* between the Moroccan and the south of Senegal waters whereas, on the other hand, *S. maderensis* is believed to perform lesser migrations around their nursery area, suggesting the existence of independent stocks at the Arguin Bank, and at the southern coast of Senegal (Boëly & Fréon, 1979; García, Tandstad, & Caramelo, 2012). These trophic and

ontogenetic migrations are related to seasonal environmental variations, which have a stronger amplitude in the southern part of the eastern edge upwelling system of the Canary Current (Boëly & Fréon, 1979). The transboundary migrations complicate the fisheries management policies, as the *S. maderensis* and *S. aurita* landings reports are usually mixed, and the migration routes as well as the existence of sub-populations for each species remain poorly understood.

According to Boëly et al. (1982), the adults of *S. aurita*, migrate from Senegal to the South of Morocco from April to September. Starting at the end of September, *S. aurita* return to Senegal, thereby passing again through Mauritanian waters. Boëly et al. (1982) further indicate areas of recruitment in Mauritania and Senegal, which are affected by the migration cycle after the respective stocks have spent their first year in the local nursery where the first spawning occurred. The seasonal primary production is likely to be the driver of such long-range migration (Boëly et al., 1982; Cury & Roy, 1988).

The recent work by Bacha, Jeyid et al. (2016), Bacha, Jehid, Vantrepotte, Dessailly, and Amara (2016) clearly indicated that the Mediterranean Sea and Atlantic Ocean *S. aurita* populations are distinct. Unlike the genetic study conducted off NW Africa (Chikhi, Agnès, & Bonhomme, 1997), the otolith shape of *S. aurita* suggests the existence of isolated groups of fish. The separation of these groups seems to be linked to oceanographic barriers and local retention areas. There is no evidence of such barriers between Senegal and Mauritanian waters. Thus, the variability of *S. aurita* abundance in Senegal in relation to local environmental fluctuations must be linked not only to population dynamics but also to migration processes.

In NW Africa, the influence of the environment on fisheries resources has been increasingly studied in recent decades (Cury & Roy, 1989; Demarcq & Faure, 2000; Faure, Inejih, Demarcq, & Cury, 2000; Caballero-Alfonso et al., 2010; Braham, Fréon, Laurec, Demarcq, & Bez, 2014; Mbaye et al., 2015;). The changes in hydro-climatic conditions are likely to be the major cause of the strong variability of coastal pelagic resources, particularly for sardinella. Off NW Africa, the coastal upwelling intensity during the upwelling season in winter and spring is an important driver of primary production (Auger, Gorgues, Machu, Aumont, & Brehmer, 2016; Lathuilière, Echevin, & Lévy, 2008), which may affect the survival of early life stages of *Sardinella* spp. (for example, Bartolino, Colloca, Sartor, & Ardizzone, 2008; Faure et al., 2000; González Herraiz, Torres, Farina, Freire, & Cancelo, 2009; Gröger, Winkler, & Rountree, 2007). The mechanisms that determine the spatial and temporal dynamics of sardinella must be elucidated for the sustainable management of these resources. An analysis of the relationship between climate variations and living resources should contribute to improve our knowledge of sardinella population and its spatial dynamics, allowing for the establishment of a rational management plan for these fisheries.

This study aims at analyzing the relationship between the environment and sardinella abundances in Senegalese waters. The objectives of the study were (i) to test the empirical predictive models of

fish abundance and (ii) to analyze the abundance–environment relationships at various time scales. Monthly abundance index (AI) of sardinella was estimated from commercial statistics over the period 1966–2011 using Generalized Linear Models (GLM) techniques. Hereafter we use the term «abundance» to refer to this abundance index. Thereafter, the seasonal variability was isolated and the inter-annual variability of the trend of abundance was correlated against five environmental indices: (i) the Coastal Upwelling Intensity (CUI) i.e., the Ekman transport from a re-analysis of alongshore wind stress, (ii) the satellite-derived Sea Surface Temperature (SST) in the coastal fringe, and large-scale climate indices: (iii) the North Atlantic Oscillation (NAO), (iv) the Atlantic Multidecadal Oscillation (AMO, Schlesinger and Ramankutty, 1994) and (v) the Multivariate El Niño Southern Oscillation Index (MEI) to account for Atlantic-Pacific teleconnections.

2 | MATERIALS AND METHODS

2.1 | Data sets

2.1.1 | Fisheries data

The Centre of Oceanographic Research of Dakar-Thiaroye (CRODT) of the Senegalese Institute of Agricultural Research (ISRA) provided data on the rate of harvest of *S. aurita* and *S. maderensis* by the small-scale fishery in Senegal. The small-scale fleets, which currently capture the bulk of the Senegalese landings, operated from fishing villages distributed along the coast (Figure 1).

Several time series provided by CRODT were used in this study. These data included: (i) annual catches of sardinella by species and per fishery from 1966 to 2011 (see Figure 2); (ii) higher time resolution data of sardinella catches of the small-scale fishery by landing port

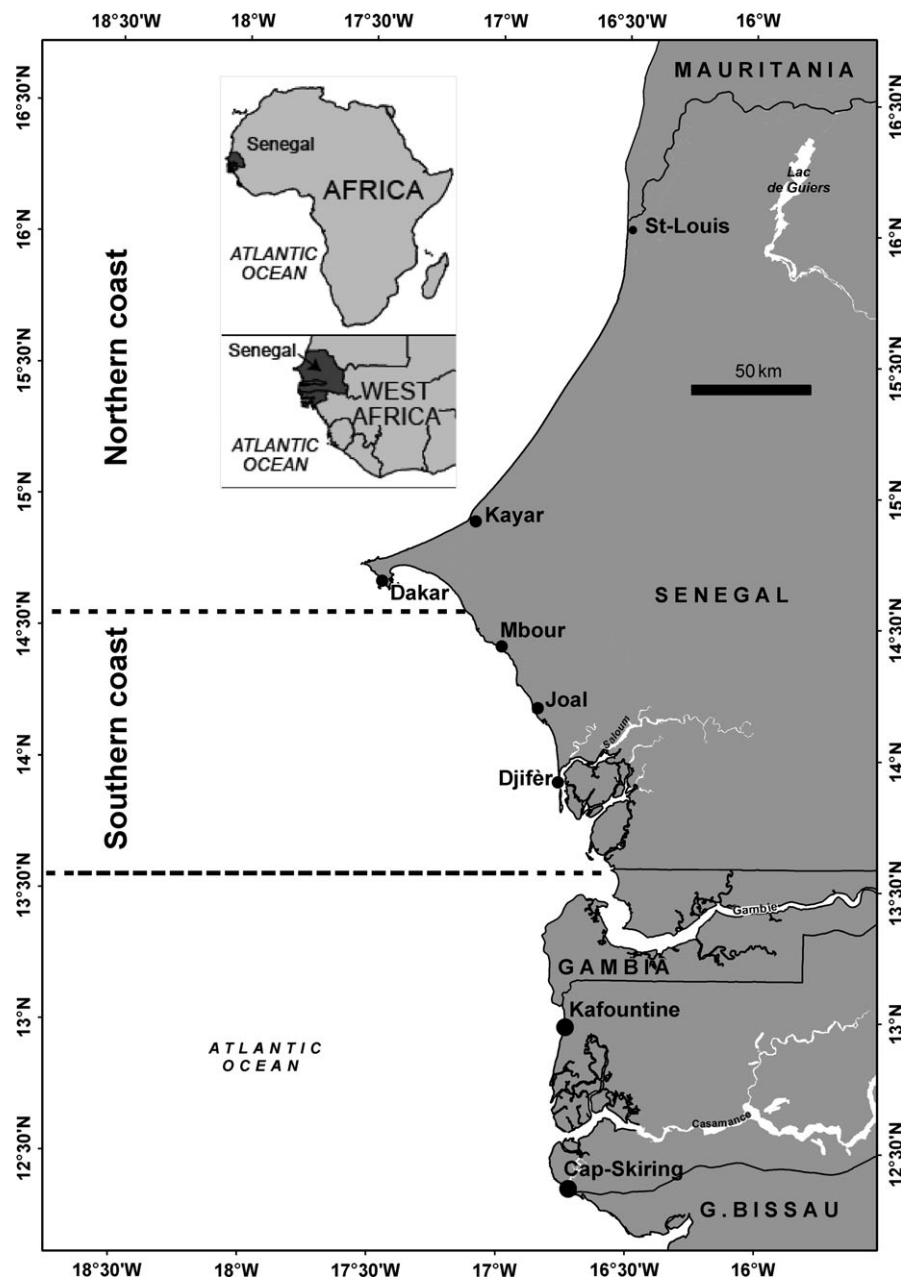


FIGURE 1 Map of the study area, the Senegalese coast showing the sardinella fishing areas from the coast to the limit of the continental shelf (isobath 200 m). The fishing villages are grouped by sub-region: the Northern coast (Saint-Louis, Kayar) including the Dakar region (Yoff, Soumbédioune, Hann) and the South of the country (Mbour, Joal) until The Gambian border

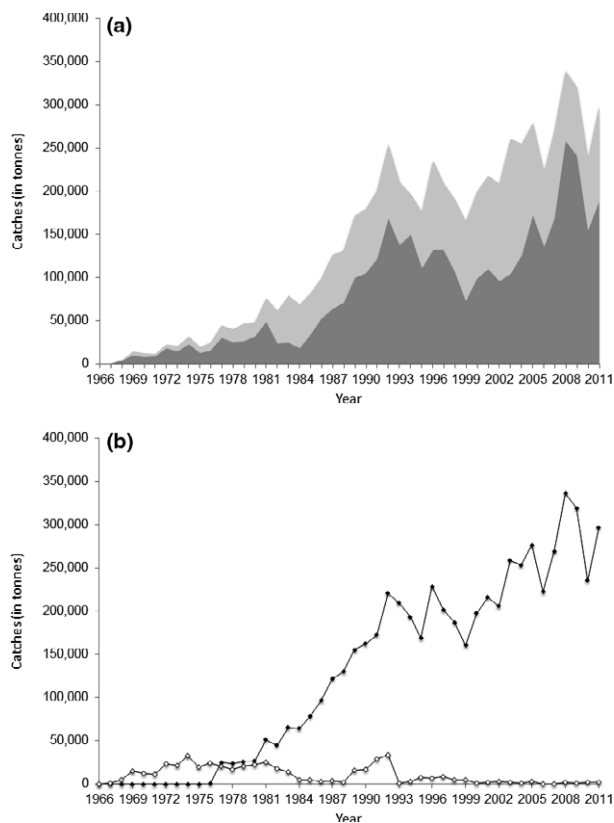


FIGURE 2 Total catches time series (tonnes) of round (*Sardinella aurita*, in dark) and flat (*Sardinella maderensis*, in grey) sardinella (a); Total catches of sardinella (*S. aurita* and *S. maderensis*) by both small-scale fishery and industrial fisheries from 1966 to 2011 in Senegal (b) (source CRODT)

from Saint-Louis to Joal and per species from 1974 to 2011 (see Figure 3a, b); and (iii) fishing effort (number of trips) per type of fishing gear (purse seine and encircling gill net) targeting sardinella from 1981 to 2010 (see Figure 3c). It is noteworthy that data on sardinella catches by the small-scale fishery were available from 1975 to 2011, nevertheless all the necessary information to estimate abundance indices (AIs) were only available over the period 2004–2011.

