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Contrasted optimal environmental windows for both sardinella species in Senegalese waters

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Abstract

We investigate *Sardinella aurita* and *Sardinella maderensis* recruitment success relative to the variability of oceanographic conditions in Senegalese waters using generalized additive models (GAM). Results show that recruitment of both species is marked by a strong intra-annual (seasonal) variation with minimum and maximum in winter and summer, respectively. Their interannual variations are synchronous until 2006 (recruitment decreasing), while from 2007 there is no synchrony. The model developed shows that sardinella recruitment variability is closely related to the tested environmental variables in the study area. However, the key environmental variables influencing the recruitment success are different for both species: the Coastal Upwelling Index and the sea surface temperature for *S. aurita* and *S. maderensis*, respectively. We report that recruitment success of *S. aurita* and *S. maderensis* are associated with distinct ranges of sea surface temperature, upwelling intensity, wind-induced turbulence, concentration of chlorophyll-*a* and north Atlantic oscillation index. Considering food security and socio-economic importance of both stocks, we recommend that consideration is given to the environmental variability in the small pelagic fish national management plans, particularly in the context of climate change.

KEYWORDS

recruitment success, *Sardinella aurita*, *Sardinella maderensis*, upwelling, West Africa

1 | INTRODUCTION

Hydroclimatic conditions along Senegalese coasts are particularly favorable to many fishes, due to enrichment by one of the most productive upwelling systems (Auger, Gorgues, Machu, Aumont, & Brehmer, 2016; Binet, 1988; Roy, Cury, Fontana, & Belvèze, 1989). Indeed, their abundance is thought to be related to the enrichment of the euphotic zone which increases primary production (Bakun, 1997; Cury & Roy, 1987; Demarcq & Samb, 1991). This eastern boundary upwelling system is characterized by a strong seasonal and interannual variability, well known to impact the fluctuations of abundance and distribution of small pelagic fishes (Bakun, 1996; Cury & Roy, 1989; Teisson, 1982).

To date, it is well established that large marine ecosystems (LME) have been continuously warming during the 1982–2006 period, and to a lesser extent the California and Humboldt LME (Belkin, 2009), also including eastern boundary upwelling systems. In California, thermal trends are extremely variable within sub-regions, as noted by Mendelssohn and Schwing (2002) between 1945 and 1990, whereas global warming is evident across the 1950–2000 period in this system (Sydeman et al., 2014). Based on in situ data, surface temperature in the Canary Current large marine ecosystem (CCLME) increased by 0.52°C from 1982 to 2006 (Belkin, 2009) and between 0.50 and 0.75°C from 1950 to 2000 (Harrison & Carson, 2007). Remote sensing observations also showed that this warming is spatially heterogeneous, particularly in the Southern part of the CCLME (Demarcq, 2009). Recent updates (A. Sarre et al., personal communication, March 2017) show extreme warming rates of 0.5°C per decade from 1982 to 2015 in the Mauritanian and Senegalese region. A depletion of phytoplankton biomass is usually associated with this warming (i.e., Richardson & Schoeman, 2004), even if moderate and spatially restricted to Mauritania and Senegal from 1998 to 2014 (Demarcq & Benazzouz, 2015). Therefore, such changes might influence the recruitment success of small pelagic fish populations (Chassot, Floch, Dewals, Pianet, & Chavance, 2011; Longhurst, 2010; Moore, Harvey, & Van Niel, 2009; Oliver & Irwin, 2008).

Round sardinella (*Sardinella aurita*) and flat sardinella (*Sardinella maderensis*), the only *Sardinella* sampled in the Senegalese area, account for more than 80% of the Senegalese artisanal fisheries total landings (Diankha et al., 2017; FAO, 2012), which are marked by strong seasonal and interannual fluctuations (Thiaw et al., 2017). Both species have short-lived, zooplankton feeders with similar shape and size (maximum fork length ~30 cm; Ba et al., 2016), and occupy almost the same geographical areas over the Senegalese continental shelf (Cury & Fontana, 1988). However, these species have some physiological differences. *Sardinella aurita* undergoes an intensive seasonal migration from Morocco to Guinea passing through Mauritania, Senegal and Gambia due to the spatial variability and strong seasonality of the Senegalo-Mauritanian Upwelling System (Boëly, 1980; Boëly & Fréon, 1979). This seasonal displacement makes its spawning heterogeneous, which occurs preferentially over the Arguin Bank (Mauritania) and the south of Cap-Vert (Senegal; Boëly, Chabanne, & Fréon, 1978; Boëly, Chabanne, Fréon, & Stéquert, 1982; Conand, 1977; Tiedemann &

Brehmer, 2017). The migration of *S. maderensis* is less marked around its nursery area (Boëly, 1982; Cury & Fontana, 1988), suggesting that this species is able to adapt more readily to environmental variations. *Sardinella maderensis* is less sensitive to climatic/environmental fluctuations than *S. aurita* and has a less flexible adaptive strategy resulting in a smaller plasticity of their biological parameters (Ba et al., 2016). Moreover, *S. maderensis* showed smaller variability of biological and demographic parameters than *S. aurita* (Cury & Fontana, 1988).

Several studies attempted to investigate the dynamic of sardinella populations in relation to environmental change. Sabatés, Martin, Lloret, and Raya (2006) showed that abundance of *S. aurita* in West Mediterranean waters is positively correlated to sea surface temperature (SST). In Mauritanian waters, it has been demonstrated that high abundance of *S. aurita* is associated with SST below 21°C (Zeeberg, Corten, Tjoe-Awie, Coca, & Hamady, 2008). Diankha, Wade, et al. (2015) suggested that important catches of *S. aurita* in Senegalese waters occur with SST ranges of 22–24°C. Recently, Bacha, Jeyid, Vantrepotte, Dessailly, and Amara (2016) demonstrated that a high part of the catch variability of *S. aurita* in Mauritanian waters could be associated with SST variations. New investigations carried out by Thiaw et al. (2017) showed that the variations in sardinella biomass in Senegalese waters were driven by environmental conditions. Similar studies on the second sardinella, i.e., *S. maderensis*, are scarce.

However, it is worth highlighting that the assessment of reliable abundance indices of small pelagic fish from artisanal fisheries landings remains complex (Ould Talib Sidi, 2005). It relies on parameters difficult to estimate such as the fishing effort (Mangel & Bede, 1985), particularly in the artisanal sector targeting the sardinella which are mainly targeted when occurring in fish school structures (Brehmer et al., 2007). The approach used in this study avoids misleading interpretation due to eventual bias in the catch per unit of effort (CPUE) estimation because the number of trips (outings) considered as fishing effort is not a proxy of the real effort. Moreover, the relationships between pelagic habitats and marine resources are fairly complex due to of their fundamentally non-linear characteristics (Boëly, 1982; Rothschild, 2000). This is why links between the fluctuations of environmental conditions and the abundance of sardinella is still not well understood and difficult to predict for management and decision making support.

This study contributes to a better understanding of the relationships between environmental variability and the local abundance fluctuations of sardinella. It aims to define the environmental conditions associated with recruitment success of *S. aurita* and *S. maderensis* in Senegalese waters, based on the monitoring of landings per size classes. The influence of four environmental variables on the recruitment of both species is tested and quantified over one decade.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is the Senegalo-Mauritanian upwelling system (Figure 1), a part of the Canary Current Large Marine Ecosystem

