Oceanologia (2021) 63, 1—11

Available online at www.sciencedirect.com

ScienceDirect

journal homepage: www.journals.elsevier.com/oceanologia

OCEANOLOGIA

ORIGINAL RESEARCH ARTICLE

Long term variation of sardine *Sardina pilchardus* spawning along the Atlantic coast of northwest Africa (21—26°N): characterization and spatiotemporal variability in spawning habitat

Hinde Abdelouahab[a,*], **Amina Berraho**[a], **Tarik Baibai**[a], **Jamila Larissi**[a], **Said Charib**[a], **Aziz Agouzouk**[a], **Ahmed Makaoui**[a], **Omar Ettahiri**[a], **Ahmed Errhif**[b]

[a] *Institut National de Recherche Halieutique, Casablanca, Morocco*
[b] *University Hassan II of Casablanca, Faculty of Sciences, Ain Chock, Casablanca, Morocco*

Received 3 February 2020; accepted 25 August 2020
Available online 3 September 2020

KEYWORDS
Sardine;
Spawning habitat;
Environment;
Time series;
Sea surface temperature

Abstract Small pelagic fish such as sardine show strong recruitment variability often associated with environmental changes influencing the spawning process and ultimately, affecting population dynamics. Sardine (*Sardina pilchardus*, Walbaum 1792) is one of the most exploited pelagic species along the northwest African coast. The main spawning occurs during the cold season (autumn—winter). A time-series autumn—winter surveys extending from 1994 to 2015 sampled sardine eggs, along the southern area of the Moroccan Atlantic coast (26°N—21°N) were analyzed. The present work focuses on examining the inter-annual variability of the spawning habitat by analyzing the spatial-temporal variability of sardine egg distribution and density extracted from the data collected over the period 1994—2015. Generalized additive models (GAM) were used to detect the relationships between the sardine distribution, expressed as

* Corresponding author at: Institut National de Recherche Halieutique, 2 Bd Sidi Abderrahmane, Casablanca, Morocco.
E-mail addresses: hind.abdelouahab@gmail.com (H. Abdelouahab), aminaberraho@gmail.com (A. Berraho), baibaitarik@gmail.com (T. Baibai), larissijamila@gmail.com (J. Larissi), saidcharib@gmail.com (S. Charib), oceanosaad@gmail.com (A. Agouzouk), oceanomakaoui@gmail.com (A. Makaoui), omarettahiriomar@gmail.com (O. Ettahiri), aerrhif@gmail.com (A. Errhif).
Peer review under the responsibility of the Institute of Oceanology of the Polish Academy of Sciences.

ELSEVIER Production and hosting by Elsevier

https://doi.org/10.1016/j.oceano.2020.08.006

egg density and the presence or absence data and relevant hydrobiological environmental variables, such as salinity, temperature and zooplankton biomass. The generalized additive models showed significant relationships between the environment variables (SST, SSS and Zooplankton biomass) and sardine density, but not with sardine presence. Given that the study area is characterized by high mesoscale features and significant upwelling activities, the variability of upwelling processes could explain the changes of spawning ground position and thermal window.

1. Introduction

The Moroccan Atlantic coast (36°N—21°N), located in the central canary current system, is characterized by the presence of one of the four world's major coastal upwelling systems with year-round activity (Aristegui et al., 2009; Benazzouz et al., 2015; Makaoui, 2008). In fact, the Moroccan coastal upwelling is evidenced at the surface by cold waters near the coast in response to the intensification of northeasterly winds and Ekman transport along the Moroccan continental shelf. The upwelling process promotes high primary productivity by dispersing nutrients elements and organisms over the surface layer, favoring the blooming of phytoplankton concentration and the decrease in sea surface temperatures in onshore direction. Moreover, the Moroccan upwelling region supports the highest fish abundance, because of high year-round productivity and favorable environmental conditions for larval survival and recruitment (Abdelouahab et al., 2017; Berraho, 2007; Brochier et al., 2009; Ettahiri et al., 2012), the majority of catches are composed of small coastal pelagic similar to those encountered in other coastal upwelling systems, with a domination of the European sardine (*Sardina pilchardus*).

The European pilchard *Sardina pilchardus* (Walbaum, 1792) is an important, commercial pelagic fish species in the north-west coast of Africa and especially in Morocco, with a wide distribution area in the Mediterranean Sea, and the northeastern Atlantic Ocean from the North Sea to Senegal (Parrish et al., 1989). Northern and southern limits seem to be related to the average water temperature, being located within 10 and 20°C isotherm (Furnestin, 1945). Spawning occurs in open waters and larvae remain in plankton for long periods (Olivar et al., 2001). In the Moroccan area, the exploitation of the southern stock started in the late 1950s. Thus, the long-term catch of sardine shows a gradual increase with peaks of landings of sardine in the 1970s followed by a decrease in the 1980s and an increase again in the 1990s to ≈1 million tons per year (Kifani, 1998). The constant exploitation of this resource (for several decades) makes Morocco the leader among the sardine-producer countries (where the total sardine catch represents approximately 80% of the total Moroccan catch in 2017, particularly in the southern region of Morocco, between Cape Blanc (21°N) and Cape Boujador (26°N)). In this area, sardine main spawning season occurs during the cold season from autumn to winter (Abdelouahab, 2018; Berraho, 2007, Ettahiri et al., 2012), and is characterized by high productivity due to the permanent upwelling activity in the area which promotes food availability for larval feeding.

Worldwide, small pelagic fish species stocks, exhibit strong inter-annual fluctuations and instabilities, especially in the upwelling areas (Arístegui et al., 2009; Brochier et al., 2009; Giannoulaki et al., 2013). Many hypotheses have been reported to explain biomass fluctuations. Regardless overfishing, fluctuations may be the effect of climate changes (Alheit et al., 2012; Bonanno et al., 2016; Malta et al., 2016), or other environmental conditions (hydrodynamic circulations, water temperature, nutrient availability), or the location of the spawning habitat which can be a limiting factor for the survival of the eggs. The latter can also impact the juvenile stage and dispersing across different habitats while minimizing predation and maximizing food intake (Ciannelli et al., 2015; Drinkwater et al., 2010; Fréon et al., 2009). However, stock variability of small pelagic appears to be the result of a successful combination of processes enhancing eggs and larval development (Bakun, 2010).

In Morocco, the large fluctuation in the abundance of *Sardina pilchardus* species is one of the current problems of the global fishery management. This research provides information over large spatial and temporal scales, from data collected of sardine egg distribution, over the period 1994—2015, in the southern part of the Moroccan coast (21°N—26°N), which allows the tracking of the influence of the environmental conditions on the distribution of the European pilchard by defining their potential spawning habitat in the Northwest African coastal area.