The Catch Per Unit of fishing Effort (CPUEs) of the Senegalese industrial fisheries expressed in kilogram per fishing day were used to derive AIs of sardinella in Senegalese waters over the period 1966–2011. Sardinella landings, fishing days, number of trips and Balance Horse Power (BHP) of the Senegalese industrial fleet, have routinely been obtained by month and by boat, from January 1966 to December 2011. This database covers the Senegalese industrial trawlers, which operate from January to December using pelagic trawl. The data obtained include specifications of the trawlers (horsepower of the engines, length of the boat and gross tonnage) and details on fishing operations (fishing date, number of fishing days and fishing area).

Another data set was used for the size spectrum analysis; the sardinella catches landed by small-scale fisheries were sampled monthly from March 2012 to February 2013 from the three main landing sites: Kayar, Mbour and Joal (Figure 1). Purse seine and gill nets were the

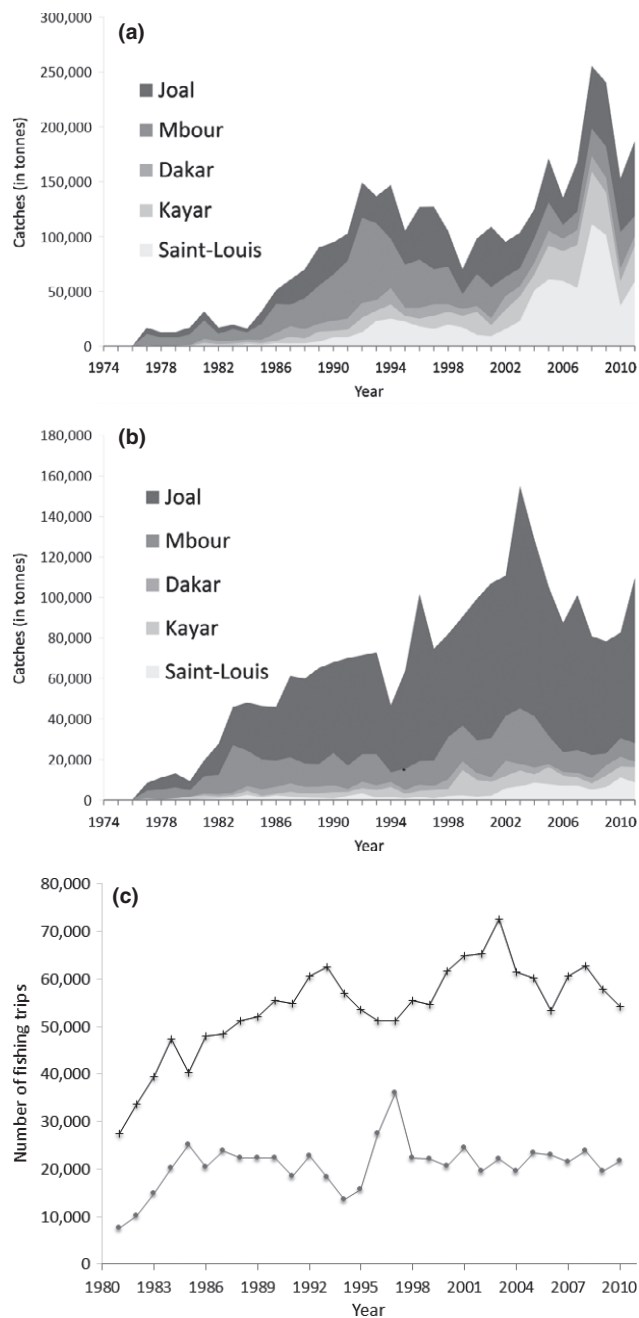


FIGURE 3 Yearly catches (tonnes) of sardinella by the small-scale fishery split by main landing sites (cf. Figure 1) in Senegal from 1975 to 2011: (a) *Sardinella aurita* and (b) *Sardinella maderensis*: Evolution of the number of fishermen trips using the purse seines (curve with cross) and the encircling gillnets (curve with point) between 1981 and 2010 in Senegal over the main landing sites (c)

main fishing gear used. The present study was based on 6,216 samples for *S. aurita* and 7,377 samples for *S. maderensis*, collected along the Northern and southern Senegalese coast in 2012–2013. Only specimens caught using purse seine nets were sampled to have the same fishing gear selectivity for monthly comparisons of the length distribution. The fork length (FL) of the fish sampled was measured to the nearest 1 mm, and the body weight was determined to the nearest 0.01 g.

2.1.2 | Environmental data

To analyze the effect of the environmental conditions on the seasonal and inter-annual variability of sardinella abundances, we used local environmental indices (CUI and coastal SST) and large-scale climate indices representative of sea level pressure patterns (NAO) and the large-scale state of SST in the North Atlantic (AMO), and of the atmospheric teleconnections between the Pacific and the Atlantic (MEI).

Coastal Upwelling Index (CUI)

We used outputs of wind stress from an atmospheric re-analysis from the National Center for Environmental Prediction and the National Center for Atmospheric Research (NCEP/NCAR, 2.5° resolution) over the period 1948–present to derive a monthly time series of CUI for the Senegalese coast. This low-resolution product is the only available product which covers the study period 1966–2011. As a first approximation, we considered the upwelling index owing to Ekman transport, omitting Ekman pumping due to wind-stress curl. Ekman transport is proportional to the wind stress, and inversely proportional to the sine of the latitude (Sverdrup et al., 1942). The volume of Ekman transport per meter of coastline (m^3/s per meter of coast) was estimated using the following equation:

$$\text{CUI} = \frac{\tau}{\rho_w f} \quad (1)$$

where τ is the along shore component of wind stress within 270 km of the coastline (positive southward), ρ_w is the seawater density (1,025 kg/m^3) and f is the Coriolis parameter ($=2 \Omega \sin(\theta)$, with Ω and θ equal to the Earth's angular velocity and latitude, respectively).

Coastal Sea Surface Temperature (SST)

As an alternative index of coastal upwelling, a monthly index of coastal SST was derived from the AVHRR Pathfinder product (1985–2009, NOAA, 4 km of resolution) for the Senegalese coast by averaging SST from the coast to the isobath 200 m where upwelling-induced SST anomalies are generally maximum (Demarcq & Citeau, 1995). Alongshore winds generate coastal upwelling through offshore Ekman transport, which brings cold water from below the seasonal thermocline (50–200 m) to the surface, especially near the coast where the upwelling flow is at its maximum. Because of the temperature difference between the coastal and offshore water masses, the surface temperature is a good descriptor of coastal upwelling.

Large-scale Atlantic climate indices

Monthly time series of NAO, AMO and MEI indices were downloaded from the period 1966–2011, from NOAA (US National Oceanic and Atmospheric Administration, <http://www.noaa.gov/>). We used the Multivariate ENSO Index (MEI, http://www.cdc.noaa.gov/_kew/MEI/) to monitor the status of ENSO during the autumn season (October–December), before the winter-spring upwelling

period (January–June) in the eastern tropical Atlantic. The MEI is a composite index of the six main observed variables over the tropical Pacific. As the MEI integrates more information than other indices, such as the SOI index based on Tahiti–Darwin pressure difference, it is thought to reflect the nature of the coupled ocean–atmosphere system better (Wolter, 1987; Wolter & Timlin, 1993). Significantly positive (negative) values of the MEI indicate El Niño (La Niña) conditions in the Pacific leading to a relaxation (intensification) of the Atlantic trade winds, and to positive (negative) coastal SST anomalies measured a few months later within the wind-driven NW African upwelling system from 10°N to 26°N (Roy & Reason, 2001).

2.2 | Statistical analysis

2.2.1 | Estimation of abundance indices using the Generalized Linear Models 'GLM'

The CPUE can be modeled as the result of an AI multiplied by the fishing power of the individual vessels, combined with a residual variability (Robson, 1966). This is usually turned into an additive relationship by logarithmic transformation, which makes it possible to use linear regression techniques to do an estimation of the unknown parameters. Linear models and their extension into GLM (McCullagh & Nelder, 1989) are nowadays widely used. They make it possible to consider several explanatory variables either categorically or continuously, but more interestingly, is their interactions. Monthly CPUEs were estimated using a GLM from the commercial industrial fishery statistics. The GLM allowed us to determine the spatial and seasonal distribution scheme of sardinella, and this scheme was used in turn for the calculation of monthly AIs (Braham et al., 2014; Gascuel et al., 2004; Meissa, Gascuel, & Rivot, 2013; Thiaw, Gascuel, Jouffre, & Thiaw, 2009).