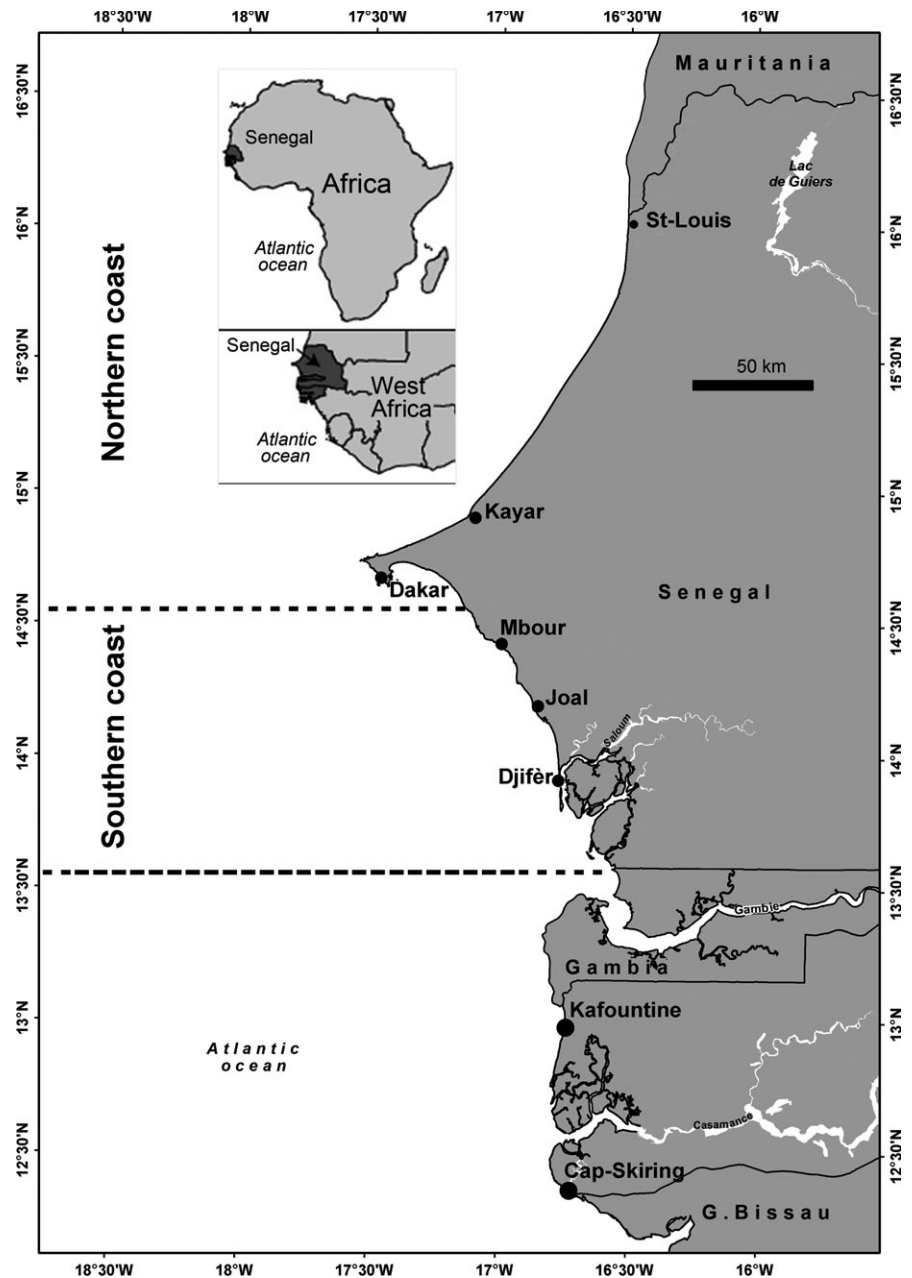


FIGURE 1 Map of the study area situated on the Senegalese coast showing the main sardinella landing ports. The landing ports are grouped by sub-region: the northern coast (e.g., Saint-Louis, and Cayar), the Dakar region (e.g., Yoff, Ouakam, Soubédioune and Hann) and the south of the country (Mbour and Joal; reproduced from Thiaw et al., 2017)

(CCLME), influenced by the Canary Current (CC) flowing along the African coast from north to south between 30°N – 10°N and offshore to 20°W (Fedoseev, 1970). This upwelling system begins in late autumn and ends in spring (Teisson, 1982). In the region north of Dakar, where the continental shelf is narrow, the upwelling occurs near the coast, while south of Dakar characterized by a larger continental shelf and the upwelling is a trapped cold water tongue in the middle of the continental shelf surrounded by warmed waters (Ndoye et al., 2014). The Senegalese upwelling is marked by great seasonal and interannual variability thought to have effects on small pelagic fish (Bakun, 1996; Cury & Roy, 1987; Fréon, 1991; Fréon & Mendoza, 2003).

2.2 | Biological fisheries data for both *Sardinella*

Landing data per size classes were used to estimate sardinella recruitment applying the virtual population analysis (VPA) cohort modeling technique widely used in fisheries science (Jones, 1984; Lassen & Medley, 2001; Pope, 1972). Monthly data were used in this work combining two data sets: (i) total landing of both sardinella species from artisanal fishing over the period 2004–2013. This data set was extracted from the database of the national Senegalese fisheries and oceanographic center the CRODT (Centre de Recherche Océanographique Dakar-Thiaroye), collected from the main Senegalese landing ports: Saint-Louis, Cayar, Yoff, Ouakam, Soubédioune, Hann, Mbour Joal, Foundiougne and Kafountine (Figure 1).

The number of trips per fishing gear was recorded on a daily basis, while landings data were randomly collected for about 5 days a week. After aggregating the data by port, gear and period (fort-nightly), total landings per port were estimated by multiplying mean landings of sampled trips by the total number of fishing trips (Chaboud et al., 2015; Thiao, 2009). Note that landings were summed per month for each landing port (Chaboud et al., 2015; Thiao, Ngom, & Thiam, 2012). (ii) A secondary data set was only used for the VPA, the monthly size distributions of both species from the same landing ports within a period of 15 months between July 2014 and September 2015. The total number of measured individuals was 96,963 split between 51,295 individuals of *S. aurita* and 45,668 individuals of *S. maderensis*. It is worth mentioning that fish samples were randomly taken while individual weights as well as size were recorded. To estimate the recruitment from VPA, the number of individuals per size classes is first transformed into size frequencies. Missing data were then substituted by the average of the corresponding missing month of the time series for the same fishing port. We assume that all monthly landings were distributed according to this average size frequency per fishing port. Then we used a size-age key to convert size class data into seasonal age groups by applying the growth equation of von Bertalanffy (Matsinos & Wolff, 2001) using the growth parameters of sardinella (Fréon, 1988). Seasonal time step (winter: January–March, spring: April–June, summer: July–September and autumn: October–December) was chosen to consider biological characteristics of both species, fast growth and short life cycle (Boëly, 1980). Seasonal and interannual sums were also computed.

2.3 | Environmental variables

Monthly data concerning five environmental variables often applied to investigate relationships between fish abundance and environmental conditions (Bacha et al., 2016; Cury & Roy, 1989; Klemas, 2012; Thiaw et al., 2017) were used in our study: sea surface temperature (SST, in °C), chlorophyll-*a* concentration (Chl-*a*, in mg/m³), wind-induced turbulence (WTI, in m³/s³) and a Coastal Upwelling Index (CUI, in m³/s³ per meter of coast) deduced from wind data and North Atlantic Oscillation index (NAO). Except NAO, all variables were averaged from the coast to the 200 m isobaths, i.e., over almost all the Senegalese sardinella habitat, the continental shelf from 12 to 17°N (Figure 1). Their seasonal and interannual means were also computed.

SST is commonly used to investigate relationships between environment and fish abundance (Kellogg & Gift, 1983; Ramos, Santiago, Sangra, & Canton, 1996). Chl-*a* is considered as an index of biological productivity (Lorenzen, 1970) and a proxy of food abundance. In this work, we used the Aqua-MODIS "Level 2" SST and Chl-*a* data from January 2004 to December 2013 obtained from the NASA Goddard Space Flight Center (GSFC) through the NASA web site (<http://oceancolor.gsfc.nasa.gov>). The spatial resolutions of these data were 4 km.

Wind speed data (m/s) from January 2004 to December 2013 were obtained from the historic reanalysis wind data, from the National Center for Environmental Prediction and the National

Center for Atmospheric Research (NCEP/NCAR, 2.5° resolution). We defined the WTI as the cube of the wind speed, similarly to early ecological studies (Bacha et al., 2016; Ueyama & Monger, 2005). CUI were estimated from the equation:

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

where τ is the along shore component of wind stress within the coastline (from Saint-Louis to Joal), ρ_w is the seawater density (1,025 kg/m³) and f is the Coriolis parameter ($2\Omega \sin(\theta)$), with Ω and θ equal to the Earth's angular velocity and latitude, respectively).

The NAO is considered to be the most important mode of atmospheric variability over the North Atlantic Ocean, and plays a major role in weather and climate variations over the North Atlantic continent (Hurrell, 1995, 1996). For this study, monthly time series of NAO indices were downloaded from the year 2004 to 2013, from the website of NOAA (US National Environmental and Atmospheric Administration, <http://www.noaa.gov/>).