2. Material and methods

2.1. Study area

In Ichthyoplankton surveys sardine egg sampling was carried out in the southern area of the Moroccan Atlantic coast, along the region Cape Blanc—Cape Boujador (21—26°N) (12 surveys: 1994—2015) (Table 1). Sampling stations were positioned to cover all the region between the coast and the isobaths 1000 m and varying slightly from year to year (Figure 1). The surveys focused mainly on the peak spawning period of sardine in this region (cold season). Ichthyoplankton samples were collected by a small 20 cm diameter bongo net geared with a 417 μm mesh. Plankton oblique

Table 1 Survey period conducted in the study area.

Years	Survey period			
	Season	Begining of the survey	End of the survey	Code
1994	Winter	17-jan	26-jan	W94
1995	Winter	25-jan	04-feb	W95
1997	Winter	20-jan	03-feb	W97
1998	Winter	06-mar	23-mar	W98
1999	Spring	12-apr	01-may	S99
2003	Autumn	26-oct	11-nov	A03
2005	Autumn	05-dec	16-dec	A05
2007	Autumn	21-nov	02-dec	A07
2009	Winter	19-dec	10-jan	W09
2011	Winter	06-jan	31-jan	W11
2013	Autumn	28-nov	25-dec	A13
2015	Autumn	20-nov	15- dec	A15

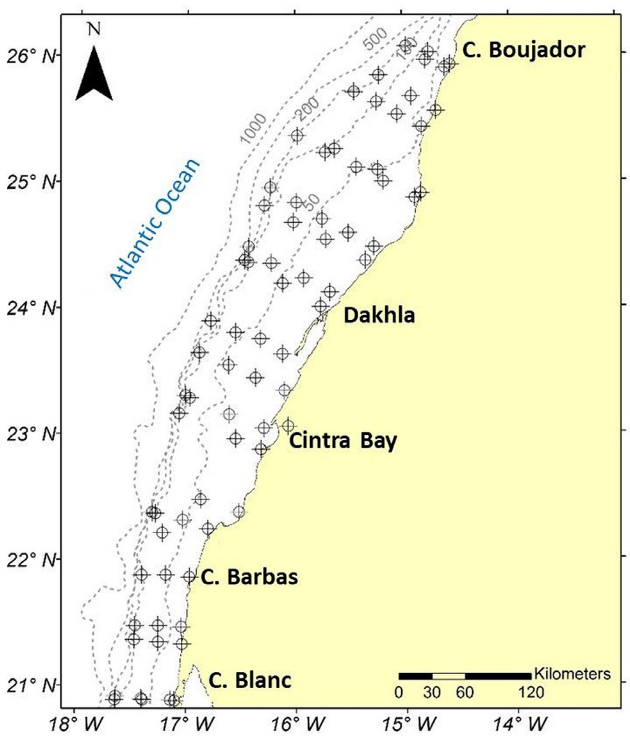

Figure 1 Example of a fish egg sampling plan network in the study area during the autumn—winter periods 1994—2015.

tows were carried out to a maximum depth of 200 m leaving 5 m over the bottom when in shallower depths. The samples were immediately preserved in 5% borax-buffered formalin. The water volume filtered was measured by a flowmeter attached to the opening of the bongo net. In the laboratory, sardine eggs were sorted from the ichthyoplankton samples and counted. The depth and water volume filtered were used to standardize abundance into egg 10 m^{-2}.

Sea Surface Temperature (SST) and Sea Surface Salinity (SSS) were recorded at each station with a SBE-911+ CTD. Zooplankton biomass (ZP) was calculated as wet weight from 5% buffered formaldehyde preserved samples (Wiebe et al., 1975) and expressed into mg m^{-3}.

2.2. Data analysis

For the long-term variation of spawning location, the centre of gravity was calculated. The centre of gravity is the mean location of the population, in our case, of the sardine eggs in the period of the 2000s. Using the following formula (Jenness, 2004), centres of gravity has been calculated:

$$\bar{X} = \frac{\sum_i fixi}{\sum_i fi} \quad \bar{Y} = \frac{\sum_i fiyi}{\sum_i fi}$$

$\bar{X}$ and $\bar{Y}$: mean longitude and latitude respectively; *fi:* sardine egg abundance at station *i; xi* and *yi:* the longitude and latitude coordinates respectively of station *i*.

The spawning habitat preference of sardine was modelled based on the egg data using Generalized Additive Model (GAM) (Wood, 2006) to detect the relationships between sardine eggs and the environmental variables SST, SSS and ZP.

The relationship between the presence/absence of sardine eggs data and density data against the environmental variables were tested by the generalized additive model (GAM). GAMs with a binomial error distribution and a logit-link function were fitted to sardine binary data, while the Gaussian distribution was used to model the density data (only on given presence density) and where depths were not beyond 500 m (where the majority of the eggs were found). This analysis was performed using R 3.0.2 (R Development Core Team 2014) and 'mgcv' package (Wood, 2001).

3. Results

3.1. Inter-annual variability of spawning distribution and location

The distribution of sardine eggs abundances varied considerably from year to year and from decade to decade showing a large degree of inter-annual variability of sardine egg distribution during the 2000s (Figure 2). Generally, the observed egg distributions were restricted to near-shore waters except for few stations whose depth exceeded 500 m.

In the period of 1990s, high abundances were reported during 1994, 1995 and 1999 (maximum abundance: 23529 egg 10 m^{-2} in 1995), whereas the lowest abundances were recorded in 1997 (maximum abundance: 216 egg 10 m^{-2}). In terms of spatial distribution, sardine eggs were concentrated between Dakhla and Cape Boujador during 1994, 1995 and 1997, whilst eggs were recorded more in the south, between Cintra bay and Dakhla in 1998—1999.