Based on the detailed data obtained from Senegalese industrial trawlers, mean CPUE, expressed in kg of sardinella per fishing day, were calculated per boat, fishing area, year and month. Based on their engine power, the boats were placed in categories that are referred to as “engine power-classes”. The CPUE is the response variable of the model and its dependent factors are: the year, the month, the fishing area and the engine power-class of the fishing boats. Sardinella can be off-loaded in almost every fishing trip, and the occurrence of this species in the catches is therefore close to 1. Hence, a Gaussian model is used to estimate monthly abundance. The model is expressed as follows:

$$\ln \text{CPUE}_{y,m,z,i} = \ln A_{y,z} + \ln d_m + \ln P_f + \ln \varepsilon_{y,m,z,f} \quad (2)$$

where $\text{CPUE}_{y,m,z,i}$ is the catch per unit of effort of the year (y), the month (m), the area (z) and boat (i) (belonging to the engine power-class (f)), $A_{y,z}$ is the combined statistical effect of year and area, d_m is the monthly effect, P_f is the engine power-class effect, and $\varepsilon_{y,m,z,f}$ is the normally distributed residual. It is noteworthy that $A_{y,z}$ can be interpreted as a monthly abundance index in the fishing area under the assumption of a constant year-to-year seasonality of CPUE, and a constant fishing efficiency per engine power-class. Conversely,

such an index is not biased by changes in the spatial fishing patterns or by an increase in the engines' power. However, changes in the seasonal pattern cannot be investigated using abundance index from this method.

GLM models were fitted using a negative log-like loss function. The Akaike Information Criterion AIC (Akaike, 1974) was calculated to measure the goodness of fit, with low values representing the best compromise between the model and the observed data. Statistical analyses were carried out using R software (version 3.1.2). To fit the distribution of residuals, a Gaussian error model was the most appropriate according to the goodness of fit values for various statistical models. In GLM modeling, it was assumed that the response variable (CPUE) follows a Gaussian distribution, which is normally appropriate for describing spatial heterogeneity and abundance data (e.g., Bellido, Pierce, & Wang, 2001; Maravelias, 1997; Swartzman, Huang, & Kaluzny, 1992).

2.2.2 | Exploratory abundance data analysis

A boxplot analysis was carried out to describe the seasonal cycle of sardinella abundance estimated by GLM off Senegal. Monthly abundances were averaged over each season to obtain a time series of abundance per season.

2.2.3 | Time series analysis

The monthly time-series of sardinella abundance were analyzed to determine the main factors affecting their variability. First, a seasonal decomposition was conducted on AIs and environmental indices: CUI, SST, NAO, AMO and MEI. For example, as sardinella abundance (R_t) shows a strong seasonal cycle, the signal was decomposed into a combined trend and cycle component (p_t), a seasonal component (s_t) and a residue component (u_t) (Cleveland, Cleveland, McRae, & Terpenning, 1990) using the package STL in R software.

$$R_t = p_t + s_t + u_t \quad (3)$$

There are sophisticated procedures to carry out seasonal decomposition nevertheless in this study, we used the method of Census II (Makridakis, Wheelwright, & McGee, 1983) for its flexibility and simplicity. The seasonal decomposition is with a homogeneous variance, with or without long-term trend, and is applied on log-transformed and differentiated data (González Herraiz et al., 2009).

2.2.4 | Relation abundance versus environment

Monthly time series of environmental indices were averaged over winter (January–March), spring (April–June), summer (July–August) and autumn (September–December) seasons to obtain time series of environmental indices per season of the year, so-called “seasonal time series”. Pearson's correlations between seasonal time

series of the environmental indices and time series of the annually averaged trend components of sardinella abundance (AIs) were computed taking into account a time lag of 0–10 years (see Table 1). These are used in explaining the part of the yearly variations that is related to the intensity of the coastal upwelling and the coastal SST along the Senegalese coast, and the predictive potential of local environmental conditions (CUI and coastal SST) and large-scale climate indices representative of sea level pressure patterns (NAO) and the large-scale state of SST (AMO) in the North Atlantic.

The relationships between log-transformed abundance (log AI) and the annual and seasonal average of environmental explanatory variables (SST, CUI, AMO, MEI, NAO) were further investigated using Generalized Additive Models (GAMs), thereby allowing non-linearity in the relationships to be taken into account. As log AI was normally distributed we used a Gaussian GAM with identity link. For all continuous explanatory variables, degrees of freedom were constrained to be less than five to avoid over fitting. Models were fitted using a backwards selection starting with full models and removing explanatory variables with non-significant partial effects. The Akaike Information Criterion (AIC) was used to choose the best fitting model (lowest AIC). More information about these techniques can be found in Zuur, Ieno, and Smith (2007).

3 | RESULTS

3.1 | Harvests of the small-scale fishery

In Senegal, the harvests of sardinella varied between seasons and years, with a clear increase over the period between 1966 and 2010 (Figure 2a). *Sardinella aurita* harvests were always higher than those of *S. maderensis*, especially between 1966–1998 and 2005–2011. Over the 1999–2004 period, the annual harvest of both sardinella species was similar, with a slightly higher harvest of *S. maderensis* (on average 115,163 tons, against 100,086 tons for *S. aurita*).

The Senegalese small-scale fishery provided the main part of the total landings of sardinella (Figure 2b) and is the biggest one in the sub-region. The villages of Mbour and Joal (Petite Côte, Figure 1) were the main landing sites of *S. aurita* in the 1990s and in the early 2000s (Figure 3a). Both villages had earlier shown a spectacular increase in landings in the 1980s, with landings at each site increasing from less than 10,000 t/year to around 40,000 t/year. However, after 2004, the largest landings of *S. aurita* were recorded in Saint-Louis (Figure 3a). Landings at Kayar (North of Dakar) have also increased concomitantly. As for *S. maderensis* landings, they were also essentially concentrated in the Petite Côte (Figure 3b). By far, Joal has always been the main landing site. The harvests here increased steadily from 1981 to 2003, and rose to a peak of more than 100,000 t/year, but thereafter, declined to less than 60,000 t/year in the year 2010. Landings at Mbour are much less important (~20,000 t/year), but they follow the same temporal pattern.

TABLE 1 Pearson's correlations between "seasonal time series" of the environmental indices (explanatory indices) and time series of the annually averaged trend components of (a) *Sardinella aurita* and (b) *Sardinella maderensis* abundance indices (AI) taking into account a lag of 0–10 years

Environmental Index		Mean AI (1966–2011)	0	1	2	3	4	5	6	7	8	9	10
(a) <i>S. aurita</i> – Lag (in years)													
CUI (1966–2011)													
Annual	versus	Annual	0.20	0.22	0.18	0.13	0.20	0.21	0.12	0.07	0.02	–0.06	–0.20
Winter	versus	Annual	–0.02	–0.03	0.02	–0.05	–0.01	0.05	0.04	0.01	–0.01	–0.09	–0.14
Spring	versus	Annual	0.38**	0.37*	0.27	0.20	0.18	0.09	–0.04	–0.06	–0.07	–0.09	–0.22
Summer	versus	Annual	0.03	–0.03	0.00	0.07	0.08	0.04	0.01	0.08	0.06	0.05	–0.06
Fall	versus	Annual	0.12	0.18	0.12	0.18	0.31*	0.36*	0.31	0.22	0.14	0.10	–0.03
SST (1985–2009)													
Annual	versus	Annual	0.11	0.04	–0.06	–0.04	–0.12	–0.09	–0.03	–0.13	–0.17	–0.09	–0.04
Winter	versus	Annual	0.16	0.14	0.09	0.15	0.05	–0.03	–0.06	–0.15	–0.20	–0.12	–0.17
Spring	versus	Annual	0.06	0.01	–0.07	–0.08	–0.13	–0.04	0.03	–0.11	–0.16	–0.11	0.01
Summer	versus	Annual	–0.03	–0.04	–0.16	–0.17	–0.17	–0.08	–0.01	0.06	0.10	0.12	0.05
Fall	versus	Annual	–0.00	–0.11	–0.14	–0.13	0.14	–0.13	–0.03	–0.07	–0.05	–0.03	0.09
NAO (1966–2011)													
Annual	versus	Annual	–0.11	–0.04	0.11	0.16	0.21	0.19	0.26	0.34*	0.28	0.20	0.23
Winter	versus	Annual	0.08	0.04	0.24	0.29	0.32*	0.26	0.25	0.27	0.25	0.21	0.16
Spring	versus	Annual	–0.01	0.05	0.15	0.14	0.20	0.23	0.24	0.26	0.22	0.21	0.13
Summer	versus	Annual	–0.10	–0.01	0.03	–0.01	0.01	0.04	0.11	0.08	0.02	–0.01	0.03
Fall	versus	Annual	–0.22	–0.26	–0.15	–0.04	–0.03	–0.07	0.03	0.17	0.15	0.06	0.20
AMO (1966–2011)													
Annual	versus	Annual	0.09	0.00	–0.03	0.03	0.01	0.03	0.07	0.00	–0.09	–0.12	–0.05
MEI (1966–2011)													
Fall/Year	versus	Annual	–0.11	–0.09	–0.01	0.03	0.03	0.05	0.22	0.24	0.16	0.13	0.19
(b) <i>S. maderensis</i> – Lag (in years)													
CUI (1967–2011)													
Annual	versus	Annual	0.24	0.19	0.22	0.02	0.01	0.02	0.09	0.17	0.00	–0.11	–0.35**
Winter	versus	Annual	0.02	–0.08	0.12	–0.15	–0.07	0.03	0.11	0.09	0.06	–0.09	–0.22
Spring	versus	Annual	0.32*	0.25	0.09	0.01	–0.06	–0.10	–0.12	0.03	–0.09	–0.02	–0.21
Summer	versus	Annual	0.05	–0.08	0.07	0.15	0.03	–0.07	–0.13	0.01	–0.01	0.08	–0.15
Fall	versus	Annual	0.23	0.36**	0.27	0.27	0.23	0.14	0.21	0.27	0.02	–0.12	–0.28
SST (1985–2009)													
Annual	versus	Annual	–0.01	–0.10	–0.25	–0.02	–0.25	–0.17	0.02	–0.17	–0.16	0.05	0.24
Winter	versus	Annual	0.07	–0.02	0.16	0.21	–0.06	–0.26	–0.15	–0.15	–0.19	0.06	–0.01
Spring	versus	Annual	–0.05	–0.11	–0.21	–0.06	–0.20	0.05	0.17	–0.15	–0.24	–0.15	0.19
Summer	versus	Annual	–0.09	–0.06	–0.08	–0.13	–0.26	–0.04	0.03	0.08	0.21	0.26	0.17
Fall	versus	Annual	–0.00	–0.10	–0.17	–0.22	–0.20	–0.14	0.02	–0.13	–0.01	0.08	0.41**
NAO (1967–2011)													
Annual	versus	Annual	–0.18	–0.32*	–0.04	0.01	0.14	0.03	0.07	0.27	0.24	0.12	0.03
Winter	versus	Annual	–0.11	–0.09	0.12	0.10	0.00	–0.08	–0.01	0.14	0.22	0.16	–0.01
Spring	versus	Annual	–0.00	–0.11	0.02	–0.08	0.20	0.24	0.11	0.18	0.13	0.15	0.06
Summer	versus	Annual	–0.17	–0.15	–0.00	–0.02	0.00	–0.08	0.11	0.14	0.12	0.07	–0.04
Fall	versus	Annual	–0.14	–0.41**	–0.21	0.02	0.12	–0.02	–0.04	0.15	0.10	–0.08	0.06