2.4 | Statistical modeling approach

The general additive model (GAM) of Hastie and Tibshirani (1986) was used: (i) to quantify the contribution of the climatic variables; and (ii) to investigate ranges of each environmental variable associated with high recruitment success. Unlike in general linear models (GLM), GAM do not require any prior assumption on the functional link between each variable and the recruitment index. These relationships are modeled with continuous smoothing functions. The dependent variables (*S. aurita* and *S. maderensis* recruitment) were modeled as the additive sum of non-parametric functions of covariates. The explanatory variables included in the model were: SST, Chl-*a*, WTI, CUI and NAO. The "mgcv" package in the R software (Wood, Scheipl, & Faraway, 2013) was used. The Gaussian distribution and the smoothing function "ti" were applied because they provided the most natural fit for the transformed recruitment data after a stepwise procedure. It ("ti") excludes the basic functions associated with the "main effects" of the marginal smooth, plus interactions other than the highest order specified (Wood et al., 2013). The degree of freedom for each spline smoother was set to 4 to avoid overfitting. The time unit for environmental variables is season as recruitment was estimated by season in order to consider the biology of these species (Boëly, 1982). The seasonal and interannual means of these five variables were also computed.

The GAM applied for each species was formulated as:

$$\begin{aligned} \text{Model} = \text{gam}(\text{recruitment}) \sim & \text{ti}(\text{SST}, k = 4) + \text{ti}(\text{Chl-}a, k = 4) \\ & + \text{ti}(\text{WTI}, k = 4) + \text{ti}(\text{CUI}, k = 4) + \text{ti}(\text{NAO}, k = 4), \quad (2) \\ \text{data} = & \text{input data, family} = \text{Gaussian}. \end{aligned}$$

The date included in the model consisted of seasonal data from 2004 to 2013, so the number of observations are $n = 40$.

The relative importance of each variable in the total deviance was determined from the "relaimpo" R package (Tonidandel & LeBreton, 2011). The application of this package allows the partition of the total explained deviance among the four predictors to better understand the role played by each one.

The variance inflation factors (VIFs) were calculated for all environmental variables in order to detect possible high dimensional collinearities (Zuur, Elena, & Chris, 2010). In fact, it was suggested by these authors that covariates with VIFs >5 are highly collinear. However, all VIF values calculated here were <2.

3 | RESULTS

3.1 | Variability of *Sardinella aurita* and *S. maderensis* recruitment

Sardinella recruitment in Senegalese waters is characterized by a marked seasonal variability (Figure 2a,b). For both species, the recruitment showed maximum and minimum values in summer and winter, respectively. According to their interannual variability, the highest *S. aurita* recruitments were observed in summer and spring in 2007 and 2009, respectively (Figure 2c). The lowest recruitment

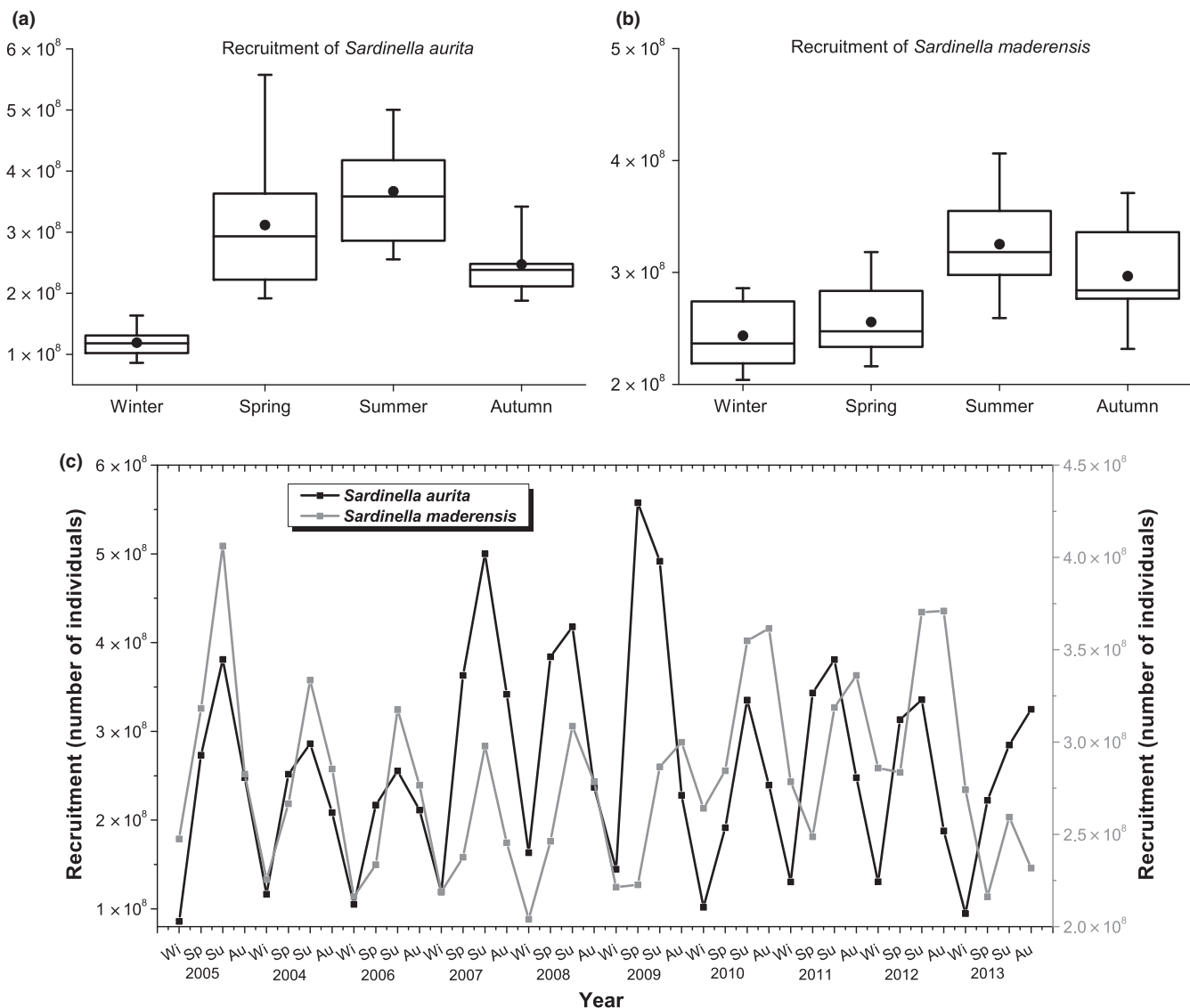


FIGURE 2 (a and b) Boxplots of seasonal variability of *Sardinella aurita* and *Sardinella maderensis* recruitment in Senegalese waters from January 2004 to December 2013, respectively. The whiskers correspond to the minima and maxima, the horizontal lines and the black dots in the boxes are the median and the mean, respectively. (c) Interannual variability of *Sardinella aurita* recruitment (black line) and *Sardinella maderensis* recruitment (grey line) in Senegalese waters from January 2004 to December 2013. The black and grey dashed lines correspond to the fitting curves for *S. aurita* and *S. maderensis*, respectively. Wi, Winter (January–March); Sp, Spring (April–June); Su, Summer (July–September) and Au, Autumn (October–December)

of *S. aurita* was noted in winter in 2004. For *S. maderensis*, the highest recruitment was recorded in summer 2004, and the lowest in winter in 2008 and 2013 (Figure 2c). The recruitment is synchronous (and decreasing) for both species until 2006, while from 2007 no synchrony is observed.

3.2 | Variability of the environmental variables

Except for the NAO index, the other tested variables showed that Senegalese waters are characterized by a strong season to season variability in environmental parameters (Figure 3). SST showed a maximum and a minimum in summer and winter, respectively (Figure 3a). The Chl-*a* showed a downward trend with a peak in spring and minimum values in autumn (Figure 3b). Maximum and minimum values of WTI and CUI are associated with winter and summer seasons, respectively (Figure 3c,d).

The interannual variability of these variables shows a marked pattern. The SST showed that summer in 2005 and winter in 2009 were the warmest and coldest periods of our time series (Figure 4). The summers in 2006, 2011 and 2010 corresponded to periods of lowest primary production while the highest values were recorded in spring 2011 and 2012 (Figure 5). The WTI time series variability showed higher values in winter in 2009 and 2011, and lower in summer in 2006 and 2009 (Figure 6). With respect to CUI interannual variations, the weakest intensity in winter occurred in 2008, while the strongest were recorded in 2009 and 2011 (Figure 7). As for the

NAO year to year variation, the lowest and highest values were associated with spring and autumn 2008 and 2011, respectively (Figure 8).