In the 2000s, high to medium sardine eggs abundances were found in 2003—2009, particularly between Cape Barbas and the northern part of Dakhla, except for the 2005, where the spatial distribution is patchy and spreads over the most shelf of the region of Cape Blanc. Besides, in 2011—2015, sardine egg abundance tends to decrease despite the high values recorded in only one station in 2013 (68539 eggs 10 m^{-2}). Spatially, sardine eggs were distributed between Cintra Bay and Dakhla during 2002—2007, while eggs were

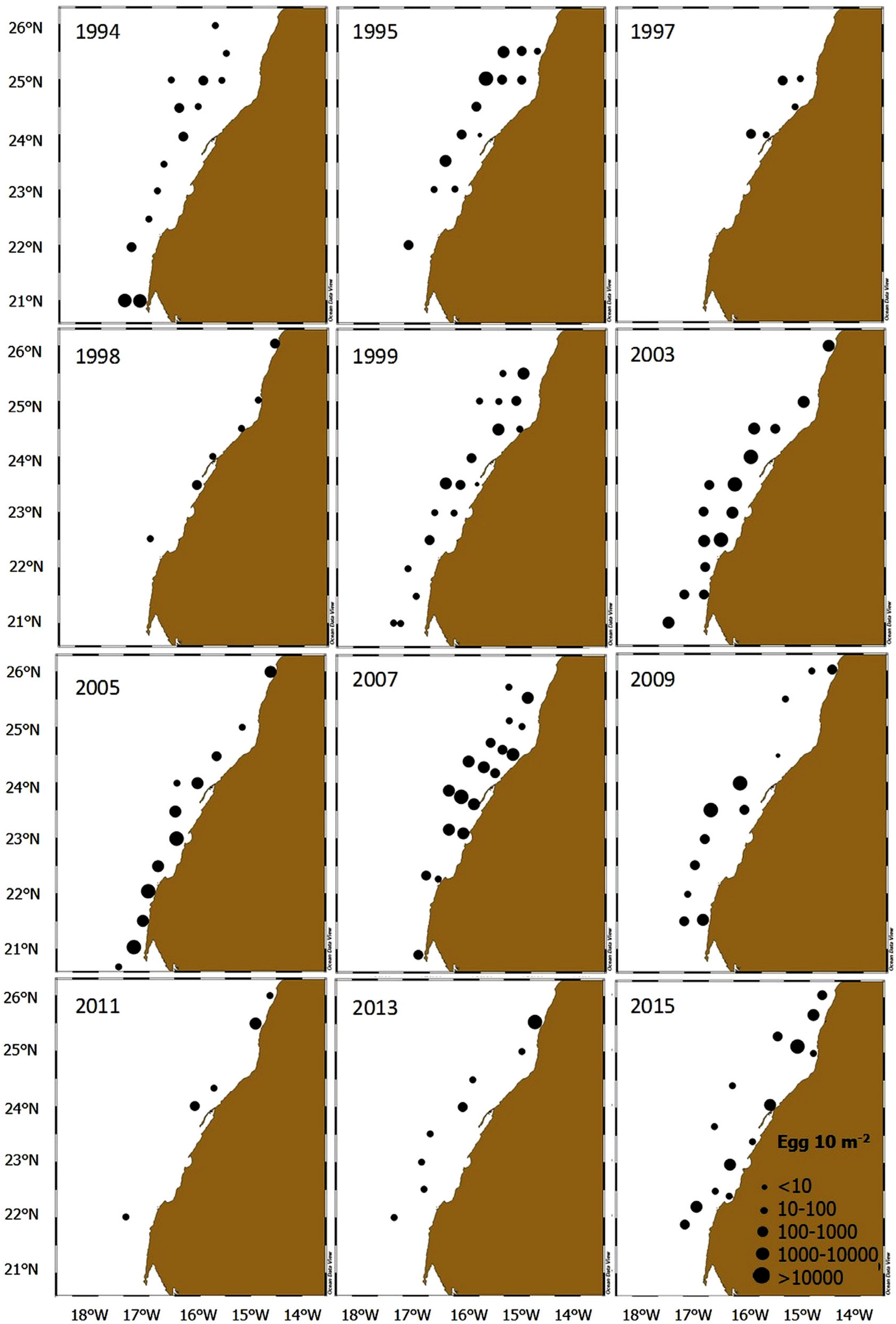

Figure 2 Distribution of sardine egg abundance (egg m^{-2}) in the study area during the autumn-winter periods 1994—2015.

Table 2 Results of Generalized Additive Models (GAMs) for sardine eggs.

	Presence/abscence				
	Estimate	SE	Z	p-value	p
Intercept	-0.3064	0.1042	-2.94	0.00328	**
Term	**edf**	**Ref.df**	X^2	**p-value**	**p**
SST	1.000	1.001	1.195	0.274	n.s
SSS	1.656	2.030	1.850	0.402	n.s
ZP	1.492	1.830	2.765	0.216	n.s
	Given presence data				
Term	Estimate	SE	Z	p-value	p
Intercept	56.927	0.1617	35.22	<2e-16	***
Term	**edf**	**Ref.df**	*F*	**p-value**	**p**
SST	1	1	9.585	0.00231	**
SSS	1	1	5.855	0.01663	**
ZP	1	1	7.480	0.00693	*

Code of significance: *** 0.001; ** 0.01; * n.s.

found further north (southern part of Cape Boujador) in 2011—2015.

3.2. Long term variation of spawning location

To show the long-term variation, centers of gravity of spawning location were calculated based on the location of each grid weighted by the number of eggs for each year. Generally, all sardine spawning areas were coastal areas where maximum depths were not over 50 meters' depth.

During the period of 1990s, the main spawning area of sardine was observed between Dakhla (24°N) and the south of Boujador (25°N). Throughout the 2000s, the mean centres spawning gravity location showed changes between 2003—2009 and 2011—2015 (Figure 3). The spawning position was found concretely around Dakhla. Thus, in the early 2000s, the spawning location was observed between Cintra Bay and Dakhla, with the exception of 2005, where the main spawning occurred further down south, particularly near Cape Barbas. Contrarily, during the period from 2011—2015, a shift of the spawning location of sardine was observed towards the north of Dakhla.

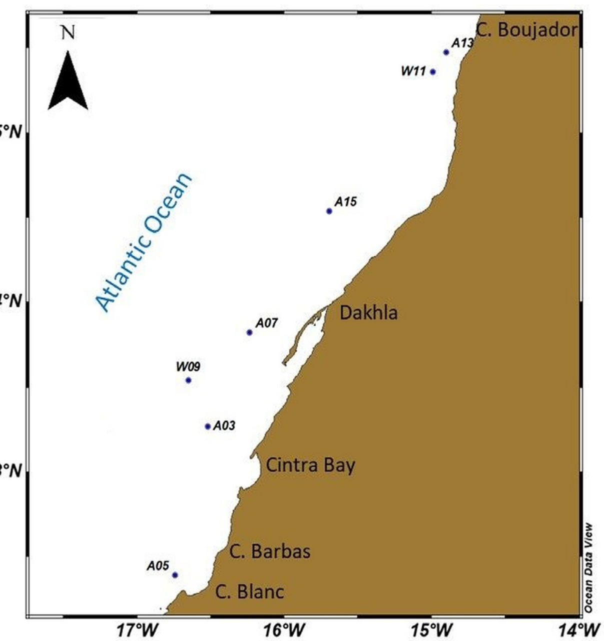

Figure 3 Centres of gravity of spawning location of sardine in the study area.