(Continues)

TABLE 1 (Continued)

Environmental Index		Mean AI (1966–2011)	0	1	2	3	4	5	6	7	8	9	10
AMO (1967–2011)													
Annual	versus	Annual	0.21	0.21	0.02	0.07	0.07	0.11	0.13	0.07	−0.01	−0.09	0.07
MEI (1967–2011)													
Fall/Year	versus	Annual	−0.14	−0.00	−0.10	−0.01	0.13	−0.00	0.17	0.19	0.11	−0.05	−0.01

Significance of Pearson's correlations: p -value < .1 (bold), * p -value < .05, ** p -value < .02.

3.2 | Fishing effort

The evolution of fishing effort differs according to the type of fishing employed. The average number of operational units was estimated to be 18,000 canoes (DPM, 2012). The small-scale fishery used two main fishing gears to target sardinella; the purse seine (far more efficient especially for *S. aurita*) and encircling gillnet.

Over the past three decades, the fishing effort of purse seines has increased (Figure 3c). Indeed, it almost doubled in 12 years from 27,441 fishing trips in the year 1981 to 62,470 fishing trips in the year 1993. After this period, the effort became relatively stable at around 60,000 fishing trips. However, since 2004, the fishing effort of purse seines generally decreased. The same trend was noted for encircling gillnets, but the fishing effort of the purse seine is more important (Figure 3c).

The industrial fleet consisted of small semi-industrial seiners, large trawlers and foreign industrial seiners. The national industrial fleet targeting sardinella consists of a limited number of "sardiniers" that operated from Dakar. This fleet started in the early 1960s with 7–10 fishing units, but over the years it has steadily declined, and only 1–2 fishing units were active in recent years. The industrial fishing effort also shows a decreasing trend with very low effort levels in recent years. With the departure of the Russian ships in 2013, the overall number (national plus foreign boats) of active fishing boat targeting sardinella has not exceeded six boats per year.

3.3 | Abundance indices from small-scale and industrial fisheries data

Data on catches of sardinella by the small-scale fishery per fishing port were available from 1975 to 2011, but all the necessary information to estimate the AIs were only available from 2004 to 2011. First, we verified that the variability of AI obtained from small-scale and industrial fisheries was comparable from 2004 to 2011 (adjusted $R^2 = 0.39$, $p < .001$). According to this result and under the hypothesis that 1966–2004 was also comparable, we select the longer time series of AI estimated using data from the industrial fishery, from 1966 to 2011, to explain the seasonal and inter-annual variability of sardinella abundances observed from the harvests by small-scale fishery in Senegalese waters.

For *S. aurita*, the selected factors for the GLM were the year, month, fishing area, fishing powers (GRT) and the number of fishing strokes. This GLM explained 32.3% of the total deviance observed in

the abundance data set (Table 2a). The yearly effect explained the largest part of the total deviance (22.8%). The monthly effect is also important and explained 7.0% of the total deviance. These indicate that the sardinella stocks' abundance varied widely between years, and seasonally, within years (Figure 4). The factor area was significant, indicating a spatial distribution of abundance, with the *S. aurita* populations found in larger population number in the coastal area of the Petite Côte, corresponding to the main area of reproduction and nurseries for this species.

For *S. maderensis*, the fitting GLM model explained 23.8% of the total deviance (Table 2b). The same factors are retained as before. However, this species was equally distributed in the North (Grande Côte) and the Petite Côte. While this is in contrast with artisanal catches, the *S. maderensis* abundance was generally lower than that of *S. aurita* (Figure 4), which seems to be reflected in the catches.

3.4 | Seasonal variability of the AIs

3.4.1 | Seasonal variability of *S. aurita* abundance

The boxplot presented in Figure 5a shows that 23.94%, 30.32%, 18.14% and 27.60% of the abundance of *S. aurita* were caught in winter, spring, summer and autumn, respectively, as estimated by GLM. The abundance displays a strong inter-annual variability, but the maximum (resp. minimum) values of abundance were always observed in spring and autumn (resp. summer and autumn). The same seasonal pattern emerged from the seasonal decomposition analysis. The latter showed that the *S. aurita* abundance has the main abundance peak between March and July and a second weaker peak between October and December. The residual component does not present any trend; its average is null and shows high volatility when large changes are observed on the trend component.

The *S. aurita* abundance presents a bimodal seasonal cycle with two peaks, one in spring and another but less pronounced in autumn, and a minimum in August (Figure 5a). In contrast, environmental indices (SST and CUI) present a unimodal seasonal cycle (Figure 6). The coastal SST is low from January to June (minimum in February–March) and high from July to December (maximum in September–October). The seasonal cycle of SST and CUI are naturally opposed with the cold season corresponding to strong wind-induced upwelling (Figure 6). So, the bimodal seasonal cycle of *S. aurita* abundance cannot be fully explained by the seasonality of upwelling-favorable wind and SST. Nonetheless, minimum abundance is found during the seasonal relaxation of coastal upwelling in summer.

TABLE 2 Goodness-of-fit statistics for the GLM fitted to (a) *Sardinella aurita* and (b) *Sardinella maderensis* catch per unit of effort CPUE (variance function: Gaussian; link function: log) deviance; F and $P(F)$ are the values for the last variable included in each model; residual deviance and percentage of deviance explained are the values for the model

Variables	df	Deviance	Residual df	Deviance residual	% Deviance explained	P(F)
(a) for <i>S. aurita</i>						
NULL			10,141	27,300		
Year	45	6211.5	10,096	21,088	22.75	<2e-16
Fishing area	8	36.6	10,088	21,052	0.13	.01058
Month	11	1909	10,077	19,143	6.99	<2e-16
Fishing powers (GRT)	10	435.5	10,067	18,707	1.60	<2e-16
Number of fishingstrokes	2	211.2	10,065	18,496	0.77	<2e-16
(b) for <i>S. maderensis</i>						
NULL			6,929	12,585		
Year	44	1341.25	6,885	11243.8	10.66	<2.2e-16
Month	11	982.21	6,874	10261.6	7.80	<2.2e-16
Fishing area	4	65.08	6,870	10196.5	0.52	1.89E-09
Fishing powers (GRT)	9	522.18	6,861	9674.3	4.15	<2.2e-16
Number of fishing strokes	2	85.63	6,859	9588.7	0.68	5.00E-14

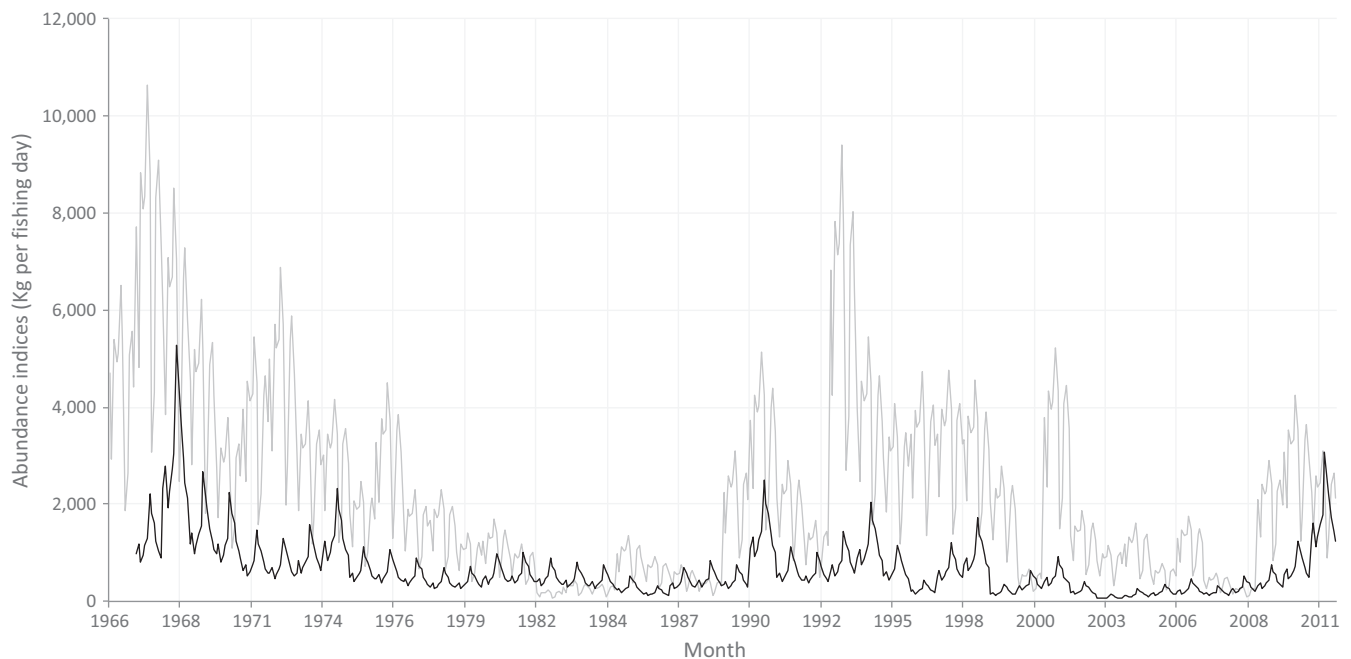


FIGURE 4 Abundance indices of *Sardinella aurita* (white line) (1966–2011) and *S. maderensis* (dark line) (1967–2011) estimated from industrial fishery in Senegal