3.3 | Effect of the environmental variables on *S. aurita* recruitment

The relationships between *S. aurita* recruitment and the selected variables generated by the GAM showed that each variable had a specific influence on *S. aurita* recruitment (Figure 9, first row). SST showed a positive effect on *S. aurita* recruitment between 22.0 and 28.5°C (Figure 9a). A positive effect of the Chl-*a* occurs for low values (≤ 3.3 mg/m³) and high values (Figure 9b). The influence of WTI is positive for values < 150 m³/s³ (Figure 9c) while CUI showed a similar positive effect up to 1.4 m³ s⁻³ m⁻¹ (Figure 9d). The effect of NAO on *S. aurita* recruitment is dome-shaped with positive effect between -1 and 0.5 (Figure 9i). The year to year variability of the effects of the environmental variables deduced from the GAM indicates that the highest effect of the variables occurred between 2008 and 2009 (Figure 10, first row). The model reveals that the five environmental variables explained 77.6% of the deviance (Table 1a). The CUI alone explains 36.7% (55% of the total contribution). SST and WTI were the second and third most important variables explaining 16.4% and 14.5% of the variability of *S. aurita* recruitment, respectively. Chl-*a* account for 8.3% of the total deviance. The contribution of NAO is very low, $< 1\%$.

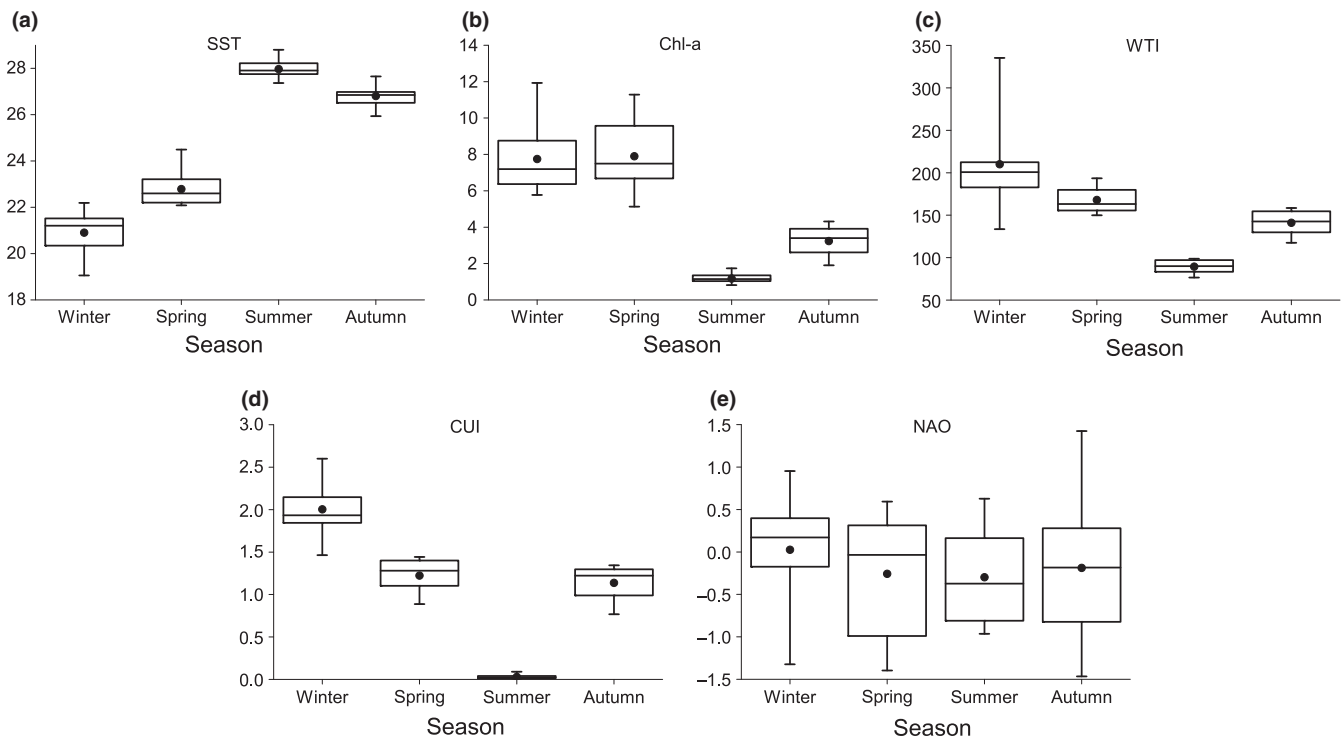


FIGURE 3 Boxplot of seasonal variability of the environmental variables tested (SST, Chl-*a*, WTI, CUI and NAO) from 2004 to 2013. SST, Sea surface temperature (°C); Chl-*a*, concentration of chlorophyll-*a* (mg m⁻³); WTI, wind-induced turbulence index (m³/s³); CUI, coastal upwelling index (m³/s³ per meter of coast); NAO, North Atlantic oscillation index. The whiskers correspond to the minima and maxima, the horizontal lines and the black dots in the boxes are the median and the mean, respectively

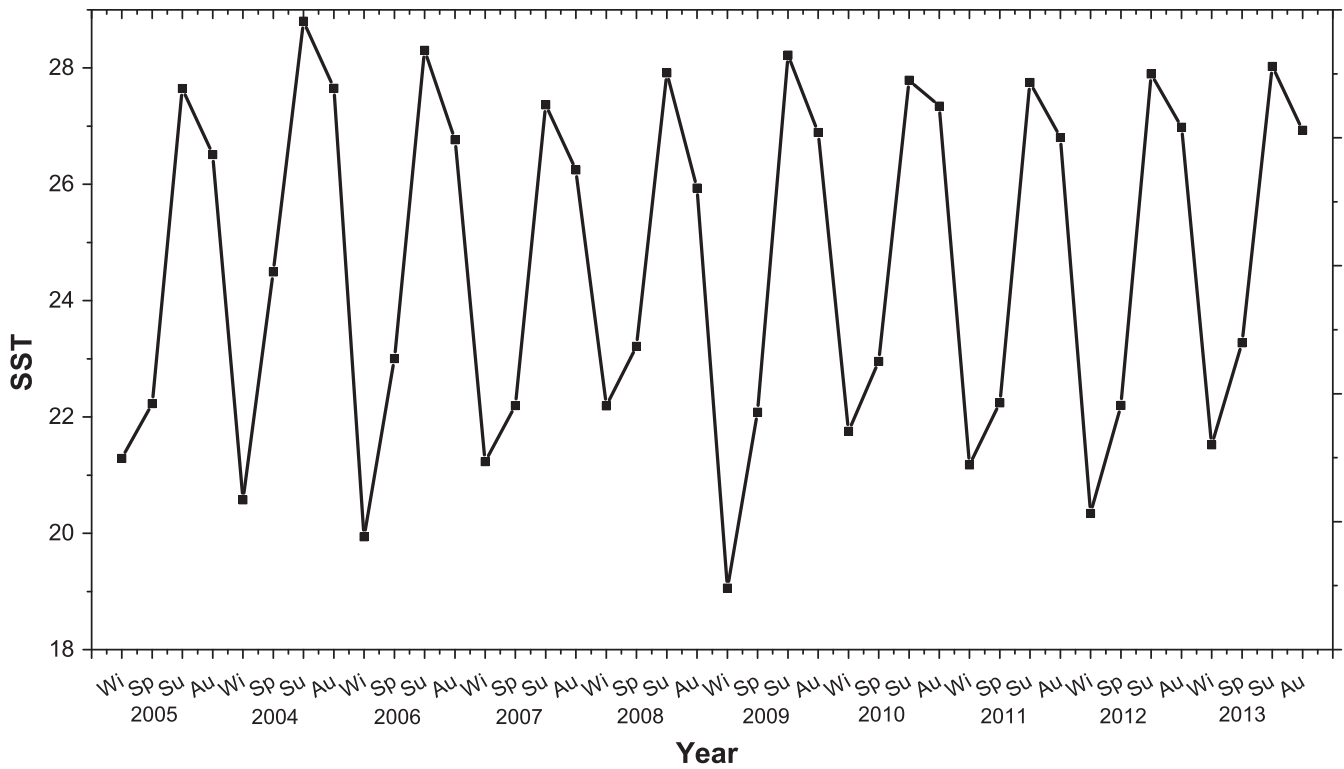


FIGURE 4 Interannual variability of the sea surface temperature (SST, °C) from 2004 to 2013. Wi, Winter (January–March); Sp, Spring (April–June); S, Summer (July–September); Au, Autumn (October–December)