3.3. Sardine spawning relationship with SST, SSS and ZP

GAM modeling was used to explore the relationship of sardine spawning with SST, SSS and ZP by using the density data and the presence/absence data of sardine eggs acquired from the time series data of surveys from 1994—2015. The results of the model are shown in Table 2. No significant relationship was detected between the presence/absence of sardine eggs with SST, SSS and ZP. However, a highly significant linear relationship between egg abundance and SST, SSS and ZP was observed. To confirm this linear relationship, a multiple regression analysis was applied verifying its statistical significance (Table 3). Figure 4 shows the GAM plot depicting the potential relationships of sardine egg abundance and SST, SSS and ZP. The results of the GAMs analysis revealed that eggs are likely to be found at surface temperatures between 18.5 and 22.5°C. Sardine eggs were associated with lower values of salinities (< 36.4 psu). Furthermore, eggs were more abundant in areas of high biomass of mesozooplankton.

3.4. Spatial-temporal dynamics of the sardine spawning habitat

The modelled potential spawning habitat of sardine covers larger areas and is patchier during the period of the 2000s (Figure 5b) than during the 1990s (Figure 5a). During the 1990s, the area with a probability of more than 50% egg presence may be considered as a favorable area for sardine

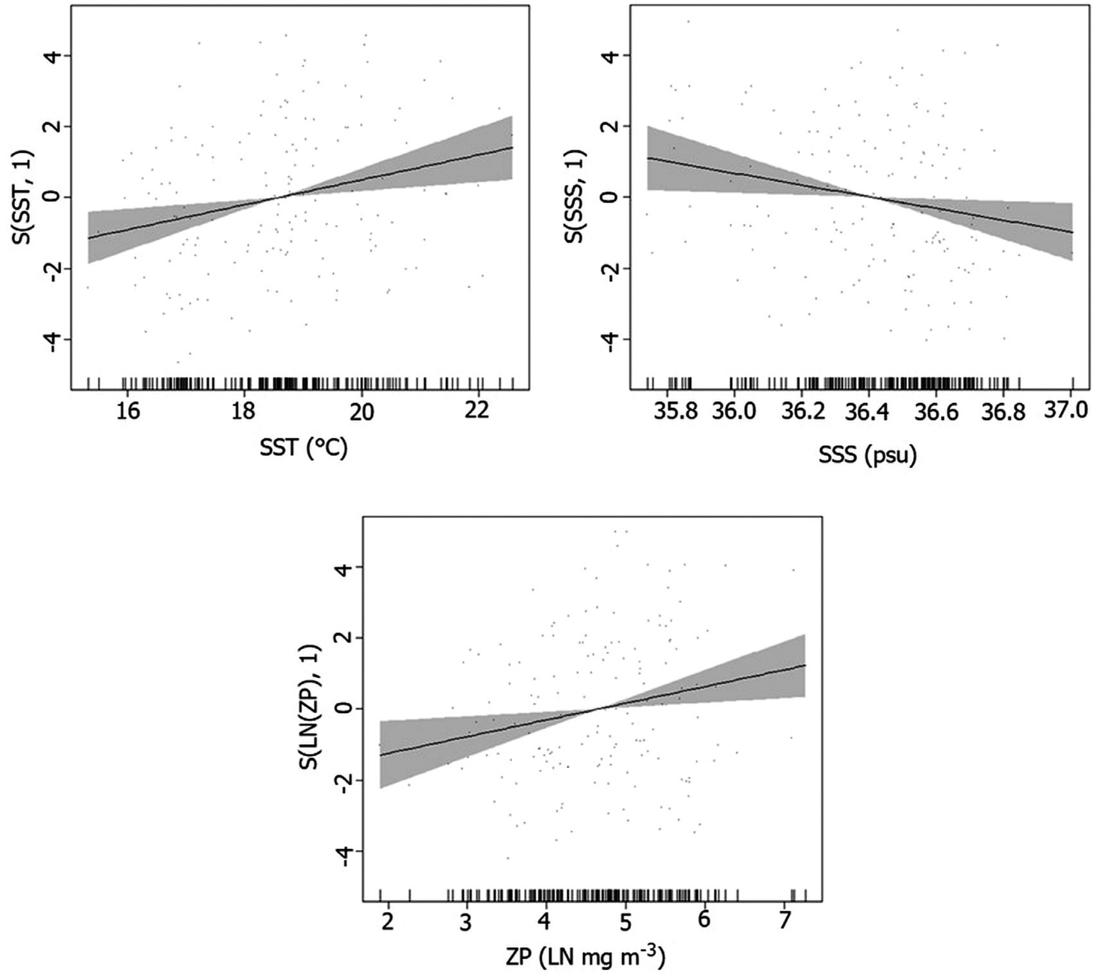

Figure 4 Results of Generalized Additive Models (GAM). The panels show the effect of SST: Sea surface temperature, SSS: Sea surface salinity and ZP: Zooplankton biomass, on the distribution of sardine eggs.

Table 3 Result of multiple linear regression between egg densities (positive stations) and environmental parameters (SST, SSS and ZP).

	Estimate	SE	t value	Pr(> |t|)	p
SST	0.318	0.114	2.785	0.006	**
SSS	−1.638	0.687	2.385	0.018	*
ZP	0.002	0.001	−2.877	0.005	**

Code of significance: *** 0.001; ** 0.01; * 0.05.

spawning. This area constricted to the coastal area between Dakhla and the southern part of Cape Boujador (Figure 5a).

During the 2000s, the potential spawning area of this species is more dispersed, from Cape Boujador to Cape Barbas (Figure 5b). However, three areas of high egg probabilities (> 75%) were identified: (1) between Cape Boujador and 25°N, (2) in the Dakhla region and (3) between Cintra Bay and Cape Barbas.

The offshore region between Cape Barbas and Cape Blanc showed a low probability of sardine egg presence in both periods of the 1990s and the 2000s. The analysis of the average and variability maps of egg presence of both periods allowed the identification of a recurrent spawning area of high egg probability (> 75%) located between Dakhla and Cape Boujador. An occasional spawning area is located between the northern area of Cape Barbas and Cintra Bay where the average probability of egg presence is high but showing high variability. Offshore areas show low average probability of sardine spawning according to data on egg presence and likewise showing low variability (Figure 5c).