3.4.2 | Seasonal variability of *S. maderensis* abundance

Contrasting with *S. aurita*, the abundance of *S. maderensis* shows an unimodal seasonal cycle with an annual maximum in summer corresponding to the relaxation of upwelling-favorable winds, and a minimum in winter/spring (Figure 5b). From winter to summer (January–July), the SST and *S. maderensis* abundance showed

similar seasonal patterns (Figure 6). Then, from summer to winter (August–December), the abundance declined whereas the SST continued to increase until October when it decreased strongly. In contrast, the *S. maderensis* abundance evolved out of phase with the CUI. The seasonal component accordingly has one maximum in summer from June to September (with an absolute maximum in July). The residuals component presents the similar patterns as for *S. aurita*.

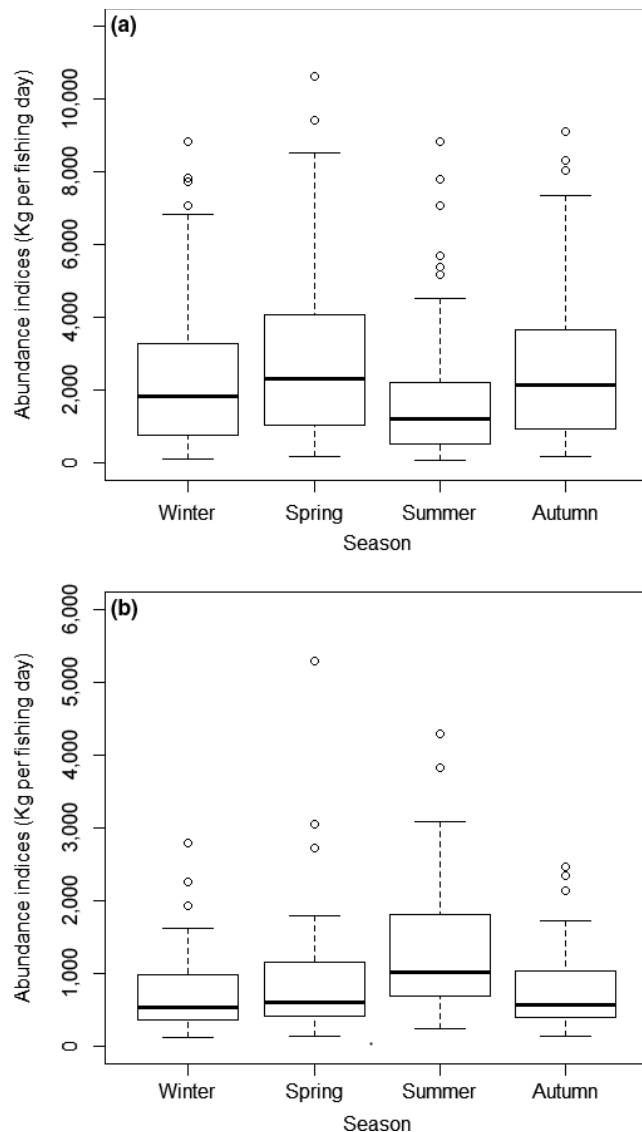


FIGURE 5 Boxplot of the monthly abundance (kg per fishing day), clustered by season of (a) *Sardinella aurita* and (b) *S. maderensis* over the period 2004–2011

3.5 | Size spectrum

The *S. aurita* size spectrum shifts toward a larger body-length during the cold season that is, the winter and spring in the Grande Côte (Figure 7) when the upwelling of nutrient-rich cold water sustains high primary production. The juveniles (<18 cm FL) of *S. aurita* were encountered on the Petite Côte mainly in winter and summer, co-occurring with the adult population (mode >23 cm FL). On the Grande Côte small proportions of juveniles were also found in summer and autumn. The smallest adult mode was found in summer on the Grande Côte (20 cm FL). The size of the adult mode was larger on the Grande Côte during winter/spring. The inverse situation was observed in summer and autumn, i.e., larger size on the Petite Côte.

For *S. maderensis*, the presence of juveniles (<18 cm FL) was observed at all seasons on the Petite Côte, to a lesser extent in

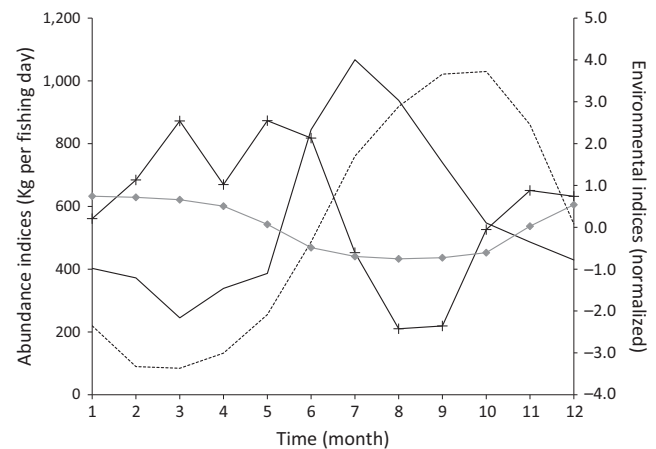


FIGURE 6 Seasonal cycles of round (*Sardinella aurita*, dark dotted line with cross) and flat (*S. maderensis*, dark line) sardinella abundance (kg per fishing day) and normalized seasonal components of the coastal sea surface temperature index (SST, dotted line, source Modis AVHRR) and the coastal upwelling index (CUI, grey line with losange) along the Senegalese coast

spring (Figure 7). On the Grande Côte, the juveniles were found only in autumn. The adult mode displayed small size variability on the Petite Côte across the seasons, being minimum in autumn (mode 21 cm FL) and maximum in spring (mode 23 cm FL). Conversely, on the Grande Côte, the adult size (FL) mode decreased from winter (24–26 cm) to spring (25 cm), summer (22.5 cm) and autumn (19 cm).

3.6 | Long-term variations

Trends of both sardinella species abundance indicated strong inter-annual and decadal variations with major peaks of abundance in the late 1960's and the 1990's, and minima in the 1980s and 2000s (Figure 8). In the Northern area, the abundance of *S. aurita* was in general, slightly lower than that of *S. maderensis*, except in 1966–1967 and 1996 (Figure 8a). In contrast, in the southern area, the abundance of *S. aurita* was significantly higher than that of *S. maderensis*, except in 1982–1983 (Figure 8b). Over the period 1966–2011, the inter-annual variability of *S. maderensis* abundance was similar to that of *S. aurita* except in the 2000s, when the abundance of *S. maderensis* increased, and the abundance of *S. aurita* decreased. The evolution of the abundances of both species of sardinella off Senegal was close, suggesting common drivers. However, both sardinella species presented different answers with regard to local environmental conditions and climate variability in the North Atlantic (see Table 1).

3.6.1 | Long-term variations for *S. aurita*

The interannual variability of the *S. aurita* abundance (annual mean) correlates positively with the CUI in spring at lag 0–2 (in years, $p < .01$, Table 1a) and also, although poorly ($p > .01$), with the autumn CUI at lag 1. However, the negative correlation found with the autumn