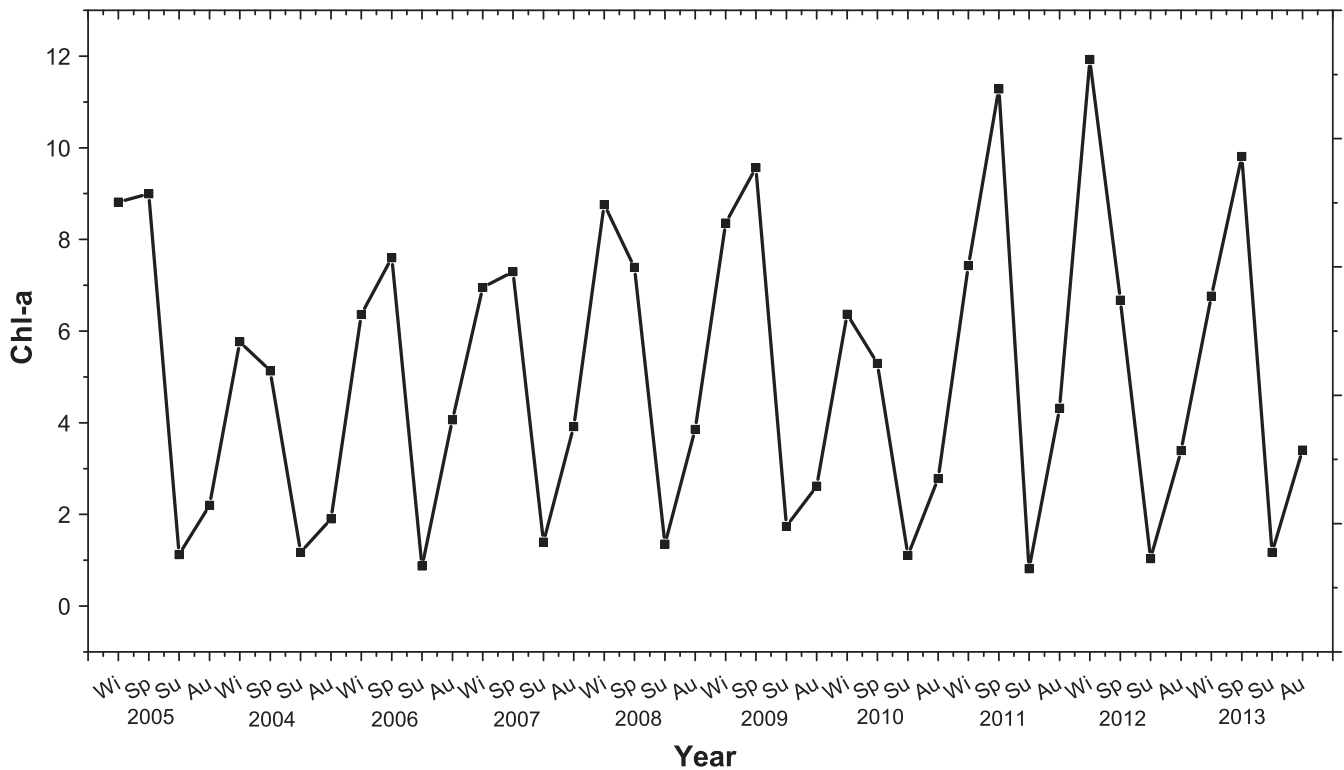


FIGURE 5 Interannual variability of the concentration of chlorophyll-a (Chl-a, mg m⁻³) from 2004 to 2013. Wi, Winter (January–March); Sp, Spring (April–June); Su, Summer (July–September); Au, Autumn (October–December)

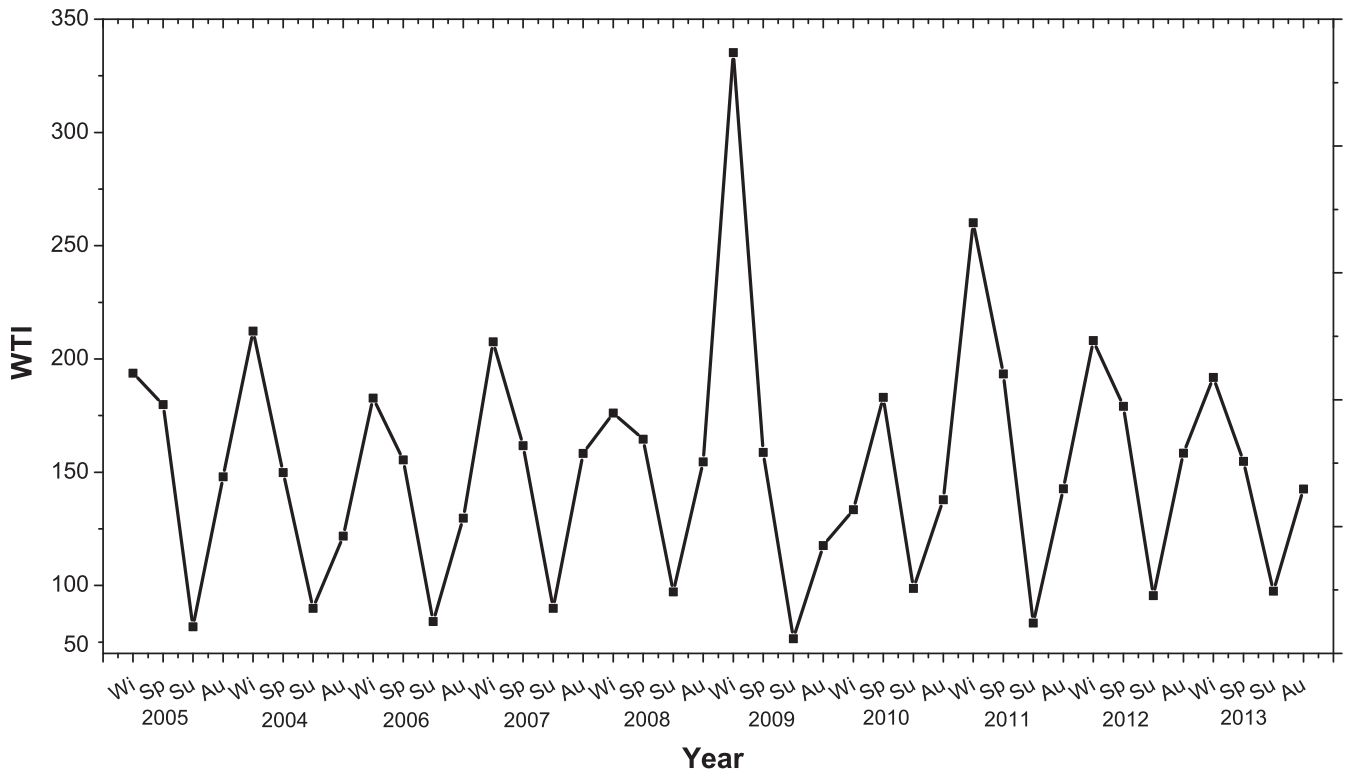


FIGURE 6 Interannual variability of the wind-induced turbulence index (WTI, m^3/s^3) from 2004 to 2013. Wi, Winter (January–March); Sp, Spring (April–June); Su, Summer (July–September); and Au, Autumn (October–December)