4. Discussion

Our samples were collected in the cold season coinciding with the peak spawning period of sardine in this area. During the study period, sardine eggs abundances varied from year to year. The distribution maps of sardine eggs revealed high abundances in the period of 2003—2009 compared to the 1990s, particularly in the coastal areas. In the winter of 1997/1998, a decrease of the sardine eggs abundances was observed. Indeed, the Moroccan stock of sardine has experienced dramatic changes in terms of abundance, especially during the 1997/1998 spawning season. This period corresponds to an El Niño warming trend that increased

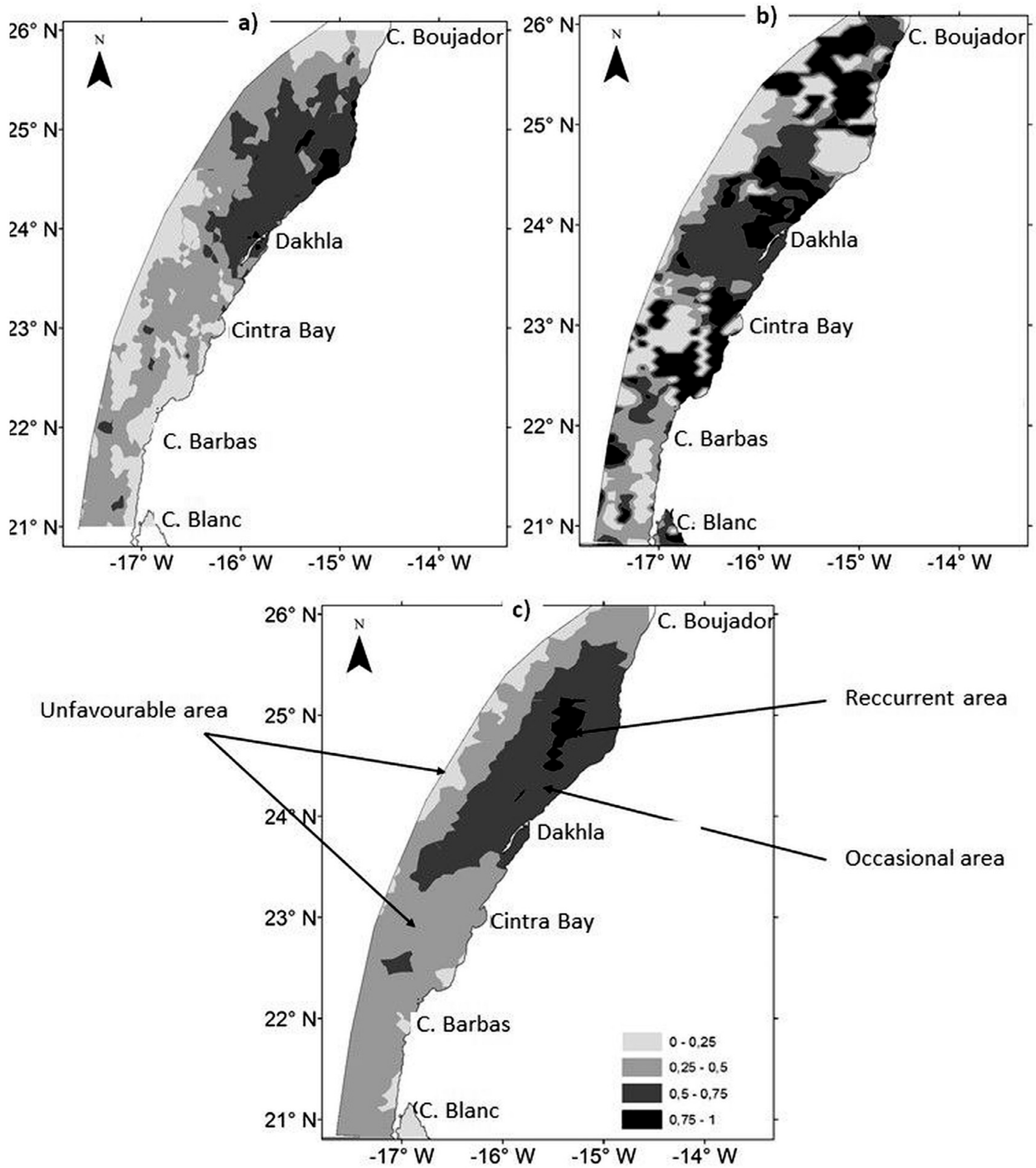

Figure 5 Spatial location of recurrent, occasional and unfavourable sardine spawning area (Grey scale is proportional to the probability of presence of eggs). Top left (a): average map of sardine spawning area for the period of 1990′s. Top right (b): variability map of sardine spawning area for the period of 2000′s. Bottom (c): average map of the probability of presence of eggs for the period of 1994—2015.

temperatures in the study area (INRH, 2002) which may have affected the optimal temperature regime for sardine spawning.

The period 2011—2013 showed low sardine egg abundances which only increased slightly in 2015. Considering the sampling periods of each decade (in winter of 1990s and in late autumn of 2000s), spawning variability between the two decades can be attributed to seasonal variations, jointly with the inter-annual variability of the environmental conditions. Petitgas et al. (2013) found strong sardine spawning variability in the Bay of Biscay, which corresponded to inter-annual differences in temperature.

In the 1994—1999 period, the spawning ground of the southern population of sardine was found between Dakhla (24°N) and the south of Cape Boujador (26°N) (Berraho, 2007; Ettahiri et al., 2012). During the period of autumn-winter of the 2000s, sardine spawning grounds were located in the south, particularly between Dakhla (24°N) and Cintra Bay (23°N), except for the year 2005 and the period between 2011—2015. The high variability in the distribution of eggs between the spawning years and within the same area is probably driven by environmental conditions. Indeed, the inter-annual variability of the spawning ground of sardine is related to the variability of the environmen-

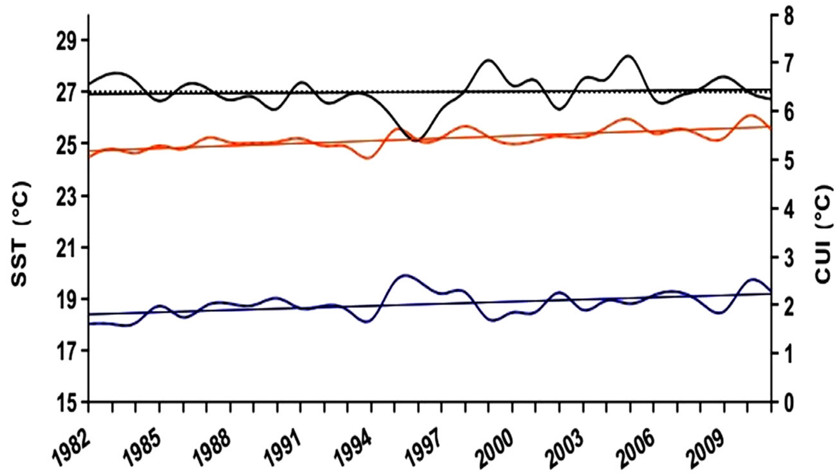

Figure 6 The annual-mean SST (Sea surface temperature) during 1982—2011 for SST_{max} (red line), SST_{min} (blue line) and CUI (Coastal upwelling index; thick black line) (Benazzouz et al., 2015).