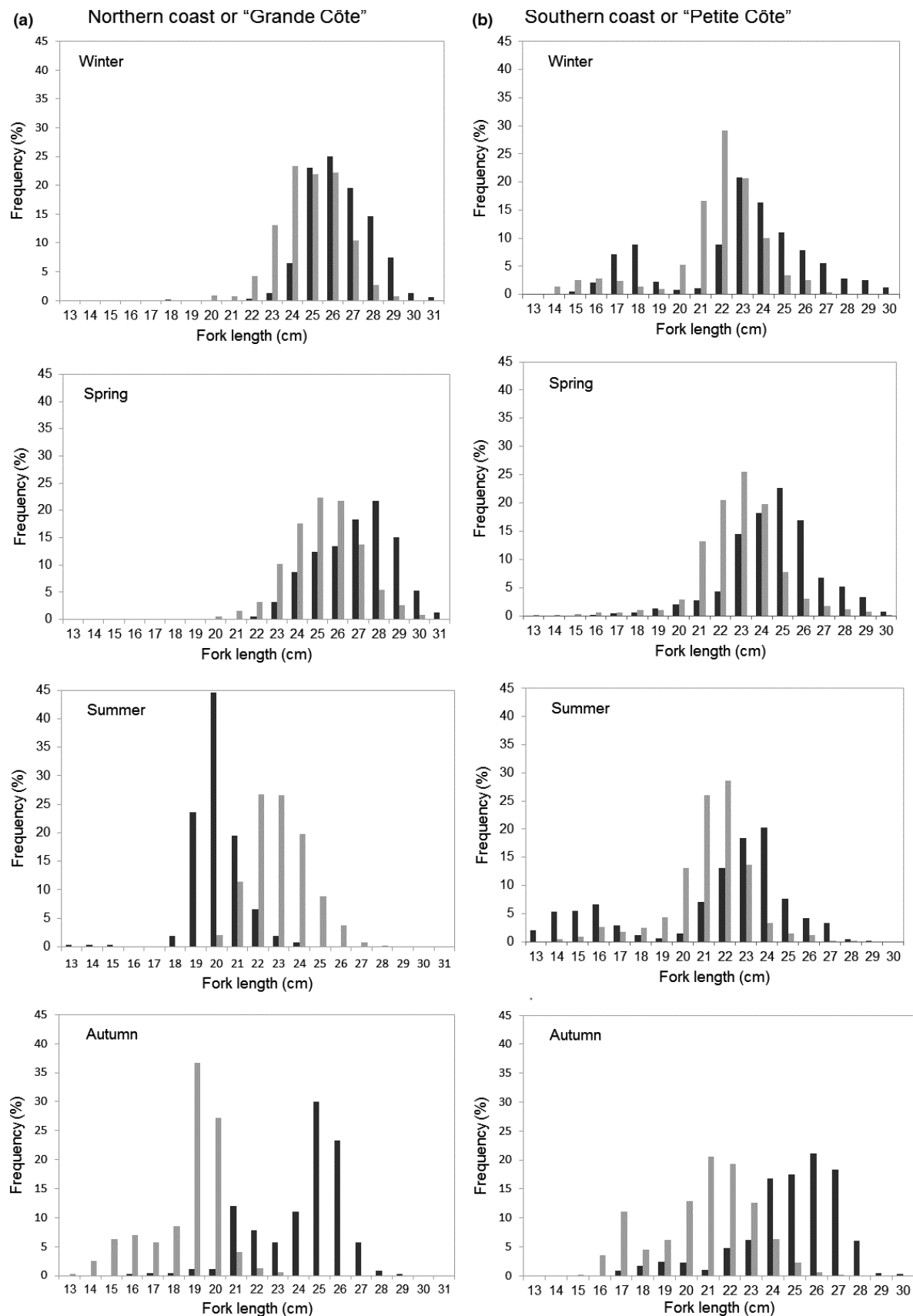


FIGURE 7 Length distribution (fork length in cm) of quarterly catches (2012–2013) of sardinella landed by the Senegalese small-scale fishery using purse seine fishing gear (a) in the Northern area (see Figure 1) and (b) in the Southern area. *Sardinella aurita* in dark, and *S. maderensis* in grey

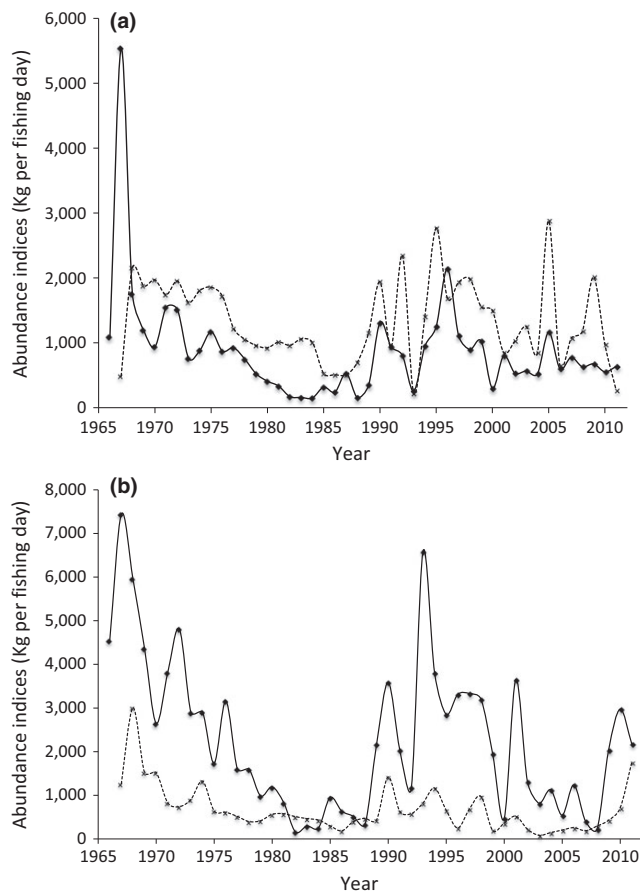


FIGURE 8 Yearly abundance (kg per fishing day) of round sardinella (*Sardinella aurita*, dark full line with points) and flat sardinella (*S. maderensis*, dark dotted line with cross) over the period 1966–2011 in (a) the Northern coast and (b) the Southern coast of Senegal

TABLE 3 Results for the generalized additive models fitted to the annual abundances of (a) *Sardinella aurita* and (b) *Sardinella maderensis* with environmental indices in Table 1 as explanatory variables

GAM variables	e df	Ref.df	F	p-value
(a) for <i>S. aurita</i>				
IASR ~ s(CUI in Spring, lag = 0) + s(CUI in Fall, lag = 5) + s(NAO annual, lag = 7))				
s (CUI in Spring (lag = 0))	7.286	8.164	8.538	3.74E-05
s (CUIFall (lag = 5))	8.210	8.736	4.624	.0234
s (NAO annual(lag = 7))	3.302	3.924	12.013	2.84E-05
(b) for <i>S. maderensis</i>				
IASR ~ s(NAO annual, lag = 1) + s(CUI in Spring, lag = 0)				
s (NAO annual, lag = 1)	2.07	2.476	14.36	.000198
s (CUI in Spring, lag = 0)	1	1	6.29	.025973

CUI, Coastal Upwelling Index; NAO, North Atlantic Oscillation.

NAO index at lag 1 was surprising as upwelling-favorable winds are supposed to be reduced during negative NAO phases.

The annual abundance also correlated positively with the autumn CUI at lag 4–6, this time corresponding to a positive

correlation with the winter NAO index at lag 3–5. Additionally, the annual NAO index (winter-spring) positively correlated with the annual abundance at lag 7–8. In winter, the expression of NAO patterns is the most intense and the coastal upwelling is particularly active off Senegal. The NAO indeed explains as much as 53% of the variability of wind stress delivered by Northeastern Trade Winds along the NW African coast (Meiners, Fernández, Salmerón, & Ramos, 2010).

It is noteworthy that no significant correlations were found with the coastal SST, MEI and AMO indices, the latter contrasting with a multi-decadal modulation of small pelagic fish catches observed in the eastern North and Central Atlantic (Alheit et al., 2014).

The use of non-linear GAM models in place of linear regressions taking each environmental index separately as an explanatory variable did not demonstrate any additional significant relationship that our linear analysis could have missed (see Table 1a) with the *S. aurita* abundance (not shown). The GAM model was run considering the annual time-series of the environmental indices to identify the most significant environmental drivers of *S. aurita* abundance among those previously identified (see above). The results showed a significant correlation with the mean annual abundance (with lag, see Table 1). This model suggested that the *S. aurita* abundance is mainly explained by the spring CUI (lag 0) and the annual NAO index (winter-spring, lag 7), and, less, by the fall in CUI (lag 5) (Table 3a and Figure 9). The relationships with *S. aurita* abundance were mostly linear except that the effect of the NAO is overall evident during positive phases (Figure S1).

3.6.2 | Long-term variations for *S. maderensis*

The interannual variability of *S. maderensis* abundance (annual mean) correlated positively with the CUI in spring at lag 0 (Table 1b) implying a direct effect of upwelling-favorable wind anomalies at the end of the upwelling season. A positive correlation, this time significant, was also found with the autumn CUI (Table 1b) at lag 1–3 which confirms that the duration of the upwelling season is important to explain interannual fluctuations of sardinella abundance, especially the precocity of the upwelling season for *S. maderensis*. As for *S. aurita*, the latter correlation was surprisingly accompanied by a negative correlation with the autumn NAO index at lag 1. In contrast, the annual abundance of *S. maderensis* was positively correlated, although poorly ($p > .01$), with the AMO index at lag 0–1 (Table 1b) in agreement with the analysis of fish catches by Alheit et al. (2014).

As for *S. aurita*, no additional environmental explanatory index of *S. maderensis* abundance emerged from the use of non-linear GAM models. However, a GAM modeling approach similar to that used for *S. aurita* (see Section 3.6.2) showed that the *S. maderensis* abundance was mainly explained by the annual NAO index (lag 1) and, less, by the effect of the spring CUI (lag 0) (Table 3b and Figure 10). It is noteworthy that the relationship with the annual NAO index was non-linear as only weak negative anomalies of *S. maderensis* abundance were observed during positive phases of the NAO, with respect to negative phases (Figure S2).

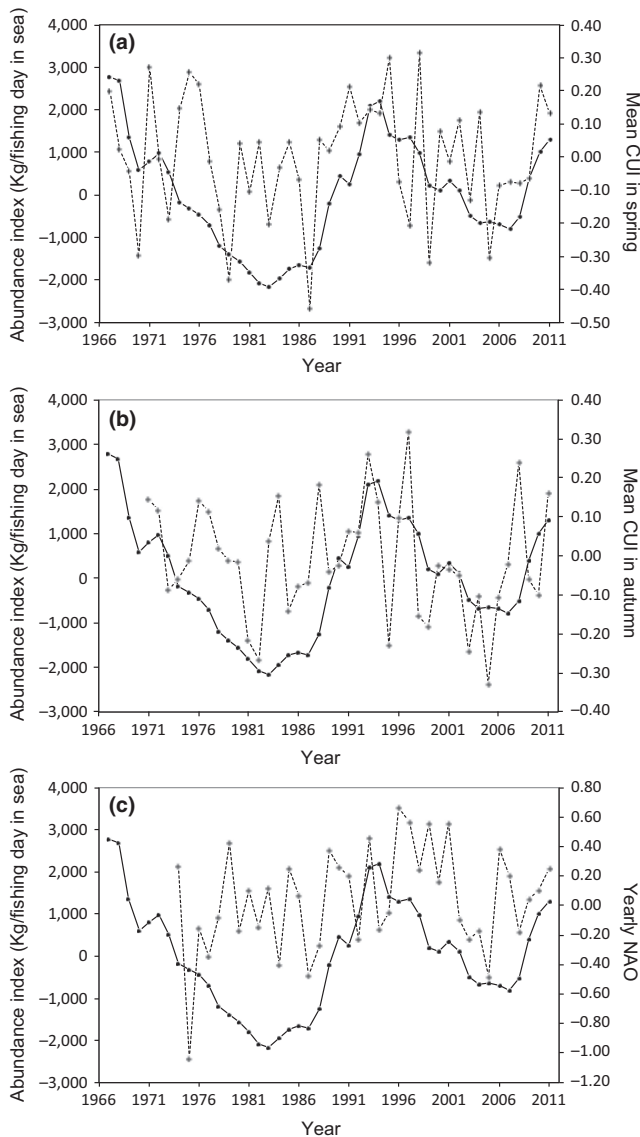


FIGURE 9 Interannual time series of the index of *Sardinella aurita* abundance in Senegalese waters (dark full line), and (a) the coastal upwelling index CUI in spring (lag = 0), (b) the CUI in autumn (lag = 5) and (c) the yearly North Atlantic Oscillation NAO (lag = 0) (dark dotted line)

4 | DISCUSSION

Results from this study will help to identify the relationships between the variability of sardinella abundance and the environmental conditions. We base our time series analysis on a 46-year data set of monthly observations of the *S. aurita* and *S. maderensis* fisheries off the Senegalese waters.