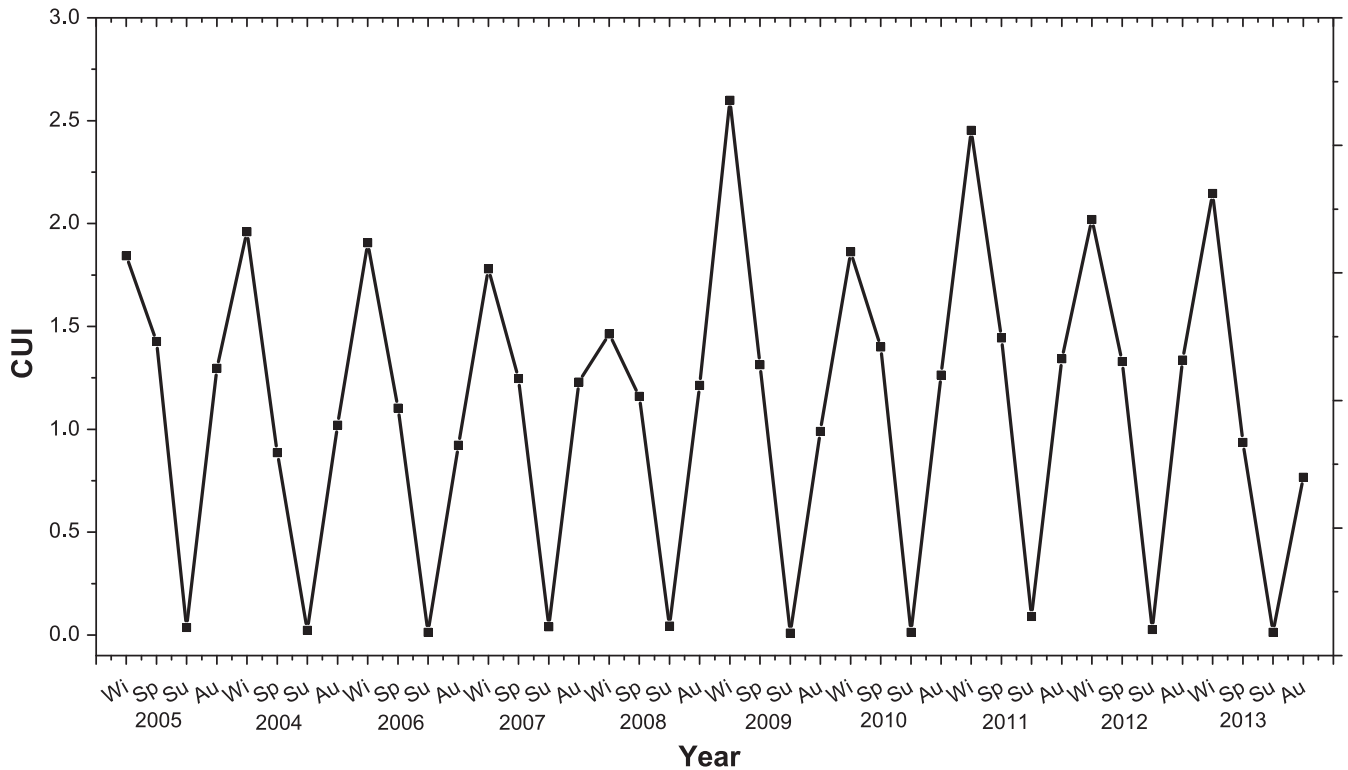


FIGURE 7 Interannual variability of the coastal upwelling index (CUI, m^3/s^3 per meter of coast) from 2004 to 2013. Wi, Winter (January–March); Sp, Spring (April–June); Su, Summer (July–September); and Au, Autumn (October–December)

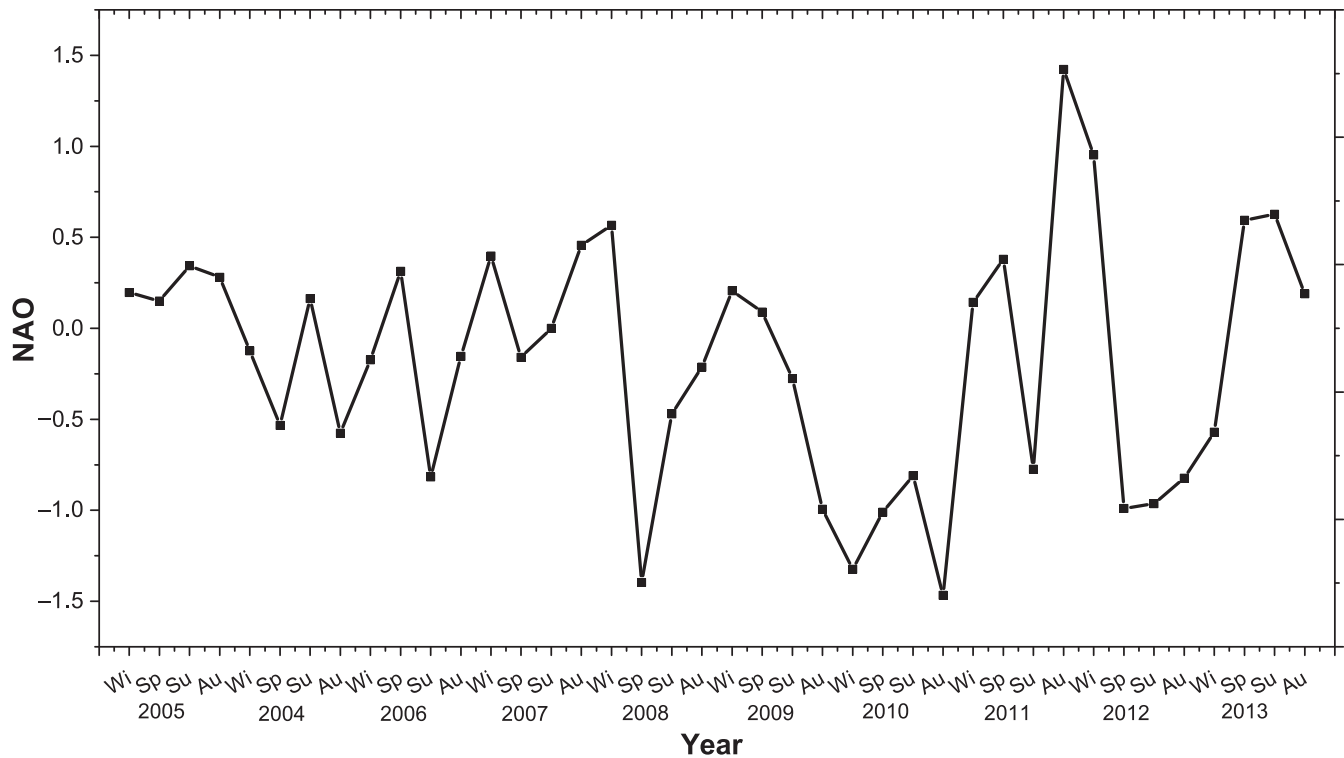


FIGURE 8 Interannual variability of the North Atlantic oscillation index (NAO) from 2004 to 2013. Wi, Winter (January–March); Sp, Spring (April–June); Su, Summer (July–September); Au, Autumn (October–December)

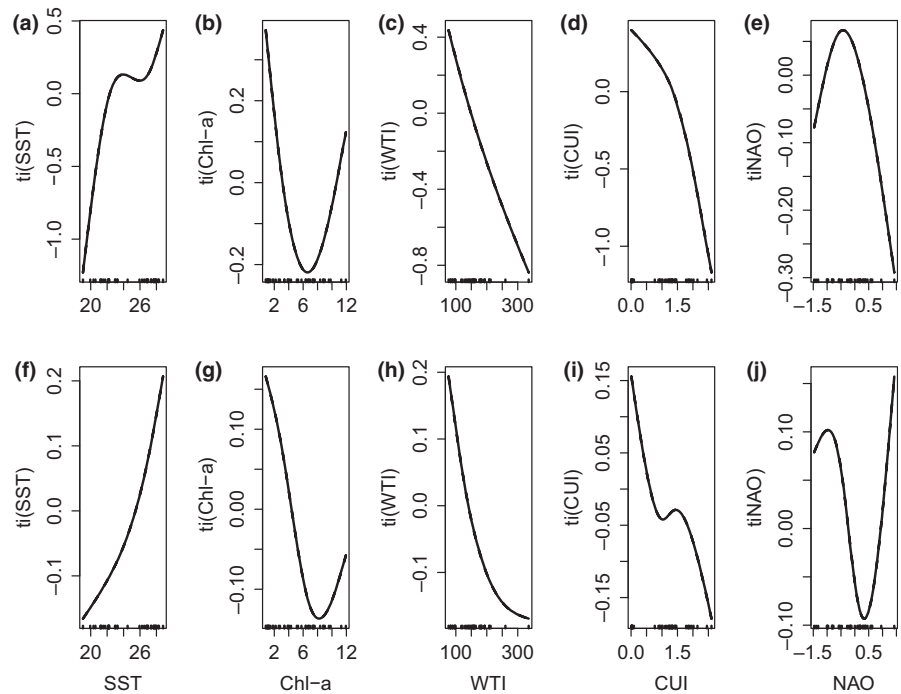


FIGURE 9 General additive model GAM-derived effect of environmental variables (SST, Chl-*a*, WTI, CUI and NAO) on *Sardinella aurita* (first row) and *Sardinella maderensis* (second row) recruitment from January 2004 to December 2013. SST, sea surface temperature (°C), Chl-*a*, concentration of chlorophyll-*a* (mg m^{-3}); WTI, wind-induced turbulence index (m^3/s^3); CUI, coastal upwelling index (m^3/s^3 per meter of coast); NAO, North Atlantic oscillation index; “ti”, smoother function used