tal parameters (Berraho et al., 2005; Ettahiri et al., 2012) which are influenced by the global environmental changes. During the last decade, fish populations have decreased, particularly regarding small pelagic fish stocks (INRH, 2014). Bakun and Cury (1999) have noted that changes in the wind intensity and the onset of the upwelling season can also be related to changes in the main atmospheric circulation patterns such as the North Atlantic Oscillation (NOA) and the Pacific Decadal Oscillation (PDO) (Guisande et al., 2004; Lindegren et al., 2013) and may cause fluctuations in the abundance of the small pelagic year per year. In general, the spawning habitat of small pelagic must conform to having suitable hydrophysical conditions (e.g., temperature, salinity and availability of food), the necessary trophic resources, and the coexistence of relatively few predators (Weber et al., 2015). In the Moroccan coast off Northwest Africa, sardine spawning is observed within an optimal temperature range of 16—18.5°C (Ettahiri et al., 2003; Furnestin and Furnestin, 1959).

Generally, a preferential spawning habitat must comply with favorable conditions for spawning of a given species, particularly defined by its hydroclimatic features and the necessary trophic resources, as well as, being surrounded by few numbers of the predator spectrum (Weber et al., 2015). The optimum spawning habitat of sardine off NW Africa has been defined by assessing the link between sardine egg densities and their presence/absence data with the implementation of a Generalized Additive Model (GAM). The relative presence/absence egg data did not show any significant relationship with SST, SSS and ZP. However, the results of the Generalized Additive Model indicate a significant linear relationship ($p < 0.05$) between the referred environmental variables and the egg density data. The predicted model showed that sardine was mostly to be found at sea surface temperatures between 18 and 22°C. However, the results of the quotient analysis carried out in the 1990s showed that the preferred temperature ranges from 15.5 to 17.5°C (Berraho, 2007; Ettahiri et al., 2012). The results of the GAMs imply that the preferred temperature range for the sardine spawning has shifted to a higher temperatures regime possibly consequent with the global warming trend in this region (Benazzouz, 2014). Changes in the preferred environmental conditions may also be due to a direct consequence of changes in the location of sardine spawning grounds through time, as reported in previous studies (van der Lingen et al., 2001, 2006). In the southern Benguela region, sea surface temperature experienced a warming trend during the 2000s period which accounted for the changes in the spawning distribution patterns as suggested by Roulaut et al. (2010) and which was confirmed by a gradual eastward shift of spawning habitat of sardine as a response to this warming (Mhlonogo et al., 2015). In this climatic context, Peck et al. (2013) argued that sardine is an excellent bio-indicator of the climate-driven changes in marine systems. Indeed, these authors suggested a dependence of preferred SST ranges for the European sardine spawning in the function of their geographical location. Thus, at decadal scales, these thermal preference variations for spawning can be attributed to significant sea surface temperature variability, as supported by Benazzouz et al. (2014; 2015) that found significant changes in temperature between the 1990s and the warming trend beyond the 2000s. This warming trend is observed in the coastal and oceanic parts of the Canary Current region, as observed from the thermal field trends from 1998 to 2014, also visible in the southern part of the Moroccan Atlantic (Figure 6). Similarly, thermal conditions in the Benguela current ecosystem have recently evolved towards a warming period (Rouault et al., 2010), and correspondingly, sardine and anchovy spawning distribution patterns seem to have followed accordingly to these changes (Mhlongo et al., 2015). Both species are considered climate change bio-indicators of marine ecosystems (Peck et al., 2013), due to their capacity to respond to climatic changes (Mhlongo et al., 2015). In the Benguela ecosystem, single parameter quotient applied yearly from 1988 to 2009 highlighted a wide range of the preferential temperature from 16—22°C for the Benguela sardine spawning (*Sardinops sagax*) (Mhlongo et al., 2015). The salinity range in which sardine eggs were found was wide (35.7—36.4) and within the same range described previously (Berraho et al., 2005; Ettahiri et al., 2003). The GAM's results suggest that the availability of food is one of the biotic factors involved in selecting a suitable habitat for spawning.

According to the results observed in 2004, there is a synchrony between the abundance of ichthyoplankton and zooplankton, which showed an overlap of zooplankton and fish egg distributions, promoting a favorable habitat for the future larvae. In fact, Chicharo et al. (2003) studying the nutritional conditions of sardine larvae found a significant correlation between zooplankton biomass and specifically on the microzooplankton fraction with the RNA/DNA ratio. Similarly, seasonal and annual variability of the potential spawning habitat of sardinella (*Sardinella aurita*) has been observed associated with planktonic biomass, thus providing favorable feeding conditions for larval survival after spawning (Mbaye et al., 2015).

The GAMs analysis revealed a significant relationship between sardine eggs sand zooplankton biomass, where egg abundance is related to higher zooplankton biomass. Sardine regulates trophic links between zooplankton and the upper trophic level of fish constituting a midtrophic level in highly productive ecosystems (Cury et al., 2000). In fact, most eggs are found in similar sites presenting similar environmental conditions to those in which the spawning occurred (Weber and McClatchie, 2010). These results suggest that food availability is among the biological factors contributing to the selection of suitable spawning habitat.

The temporal variability of environmental conditions not only influences spawning habitats but also impacts the spatial dynamics in terms of spawning ground's distribution of different sardine populations (Bellier et al., 2006; Gigliotti et al., 2010; Mhlongo et al., 2015; Planque et al., 2007; van der Lingen et al., 2001).

The location of suitable spawning areas was assessed based on the analysis of the probability of occurrence of eggs during two decades, the 1990s and the 2000s. As a result of this study, a strong inter-decadal variability in the spatial positioning of spawning grounds was determined. In the 1990s, a restricted area of a high probability of egg occurrence was identified near the coast at a latitude of 25°N where sardines spawned regularly every year. This was a large area characterized by its inter-annual variability of sardine egg production. In the 2000s, areas of high spawning probability were more spatially spread out. In addition, over the entire period from 1994—2015, three categories of spawning habitats were identified by Bellier et al. (2006): a) a persistent spawning area where the spawning is observed every year being delimited by 24°30—25°30′N; b) an occasional spawning area where sardines spawned variably from year to year in the spatial extension from southern Cape Boujador to Cintra Bay and c) unfavorable spawning areas where quasi-absence of sardine eggs in this area is observed which is likely due to hydrographic features causes rather than spawning.