One limit of our methodology is that the small-scale fishing effort metric recorded in Senegal, expressed in the number of fishing trip, has decreased over the past decade despite an increase in catches. Indeed, the number of fishing trips did not translate well in the effective changes in fishing effort because the increase in distance traveled and sea fishing time were not taken into account.

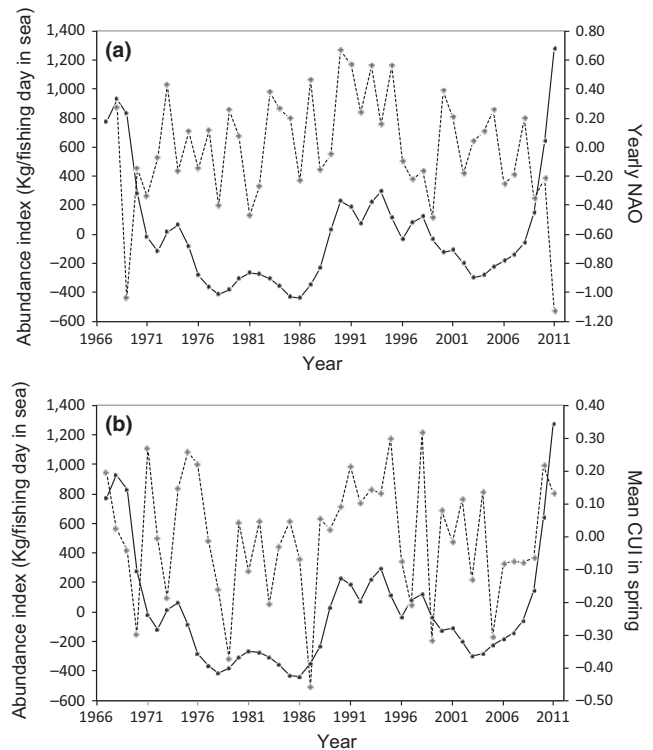


FIGURE 10 Interannual time series of the index of *Sardinella maderensis* abundance in Senegalese waters (dark full line), and (a) the yearly North Atlantic Oscillation NAO (lag = 1) and (b) the coastal upwelling index CUI in spring (lag = 0) (dark dotted line)

4.1 | Harvests and Fishing Effort

From 1974 to 2004, the yearly harvests of *S. aurita* were higher in the Petite Côte compared to the Grande Côte (Figure 3a). After 2004, a fishing agreement allowed 300 Senegalese canoes using purse seines to the fish in the Mauritania exclusive economic zone (EEZ). The landings of these canoes were recorded in Saint-Louis, which caused a sharp increase in the harvests reported in Saint-Louis over the past decade (Figure 3a). Meanwhile, the migration of the 300 canoes to the North reduced the average fishing effort in the rest of the country. The movement of these canoes may be responsible for the decrease in the landings recorded at the other fishing sites, especially in the Petite Côte. Otherwise the fishing in the Mauritanian EEZ resulted in a longer duration of the fishing trips. This might explain why, despite the increase of total landings, the fishing effort metric, the number of fishing trips recorded in Senegal has decreased over the same period (Figure 4).

A symmetric reasoning can be applied for the *S. maderensis* landings, considering that Joal account for the landings of *S. maderensis* fished further south, as Saint-Louis does for *S. aurita* fished further North (Figure 3b). This landing site is the southern fishing port in Senegal, being well connected with roads, and with extensive transformation (smoking fish) industry, allowing for easy exportation. As the horsepower of the canoes constantly increased over the last decades, the small-scale fishers increasingly caught the populations of *S. maderensis* in abundance in the South (Gambia and Casamance)

or even in the common waters of Senegal and Guinea Bissau, but the landings are almost done in Joal. The main fishing engine used to target *S. maderensis* is the encircling gill nets. The number of encircling gillnets fishing trips remained more or less constant whereas the catches of *S. maderensis* sharply increased. Here it might be due to the increase in distance traveled to the south and sea fishing time, which were not taken into account in this metric of the fishing effort. The decrease in *S. maderensis* landings after 2004 might be related to the re-allocation of the fishing effort toward *S. aurita* fisheries, according to the agreement with Mauritania that was mentioned before.

4.2 | Seasonal variability of sardinella

Monthly time series of *S. aurita* abundance showed a bimodal seasonal cycle with two peaks in spring and autumn, and an annual minimum in summer. The abundance index of *S. aurita* was maximal during the transitional phases of SST that is, from cold to warm (in spring, the highest abundance) and warm to cold (autumn) seasons (Figure 7). The low abundance of *S. aurita* was observed when the SST remained stable in cold or warm season (Figure 7).

We propose two hypotheses to explain this bi-modal cycle of the abundance index. First, during those two seasons, the harvest rate is high owing to favorable climatic conditions which facilitate small-scale fishing operations. They also correspond to periods of migration of sardinella (southward, or “descent” and Northward or “ascent”) during which fishermen easily detect fish shoals (com. pers. Moulaye MBAYE, “Comité Local de Pêche Artisanale” CLPA Saint-Louis). Second, the spring might be the period of maximum sardinella accumulation in Senegal because, during this period, fish coming from Mauritania may end their southward migration and fish having previously migrated further south may begin their Northward migration (Boëly et al., 1982). Conversely, the peak of abundance during the autumn might be due to the convergence of *S. aurita*, which continue to migrate from South to North (where the upwelling intensity was high last winter) with those in Mauritania that are beginning their Southward migration. Similar bimodal patterns were also found for other fish species such as octopus, sardine, shrimps and the whiter grouper, or “thiof” in the local name (*Epinephelus aeneus*) in NW Africa (Cury & Roy, 1988; Bacha, Jeyid et al., 2016; Bacha, Jehid et al., 2016). These authors suggested that the regional upwelling dynamics and local environmental effects might influence the migration of these species, i.e., the simultaneous relaxation and trigger of the coastal upwelling off Mauritania and Senegal, respectively.

The Senegalese small-scale fishery directed to sardinella is mainly carried out during the transition periods (May to June and November to December; Fréon, 1991), which corresponds to the period of highest abundance of *S. aurita*. The increase in harvests during the cold season was then concomitant with a size increase of the population (Figure 8). Indeed, the period of high catch of *S. aurita* corresponds to the period during which we observed the larger size of adult mode on the Petite Côte for both spring and autumn and for

the Grande Côte in spring. As fecundity is proportional to the weight of the mature individuals, this is in line with the fact that there are two annual cohorts in the *S. aurita* populations of the Senegalese waters. These two cohorts are the result of two main annual reproductive peaks (Fréon, 1988; Ndiaye, 2013).

For *S. maderensis*, the abundance was higher in summer (Figure 6), between June and September, than during the rest of the year. The juveniles were observed in autumn at the Grande Côte (Figure 8). In contrast, they were present throughout the year (but especially plentiful in autumn) in the Petite Côte. It is known that this species tolerates strong environmental variations (Cury & Fontana, 1988), which would explain why *S. maderensis* is also found in the cold Mauritanian coastal waters (Boëly & Fréon, 1979; Corten & Sadegh, 2014) and even in the colder waters of the Sahara Bank (Ettahiri, Berraho, Vidy, Ramdani, & Do chi, 2003).

The highest catch of *S. maderensis* was observed in summer along the Senegalese coast (Figure 6). At this season, the size mode of the *S. maderensis* population was highest than the *S. aurita*'s on the Grande Côte (22.5 cm FL versus 20 cm). Both these differences in size and the reduction of *S. aurita* abundance owing to its Northward migration in summer (Boëly, 1980) cause the fishermen to change their strategy by switching from the purse seine to the encircling gillnet to target *S. maderensis* (see section 3.2.).

In Senegal, the abundances indices for both sardinella species were higher in the Petite Côte than in the Grande Côte. The larger sizes of sardinella were encountered in the Northern area. In the Southern area, the sardinella encountered were generally small to medium in size. The juveniles of sardinella are always present in the Petite Côte and seasonally observed in the Grande Côte. The Petite Côte is the main spawning and nursery area for both sardinella species. This coastal area is characterized by a broad and shallow continental shelf, which leaves an inshore well-mixed zone acting as a retention area for fish larvae (Demarcq & Faure, 2000). This spatial distribution is confirmed by the observation that the Southern area is a nursery area, and the especially large individuals migrate North in deeper areas (Krakstad, Sarr, Sow, Mbye, & Skålevik, 2013).

The sardinella migration appears to be primarily driven by foraging needs and spawning preferences (Zeeberg, Corten, Tjoe-Awie, Coca, & Hamady, 2008). Sardinella adults move alongside, preferentially looking for convergence areas nearby upwelling of cold waters (Boëly et al., 1982). In the cold season, most of *S. aurita* are found in Senegalese waters where the temperature remains above 21°C. The productivity of the Senegalese waters is high during winter and spring, as a result, according to Zeeberg et al. (2008), of river run-off after the rainy season, localized upwelling, and cyclonic eddies retaining productive waters.