3.4 | Effect of the environmental variables on *S. maderensis* recruitment

The shapes of the relationship between variables SST and CUI and *S. maderensis* recruitment generated with the GAM (Figure 9, second row) are quite different from those obtained for *S. aurita* (Figure 9,

first row), while that with Chl-*a* and WTI are similar. Indeed, high recruitment is associated with high SST i.e., above 25°C (Figure 9e), instead of 22°C for *S. aurita*. High recruitment of *S. maderensis* is associated with low Chl-*a* (<4.4 mg/m^3) on the continental shelf, while a negative effect occurred above this value (Figure 9f). Positive effect of WTI is recorded for values <140 m^3/s^3 (Figure 9g). Values

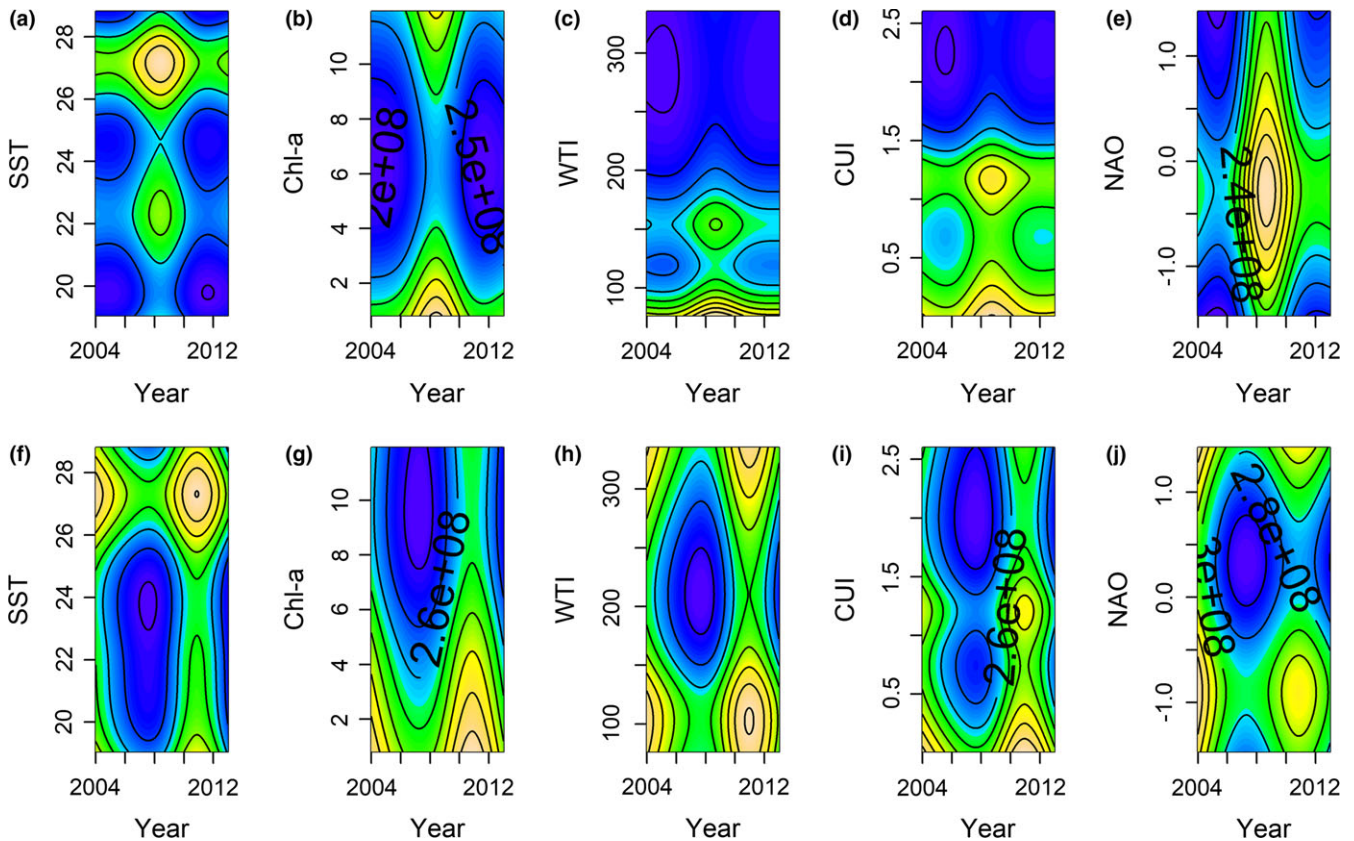


FIGURE 10 General additive model derived effect of interactions between environmental variables (SST, Chl-*a*, WTI, CUI and NAO) and temporal variable (year) on *Sardinella aurita* (first row) and *Sardinella maderensis* (second row) recruitment from 2004–2013. SST, sea surface temperature (°C); Chl-*a*, concentration of chlorophyll-*a* (mg m^{-3}); WTI, wind-induced turbulence index (m^3/s^3); CUI, coastal upwelling index (m^3/s^3 per meter of coast); NAO, North Atlantic oscillation index. Color code: blue, negative effect; green, non-significant effect; yellow and red, positive effect. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Generalized additive model (GAM) derived deviances corresponding to the quantified effect of each oceanic variable on (a) *Sardinella aurita* and (b) *Sardinella maderensis* recruitment (2004–2013)

Variable	Significance	Explained deviance (%)	Total explained deviance (%)
(a)			
CUI	<<.001	36.7	76.7
SST	<<.001	16.4	
WTI	<<.001	14.5	
Chl- <i>a</i>	<<.001	8.6	
NAO	<<.001	0.5	
(b)			
SST	<<.001	20.4	66.1
WTI	<<.001	15.9	
Chl- <i>a</i>	<<.001	14.2	
CUI	<<.001	10.5	
NAO	<<.001	5.1	

SST, Sea surface temperature (°C); Chl-*a*, chlorophyll concentration (mg/m^3); WTI, wind-induced turbulence index (m^3/s^3); CUI, Coastal upwelling index (m^3/s^3 per meter of coast); NAO, North Atlantic Oscillation index.

below $0.7 \text{ m}^3 \text{ s}^{-3} \text{ m}^{-1}$ for CUI are associated with high *S. maderensis* recruitment (Figure 9h). The effect of NAO on *S. aurita* recruitment is different from that on *S. maderensis* recruitment. Negative effect of NAO is observed between -0.2 and 1.0 (Figure 9j). The interannual variability of the effect of all variables (Figure 10, second row) shows that the environmental effects are more favorable to recruitment during two periods over the considered decade: 2004–2005 and 2010–2012. The results of the GAM (total and partial deviances) are summarized in Table 1b; the total explanation reaches 66.1% of the variation in *S. maderensis* recruitment during the study period. SST accounts for 20.4% of the total variability and is the most determinant factor. Others factors are, WTI, Chl-*a*, CUI and NAO which support 15.9%, 14.2%, 10.5% and 5.1%, respectively.

4 | DISCUSSION

The originality of this study relies on the use of recruitment estimations from the VPA method to investigate the influence of environmental conditions on the natural variability of sardinella in Senegal combined with a GAM. Previous studies were only based on CPUE

data which strongly depends on fishing effort reliability, a parameter difficult to quantify (Mangel & Bede, 1985), especially for Senegalese artisanal fisheries where the unit of effort is expressed in number of outings. This does not reflect the real changes in fishing effort due to, for example, the non-consideration of the increase of distance traveled by the canoe and fishing activity duration, as reported in Ba et al. (2017). Moreover, the quick and important development of the Senegalese artisanal fishery sector, along with structural and conjec-tural changes, makes the choice difficult for the fishing effort unit. The use of the VPA may be limited by several sources of potential uncertainties, mainly related to catch extrapolations, assessment of discards and estimation of fishing mortalities used to initiate the cohort analysis (Gascuel, 1994). In our case, because of their high demand in the fish market, discards of sardinella are not frequent. Therefore, biases related to the distribution of catches by age class could be assumed to be negligible. Moreover, the sardinella are migratory species and the two main nursery areas are situated in Mauritania (banc d'Arguin) and Senegal (petite cote); thus the sam-pling had covered a complete annual cycle, and such facts confirm our assumption that the whole populations have been sampled.

Results show that sardinella recruitment, like the environmental variables, are characterized by strong temporal variability. Both sardinella show similar seasonal variation in recruitment with a minimum and maximum in winter and summer, respectively. Winter and summer are opposite hydrological seasons. In Senegalese water, winter is char-acterized by cold waters, strong wind-induced turbulence and upwel-ling intensity, while the opposite occurs in summer. These results seem to suggest that at this stage, sardinella prefer oceanographic conditions in the summer. These results are in accordance with previ-ous studies which suggest that variability in abundance and distribu-tion of sardinella is mainly under the influence of oceanographic changes, such as cooling or warming waters (Bacha et al., 2016; Sabatés et al., 2006; Thiaw et al., 2017; Zeeberg et al., 2008).