Acknowledgements

This work was carried out in the context of the oceanographic program of the Moroccan coastal sites undertaken by the National Institute of Fisheries Research. The authors thank all the team that took part in the surveys. The authors would also like to thank the editor and the reviewers for their useful comments.

References

Abdelouahab, H., 2018. Assemblages des larves de poissons et variabilité temporelle de la phase planctonique de la sardine (Atlantique marocain), Ph.D. thesis. Hassan II Univ., Casablanca, Morocco, 194 pp.

Abdelouahab, H., Berraho, A., Baibai, T., Agouzouk, A., Makaoui, A., Errhif, A., 2017. Autumn larval fish assemblages in the northwest African Atlantic coastal zone. Chin. J. Oceanol. Limnol. 35 (3), 515—527. http://dx.doi.org/10.1007/s00343-017-5302-7

Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, A., Mathis, M., O'Driscoll, K., 2012. Climate variability drives anchovies and sardines into North and Baltic Sea. Prog. Oceanogr. 96 (1), 128—139. https://doi.org/10.1016/j.pocean.2011.11.015

Arístegui, J., Barton, E.D., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., Mason, E., Machu, E., Demarcq, H., 2009. Sub-regional ecosystem variability in the Canary current upwelling. Prog. Oceanogr. 83 (1—4), 33—48. https://doi.org/10.1016/j.pocean.2009.07.031

Bakun, A., 2010. Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: Conceptual templates and schematic constructs. J. Mar. Syst. 79, 361—373. https://doi.org/10.1016/j.jmarsys.2008.12.008

Bakun, A., Cury, P., 1999. The "school trap": a mechanismpromoting large-amplitude out-of-phase population oscillations of small pelagic fish species. Ecol. Lett. 2 (6), 349—351.

Bellier, E., Planque, B., Petitgas, P., 2006. Historical fluctuations in spawning locations of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay during 1967—73 and 2000—2004. Fish. Oceanogr 16 (1), 1—15. https://doi.org/10.1111/j.1365-2419.2006.00410.x

Benazzouz, A., 2014. Upwelling côtier et effet de la dynamique océanique à méso-échelle sur la variabilité planctonique dans le système du Courant des Canaries, Ph.D. thesis. Hassan II Univ., Casablanca, Morocco, 261 pp.

Benazzouz, A., Demarcq, H., González-Nuevo, G., 2015. Changes and trends of the upwelling intensity in the Canary Current Large Marine Ecosystem. In: Valdés, L., Déniz-González, I. (Eds.), Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem. IOC-UNESCO, IOC Tech. Series 115, Paris, 321—330.

Benazzouz, A., Mordane, S., Orbi, A., Chagdali, M., Hilmi, K., Atillah, A., Pelegrí, J.L., Demarcq, H., 2014. An improved coastal upwelling index from sea surface temperature using satellite-based approach — the case of the Canary Current upwelling system. Cont. Shelf Res. 81, 38—54. http://dx.doi.org/10.1016/j.csr.2014.03.012

Berraho, A., 2007. Relations spatialisées entre milieu et ichtyoplancton des petits pélagiques de la côte Atlantique Marocaine (Zones central et sud), Ph.D. thesis. Mohammed V Univ., Rabat, Morocco, 261 pp.

Berraho, A., Ettahiri, O., Letourneur, Y., Orbi, A., Yahyaoui, A., 2005. Importance des paramètres hydrologiques dans la distribution des oeufs et larves des petits pélagiques du sud de l'Atlantique marocain. Cybium 29 (1), 21—31.

Bonanno, A., Barra, M., Basilone, G., Genovese, S., Rumolo, P., Goncharov, S., Popov, S., Buongiorno Nardelli, B., Iudicone, D., Procaccini, G., Aronica, S., Patti, B., Giacalone, G., Ferreri, R., Fontana, I., Tranchida, G., Mangano, S., Pulizzi, M., Gargano, A., Di Maria, A., Mazzola, S., 2016. Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. Fish. Oceanogr. 25 (5), 471—490. http://dx.doi.org/10.1111/fog.12166

Brochier, T., Colas, F., Lett, C., Echevin, V., Cubillos, L.A., Tamf, J., Chlaida, M., Mullon, C., Fréon, P., 2009. Small pelagic fish reproductive strategies in upwelling systems: A natal homing evolutionary model to study environmental constraints. Prog. Oceanogr. 83 (1—4), 261—269. https://doi.org/10.1016/j.pocean.2009.07.044

Chicharo, M.A., Esteves, E., Santos, M.A., dos Santos, A., Peliz, A., Ré, P., 2003. Are sardine larvae caught off northern Portugal in winter starving? An approach examining nutritional conditions. Mar. Ecol. Prog. Ser. 257, 303—309. https://doi.org/10.3354/meps257303

Ciannelli, L., Bailey, K., Olsen, E.M., 2015. Evolutionary and ecological constraints of fish spawning habitats. ICES J. Mar. Sci. 72 (2), 285—296. https://doi:10.1093/icesjms/fsu145

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES. J. Mar. Sci. 57, 603—618. https://doi.org/10.1006/jmsc.2000.0712

Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I., Pörtner, H.O., Plovina, J.J., Takasuka, A., 2010. On the processes linking climate to ecosystem changes. J. Mar. Syst. 79 (3—4), 374—388. https://doi.org/10.1016/j.jmarsys.2008.12.014

Ettahiri, O., Berraho, A., Houssa, R., Ramzi, A., Somoue, L., Zizah, S., Machu, E., 2012. Characteristics of the spawning habitats of sardine, *Sardina pilchardus*, off the Moroccan Atlantic coast (21°N—26°N). FAO, Pêch. Aquac. 18, 157—186.

Ettahiri, O., Berraho, A., Vidy, G., Ramdani, M., Do chi, T., 2003. Observation on the spawning of Sardina and Sardinella off the south Moroccan Atlantic coast (21—26°N). Fish. Oceanogr. 60 (2—3), 207—222. https://doi.org/10.1016/S0165-7836(02)00172-8

Fréon, P., Werner, F., Francisco, P., Chavez, F.P., 2009. Conjectures on future climate effects on marine ecosystems dominated by small pelagic fish. In: Checkley, D., Alheit, J., Oozeki, Y., Roy, C. (Eds.), Climate Change and Small Pelagic Fish. Cambridge Univ. Press, 312—343.

Furnestin, J., 1945. Note préliminaire sur l'Anchois (*Engraulis encrasicolus*) du Golfe de Gascogne. Rev. Trav. Off. Sci. Tech. Pêches Marit 13 (1—4), 197—209

Furnestin, J., Furnestin, M.L., 1959. La reproduction de la sardine et de l'anchois des côtes Atlantiques du Maroc (saisons et aires de ponte). Rev. Trav. Ins. Pêches Marit. 23 (1), 79—104.