4.3 | Environmental effect on sardinella abundance

The correlation analysis first reveals that interannual fluctuations of *S. maderensis*/*S. aurita* abundance are linked positively to the coastal upwelling intensity in autumn/spring, i.e., at the beginning/

end of the upwelling season (Lathuilière et al., 2008) respectively, and to the North Atlantic Oscillation (NAO) index. The two species responded the same way to upwelling intensity, and we found no evidence of competition between them. So, these correlations may result from the delayed effect of enhanced upwelling-favorable wind intensity at the beginning of the upwelling season off Senegal, i.e., an earlier start-up of the upwelling season in autumn, matching with positive winter NAO through the enhancement of the Azores High.

The positive correlation between the *S. aurita* abundance and the CUI in spring suggested a direct influence of the duration of the coastal upwelling season, peaking in winter (Lathuilière et al., 2008). The coastal upwelling intensity was shown to be a source of interannual fluctuations observed in the coastal abundance of *S. aurita* in West Africa (Braham et al., 2014; Demarcq & Faure, 2000; Diankha et al., 2015; Mbaye et al., 2015). This pattern is also in accordance with the dynamics exhibited by other important resources in the area (for example, *Farfantepenaeus notialis* and *Octopus vulgaris*), which have similar periodicity (Thiaw, Gascuel, Thiao, Thiaw, & Jouffre, 2011; Thiaw et al., 2009). Changes in the recruitment from year to year that are due to fluctuations in environmental conditions are thought to especially affect the early life stages of several species (Bakun & Csirke, 1998; Caballero-Alfonso et al., 2010; Dawe & Warren, 1993). The latter studies suggest that food availability enhanced by coastal upwelling may be the primary controlling factor for larval sardinella survival and recruitment, which we find to translate into fish abundance.

In the NW African upwelling system, the variability of upwelling-favorable winds is positively related to the NAO (Meiners et al., 2010). The relationship between winds and small pelagic abundance depends on how wind variability affects the recruitment success, i.e., nutrient enrichment, concentration of larval food and retention of larvae, according to the “ocean triad hypothesis” (Bakun, 1996). In the Iberian upwelling, high dispersal of sardine eggs and larvae by enhanced coastal upwelling during the winter spawning season was actually proposed to explain a negative relationship between the NAO index and sardine abundance (Guisande et al., 2001; Borges et al., 2003; Santos et al., 2007). In contrast, the recruitment success and abundance of sardine are positively correlated with wind anomalies off Morocco (Roy et al., 1992; Kifani et al., 2008; Machu et al., 2009), and we found a similar relation with sardinella abundance in Senegalese waters. This suggests that the negative effect of wind speed on food concentration and larval retention does not drive the recruitment success of sardinella off Senegal. Moderate winds and a large continental shelf may explain why the latter processes are not so affected by wind variability.

An alternative or complementary explanation for the inter-annual changes in abundance may be that the sardinella abundance in Senegalese waters depends more on the inflow and outflow of sardinella due to migrations than on the local recruitment success. The *S. aurita* abundance in Senegalese waters seems mostly driven by the duration of the upwelling season (spring CUI at lag 0), whereas the *S. maderensis* abundance also depends on the precocity of the

upwelling season (autumn CUI at lag 1) and the state of the NAO during the previous year (autumn and annual NAO at lag 1, Table 1a). This may be explained by the large migrations of *S. aurita* between the Moroccan and the South of Senegal waters (Boëly, 1980) whereas, *S. maderensis* perform lesser migrations around their nursery area (Boëly et al., 1978; Garcia et al., 2012). On one hand, *S. maderensis* would mainly take advantage of an earlier start of the upwelling season off Senegal in autumn owing to poor competition for food with *S. aurita* whose populations are still in Morocco–Mauritania waters. Identically, a large-scale anomaly of SST in the North Atlantic (positive AMO index) may force the population of *S. aurita* to migrate northward very far from Senegal in summer, which would benefit locally to *S. maderensis*. On the other hand, a longer duration of the upwelling season would benefit to *S. aurita* that arrived from Mauritania during winter. The variability in the duration of the productive upwelling season has been proposed to explain abrupt changes in sardine abundance off Morocco (Machu et al., 2009). Following this idea, the longer the productive upwelling season off Senegal, the larger might be the window of time favorable to recruitment for *S. aurita* over the large continental shelf off Senegal. The role of migration dynamics on the interannual variability of fish communities' structure in a specific fishing ground is poorly known, so the latter hypotheses are speculative and should be tested using dedicated modeling approaches.

Note that the apparent discrepancy of the correlations (see Table 1) between the annual abundance of *S. maderensis* on one hand, and the spring CUI (positive) and the annual NAO index (negative) on the other hand may result from a southward shift of the Azores High especially at the beginning of the boreal winter during negative NAO phases. A weakening of the Azores High would be compensated by an anomalous southward displacement of upwelling-favorable coastal winds. This should especially favour *S. maderensis* off Senegal, since the food availability for the pool of *S. aurita* located off Morocco–Mauritania would be additionally reduced due to a reduction in wind intensity during negative NAO phases. This could explain why the *S. maderensis* abundance is overall affected during negative phases of the NAO (Figure 10b). Inversely, the *S. aurita* abundance in Senegalese waters could be maintained during negative NAO phases (Figure 10a) owing to enhanced inflow through southward migration. The decline in the NAO index is associated with the establishment of a blocking high-pressure cell over Scandinavia producing a shift of the Icelandic Low (Bersch, 2002), and this also produces a shift of the Azores High. A specific local index describing the fluctuations of both the position and intensity of the Azores High would certainly help to better link the fluctuations of sardinella abundance to large-scale atmospheric patterns in the Atlantic.

Our results suggest a persistent effect of the NAO and associated upwelling-favorable winds on *S. aurita* abundance for several years. Interannual fluctuations of *S. aurita* abundance respond positively to the winter NAO index and the autumn CUI with a time lag of 4–7 years. In the NW African upwelling system, the abundance of black hake, another highly targeted fish species off Mauritania–

Senegal, also correlates significantly though negatively with the NAO index and the intensity of upwelling-favorable winds, with a comparable time lag of 3 years (Meiners et al., 2010). For *S. maderensis* the abundance responds positively (but with poor significance, $p > .1$) to the AMO index and negatively to the winter coastal SST index, in line with enhanced coastal upwelling, with a similar delay. This suggests a primary role of food availability on *S. aurita* abundance, but in this case with a delay maybe depending on sardinella life span and migrations (Chesheva, 1998, 2006), and on the size/age structure of the catches (Meiners et al., 2010). In contrast, *S. maderensis* is better related to SST according to a greater tolerance to strong environmental variations (Cury & Fontana, 1988), and may benefit from unfavorable conditions affecting *S. aurita*.

Wind observations during the last decades (Sydeman et al., 2014) and projections from coupled ocean-atmosphere general circulation models (IPCC AR5, Stocker et al., 2013) overall agree that global warming will widen the tropical band and shift the subtropical highs poleward in the future. Although large regional and seasonal uncertainties remain, this would tend to increase (decrease) upwelling-favorable winds in poleward (equatorward) regions of EBUS (García-Reyes et al., 2015) both in terms of duration and intensity (Wang, Gouhier, Menge, & Ganguly, 2015). According to our results, the abundance of both *S. aurita* and *S. maderensis* in Senegal could then decrease in the future through a weakening of upwelling-favorable winds. Furthermore, a northward shift of the Azores anticyclone may increase the northward migrations of *S. aurita* during summer, while *S. maderensis* may stay in Senegalese waters owing to its less migratory behavior and higher tolerance to environmental fluctuations (Ba et al., 2016).

5 | CONCLUSION

Our analyses showed that the recruitment of *S. aurita* (round sardinella) and *S. maderensis* (flat sardinella) are continuous in the Petite Côte and seasonal in the Grande Côte. Larger sizes of sardinella were usually observed in the first half of the year along the coastal area, particularly in the Grande Côte. The results also illustrated that the large variations in sardinella biomass in Senegalese EEZ were driven by environmental conditions. This underlines the fact that the environmental variability should be considered in the small pelagic fishery management. Nevertheless, some abrupt changes in landings recorded in Senegal may also have other explanations.

Indeed, the analysis of the landings by site show that most of the increase in sardinella landings in Senegal over the last decades was recorded in the northern and southernmost well connected commercial landing sites limits in Saint-Louis and Joal, respectively. We suggest that the increase in landings in these two sites was due to the increasing distance of the fishing trips toward the adjacent northern and Southern waters that are in Mauritania in the north, and in Gambia, Casamance and Guinea Bissau shared waters in the South.

The precocity and duration of the coastal upwelling period off Senegal respectively influence interannual fluctuations of

S. maderensis and *S. aurita* abundances, which is attributed to distinct migration patterns. *Sardinella maderensis* may mostly depend on the coastal upwelling intensity in autumn when the migrant *S. aurita* would still be absent to compete for food. In contrast, the migrant *S. aurita* would benefit from an anomaly of coastal upwelling intensity in spring when their population is full established off Senegal. Winds are a key driver of sardinella abundance and depends on the state of the NAO (significant relationship is found with the annual NAO). The relation is at low frequency so the decadal variability of sardinella abundance could be inferred from the low frequency variability in the NAO signal. Additionally, the winter/spring NAO could be related to the *S. aurita* abundance with predictive skills at around 4–7 years. Integration of coastal primary productivity and migration patterns may drive such predictability. However, dedicated modeling approaches should be carried out to elucidate the main processes involved. Indeed, such information could be useful to further optimize the management of fish stocks and predict their response to climate change under various exploitation scenarios (Bartolino et al., 2014). Integrating the effect of environmental variability on fish stocks dynamics is central to the ecosystem approach for fisheries management in North West Africa small pelagic fisheries as well as to estimate loss and damage in this fisheries sector due to climate change.

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SUPPORTING INFORMATION

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