This study is consistent with the findings of previous work which showed that the dynamics of small pelagic are closely linked to oceanographic conditions (Bacha et al., 2016; Bakun, 1996; Cury & Roy, 1989; Diankha, Thiaw, et al., 2015; Diankha, Wade, et al., 2015; Fréon, 1991; Fréon & Mendoza, 2003; Thiaw et al., 2017). The use of GAM, which takes into account the potentially complex non-linear relationships between the covariates, allowed a better illustration of the links between *S. aurita*, as well as *S. maderensis* and the oceanographic conditions in off Senegal. The environmental variables considered in this work (SST, Chl-*a*, WTI CUI and NAO) were responsible for 76.7% and 66.1% of the variability of *S. aurita* and *S. maderensis* recruitments, respectively. The CUI and SST together accounted for 53.1% and 30.9% of the total explained vari-ance for *S. aurita* and *S. maderensis*, respectively. Our results are in accordance with those found in Mauritanian waters, showing that SST and CUI were also the main environmental parameters explain-ing the variability of *S. aurita* (Bacha et al., 2016). The CUI played the major role in *S. aurita* recruitment variability, while for *S. maderensis* the SST was the key factor. However, SST was the second most important variable in *S. aurita* recruitment variability.

The role of the upwelling intensity on *S. aurita* abundance was already well established (Bacha et al., 2016; Braham et al., 2014; Diankha, Thiaw, et al., 2015; Mbaye et al., 2015). Nevertheless, to our knowledge, studies quantifying the effect of upwelling intensity on *S. maderensis* abundance have not previously been reported. The effect of SST and CUI does not hide the influence of Chl-*a* and WTI which had significant effect on both sardinella recruitment success in this study. These observed differences might be due to their physio-logical characteristics which are relatively distinct: *S. aurita* is more sensitive to temperature and salinity fluctuation than *S. maderensis*, which tolerate higher change in salinity and temperature (Ba et al., 2016; Cury & Fontana, 1988). This is also explained by the fact that, even if both species occupy the same area in Senegal (Cury & Fon-tana, 1988), their relative abundance strongly differs between North-ern Senegal (in connection with Mauritania) and Southern Senegal (Capet et al., 2016; Ndoye et al., 2014), warmer and less sensitive to the detrimental effects of a strong upwelling season.

The role of temperature on small pelagic fish stock dynamics has been previously reported (Pepin, 1991). Temperature always affects fish populations at different stages of their life cycles, including dur-ing spawning and the development and survival of the eggs and lar-vae, as well as influencing their distribution, diet, migration pattern and schooling behavior (Gordoa, Maso, & Voges, 2000; Laevastu & Hayes, 1981; Sund, Blackburn, & Williams, 1981). Several studies have shown that abundance of sardinella is related to SST variability (Bacha et al., 2016; Diankha, Wade, et al., 2015; Sabatés et al., 2006; Thiaw et al., 2017; Zeeberg et al., 2008). However, *S. maderensis* is more associated with warmer waters (>24°C), as shown by Boëly (1979), than *S. aurita*. Furthermore, the ideal bal-ance between a moderate upwelling and warmer waters in Southern Senegal highly favors *S. maderensis* recruitment and its abundance, and makes it predominantly sensitive to environmental thermal varia-tions and prey abundance with a low direct dependency of the upwelling intensity, whose detrimental effects are low in this region, characterized by a high physical retention capability of eggs and lar-vae (Demarcq & Faure, 2000; Mbaye et al., 2015; Roy et al., 1989).

The landings of small pelagic fish in the Pacific may be related to Chl-*a* (Ware & Thomson, 2005) and the influence of Chl-*a* is more important on sardine (*Sardina pilchardus*) than on *S. aurita* in Maurita-nia (Bacha et al., 2016). We also found a moderate influence of Chl-*a* on the recruitment success of *S. aurita* because its variability seems to be partly hidden by the upwelling intensity, whose effect is a direct increase of the primary production. The apparently higher influence of Chl-*a* (14.2%) for *S. maderensis* is explained by the low influence of the upwelling intensity, and despite the fact that its pre-ferred habitat (Southern Senegal) is almost constantly enriched by both the coastal upwelling and a potential local enrichment from coastal estuaries (e.g., Saloum, Gambia mouth, Casamance river) and a much wider continental shelf versus Northern Senegal.

It is worth highlighting that the low effect of the North Atlantic Oscillation index (NAO; explaining 0.5% and 5% of *S. aurita* and *S. maderensis* recruitment variability, respectively), does not mean that its influence was negligible. We hypothesize that its influence

on sardinella was not adequately taken into account in our GAM formulation, or was expressed through another variable. In fact, several studies suggested NAO influence on marine resources were generally reflected through its effect on SST (Caballero-Alfonso et al., 2010; Diankha, Wade, et al., 2015; Ottersen, Planque, Post, Reid, & Stenseth, 2001). These findings are in accordance with this study because the effect of SST on *S. aurita* increased when NAO took into account the global model. However, findings in this study are in contrast with Thiaw et al. (2017) who found that abundance indices for both sardinella species respond to the winter NAO index. The difference with the environmental correlations we found with recruitment may be attributed to two factors. First, the average adult spatial distribution and migration patterns at the sub-regional scale may change according to large scale climate indices such as NAO, without necessarily impacting the local (national) favorability for recruitment. Second, since 2004 fishing agreements were passed with surrounding countries, especially with Mauritania, so that Sardinella landed in Senegal may contain catch outside the Senegalese Exclusive Economic Zone (EEZ; Thiaw et al., 2017).

This study highlights the existence of distinct ranges of SST, Chl-*a*, WTI, CUI and NAO associated with successful recruitment of *S. aurita* and *S. maderensis* in Senegalese waters (i.e., distinct optimal environmental windows; Cury & Roy, 1989). Indeed, higher recruitment of *S. aurita* and *S. maderensis* was associated with low upwelling intensity ($<2 \text{ m}^3 \text{ s}^{-3} \text{ m}^{-1}$ for *S. aurita* and $<1 \text{ m}^3 \text{ s}^{-3} \text{ m}^{-1}$ for *S. maderensis*), with SST ranging from 22 to 28°C for *S. aurita* and from 26 to 28°C for *S. maderensis*, low Chl-*a* ($<3 \text{ mg/m}^3$ for *S. aurita* and $<4 \text{ mg/m}^3$ for *S. maderensis*) and WTI $<150 \text{ m}^3/\text{s}^3$ for *S. aurita* and $<140 \text{ m}^3/\text{s}^3$ for *S. maderensis*. In Bacha et al. (2016), SST above 24°C positively affects the abundance of *S. aurita* in Mauritanian waters and it has been established that some species avoid entering the coldest upwelling zone (SST between 15 and 21°C; Zeeberg et al., 2008). Unfavorable conditions mainly include low temperature having a negative effect on their growth (Cole & McGlade, 1998). In addition, it was suggested that a marine environment with Chl-*a* above 0.2 mg/m^3 could support sustainable fisheries (FAO, 2003; Gower, 1986). The pioneering work of Cury and Roy (1989) suggested that in upwelling areas there is an optimal wind speed value outside which recruitment success is lower. However, such optimal wind speed values are different from those found in this study. Cury and Roy (1989) highlighted that wind speeds values outside 5–6 m/s (corresponding to WTI from 125 to 216 m^3/s^3) had a negative effect on sardinella CPUE in Senegal, whilst we found a constantly higher recruitment success for low wind values for both sardinella species. This difference is probably due to the use of distinct indices in Cury and Roy (1989), and because they have worked on the *S. aurita* CPUE as abundance index, while our study considered the recruitment.

5 | CONCLUSION

The results obtained on the estimation of *S. aurita* and *S. maderensis* recruitment in Senegalese waters showed how their success is

related to direct environmental conditions and the existence of different ranges of environmental conditions (optimal environmental windows) associated with high recruitment of *S. aurita* and *S. maderensis*. Moreover, both clupeid species present distinct responses to these environmental factors probably because of their different physiological and ecological intrinsic characteristics. The explanations of our variables are unexpectedly high (76.7% and 66.1%). In other words, we obtained a good explanation of recruitment success with only environmental variables that describe the in situ environmental conditions, or habitat of the exploited fish. As sardinella, mainly round sardinella (*S. aurita*), perform strong seasonal migration it suggests that national policy prerogatives for the management of such fisheries should be done at the regional level. Such an approach to facilitate common sub-regional management plans should allow a better mitigation of loss and damage in the fisheries sector in the context of overfishing and climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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