Giannoulaki, M., Iglesias, M., Tugores, M.P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., Bigot, J.L., Tičina, V., Pyrounaki, M.M., Tsagarakis, K., Machias, A., Somarakis, S., Schismenou, E., Quinci, E., Basilone, G., Cuttitta, A., Campanella, F., Miquel, J., Onate, D., Roos, D., Valavanis, V., 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. Fish. Oceanogr 22 (2), 69—89. https://doi.org/10.1111/fog.12005

Gigliotti, E.S., Gherardi, D.F.M., Paes, E.T., Souza, R.B., Katsuragawa, M., 2010. Spatial analysis of egg distribution and geographic changes in the spawning habitat of the Brazilian sardine *Sardinella brasiliensis*. J. Fish Biol. 77 (10), 2248—2267. https://doi.org/10.1111/j.1095-8649.2010.02802.x

Guisande, C., Vergara, A., Riveiro, I., Cabanas, J., 2004. Climate Change and Abundance of the Atlantic-Iberian Sardine (*Sardina pilchardus*). Fish. Oceanogr. 13, 91—101. https://doi.org/10.1046/j.1365-2419.2003.00276.x

INRH, 2002. Les ressources halieutiques marocaines: situation et niveaux d'exploitation. Doc. Tech. INRH, 167 pp.

INRH, 2014. Etat des Stocks et des Pêcheries Marocaines. Doc. Tech. INRH, 305 pp

Jenness, J., 2004. Weighted mean extension for Arc View3. *x*, *v*. 1.2c. Jenness enterprises

Kifani, S., 1998. Climate dependent fluctuations of the Moroccan sardine and their impact on fisheries. In: ORSTOM (Ed.), Global Versus Local Changes in Upwelling Systems. Colloq. Inst. Fr. Rech. Sci.Dev. Coop., Paris, 235—247.

Lindegren, M., Checkley, D., Rouyer, T., Maccall, A., Stenseth, N., 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. Proc. Natl. Acad. Sci. USA. 110 (33), 13577—13677. http://dx.doi.org/110.10.1073/pnas.1305733110

Makaoui, A., 2008. Etude de l'upwelling côtier de la côte atlantique marocaine et sa contribution à la sédimentologie du plateau continental, Ph.D. thesis. Hassan II Univ., Casablanca, Morocco, 163 pp.

Malta, T., Santos, P.T., Santos, A.M.P., Rufino, M., Silva, A., 2016. Long-term variations in Ibero-Atlantic sardine (*Sardina pilchardus*) population dynamics: Relation to environmental conditions and exploitation history. Fish. Res. 179, 47—56. http://dx.doi.org/10.1016/j.fishres.2016.02.009

Mbaye, B.C., Brochier, T., Echevin, V., Lazar, A., Lévy, M., Mason, E., Gaye, A.T., Machu, E., 2015. Do *Sardinella aurita* spawning seasons match local retention patterns in the Senegalese-Mauritanian upwelling region? Fish. Oceanogr. 24 (1), 69—89. http://dx.doi.org/10.1111/fog.12094

Mhlongo, N., Yemane, D., Hendricks, M., Van Der Lingen, C.D., 2015. Have the spawning habitat preferences of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the southern Benguela changed in recent years? Fish. Oceanogr. 24 (Suppl. 1), 1—14. https://doi.org/10.1111/fog.12061

Olivar, M.P., Salat, J., Palomera, I., 2001. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. Mar. Ecol. Prog. Ser. 217, 111—120.

Parrish, R.H., Serra, R., Grant, W.S., 1989. The Monotypic Sardines, Sardina and Sardinops: Their Taxonomy, Distribution, Stock Structure, and Zoogeography. Can. J. Fish. Aquat. Sci. 46 (11), 2019—2036.

Peck, M.A., Reglero, P., Takahashi, M., Catalan, I.A., 2013. Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. Prog. Oceanogr. 116, 220—245. http://dx.doi.org/10.1016/j.pocean.2013.05.012

Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H, Peck, M.A, Pinnegar, J.K., Drinkwater, K., Huret, M., Nash, R.D.M., 2013. Impacts of climate change on the complex life cycles of fish. Fish. Oceanogr. 22 (2), 121—139. https://doi.org/10.1111/fog.12010

Planque, B., Bellier, E., Lazure, P., 2007. Modelling potential spawning habitat of sardine (*sardina pilchardus*) and anchovy (*engraulis encrasicolus*) in the Bay of Biscay. Fish. Oceanogr 16, 16—30. https://doi.org/10.1111/j.1365-2419.2006.00411.x

Rouault, M., Pohl, B., Penven, P., 2010. Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. Afr. J. Mar. Sci. 32 (2), 237—246. https://doi.org/10.2989/1814232X.2010.501563

van der Lingen, C.D., Hutchings, L., Merkle, D., van der Westhuize, J.J., Nelson, J., 2001. Comparative spawning habitats of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the southern Benguela upwelling ecosystem. In: Kruse, G.H., Bez, N., Booth, T., Dorn, M., Hills, S., Lipcius, R.N., Pelletier, D., Roy, C., Smith, S.J., Witherell, D. (Eds.), Spatial Processes and Management of Marine Populations. Alaska Sea Grant Univ., Fairbanks, 185—209.

van der Lingen, C.D., Shannon, L.J., Cury, P., Kreiner, A., Moloney, C.L., Roux, J-P., Vaz- Velho, F., 2006. Resource and

Ecosystem Variability, Including Regime Shifts, in the Benguela Current System. Large Mar. Ecosyst. 147—184. https://doi.org/10.1016/S1570-0461(06)80013-3

Weber, E.D., Chao, Y., Chai, F., McClatchie, S., 2015. Transport patterns of Pacific sardine *Sardinops sagax* eggs and larvae in the California Current System. Deep-Sea Res. I. 100, 127139. https://doi.org/10.1016/j.dsr.2015.02.012

Weber, E.D., McClatchie, S., 2010. Predictive models of northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* spawning habitat in the California current. Mar. Ecol. Prog. Ser. 406, 251—263.

Wiebe, W.J., Johannes, R.E., Webb, K.L., 1975. Nitrogen fixation in a coral reef community. Science 188 (4185), 257—259. https://doi.org/10.1126/science.188.4185.257

Wood, S.N., 2001. mgcv: GAMs and Generalized Ridge Regression for R. R News 1 (2), 20—25

Wood, S.N., 2006. Generalized Additive Models: An Introduction with R. J. Stat. Softw. Chapman et Hall/CRC, Boca Raton, 410 pp.