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Variability of key biological parameters of round sardinella Sardinella aurita and the effects of environmental changes

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Abstract :

We examined growth rates and reproductive characteristics of Sardinella aurita off Senegal and other coastal areas over a 20 year period (1995-2014) to determine how they relate to variations in environmental characteristics of coastal waters. Based on fish length-frequency data and a coastal upwelling index, we found that S. aurita recruitment tends to occur during the periods of most intensive upwelling (March-April off Senegal). Peak reproduction corresponds to periods of low sea-surface temperature (in February or March). The sex ratio was remarkably consistent during the 30 year study period and so was not affected by environmental changes. We hypothesise that S. aurita takes advantage of the higher zooplankton productivity that occurs in coastal waters when upwelling brings nutrient-rich water to the surface (i.e., it increases its growth rate and accumulates energy reserves for spawning). Growth performance appears to be strongly dependent on environmental conditions. The timing of spawning seems to occur when food (zooplankton) is most available for supplying the energy requirements needed by adults for spawning and early development of larvae. Environmental changes seem to have a significant effect on S. aurita growth and reproduction, which endorses their high phenotypic plasticity.

Keywords : data poor fisheries, environmental variability, size structure, small pelagic, spawning period, west Africa

1. INTRODUCTION

The Canary Current off the West Africa coast initiates an upwelling zone that modifies the trophic structure of coastal ecosystems profoundly (Auger et al., 2016). The coastal upwelling region from 10° N to 35° N has been identified as one of many large marine ecosystems ("LMEs") of the world, with the southern part of this LME represented by the Senegal-Mauritanian upwelling system (Auger et al., 2016). In the more southern portion of this system off Senegal (between 12° N and 17° N, upwelling occurs only during the winter-spring period. This upwelling is a response to the southern extension of the trade wind, which is defined by the position of the Intertropical Convergence Zone (Auger et al., 2016). The wind-forced upwelling of deep, nutrient-rich water is responsible for high primary productivity (of phytoplankton) in coastal waters, which provides the energy (food) for higher trophic levels. In the Senegal-Mauritanian region (10°–19° N), the geographic expansion of offshore phytoplankton production that occurs during winter and spring is followed by an abrupt decline in summer production (Auger et al., 2016). Bakun (1990) hypothesized that climate change may lead to an intensification of coastal upwelling in response to increasing favourable upwelling wind, and Barton et al. (2013) has predicted there is an increase in SST in general. In either case, changes in the upwelling intensity of the Senegal-Mauritanian system will influence the abundance of small pelagic fish, including *Sardinella aurita* (round Sardinella) and *Sardinella maderensis* (flat Sardinella) (Thiaw et al., 2017; Diankha et al., 2018). Thiaw et al. (2017) and Diankha et al. (2018) report that abundance and recruitment success of *S. aurita are* associated with distinct ranges of sea surface temperature, upwelling intensity, wind-induced turbulence, concentration of chlorophyll-a and north Atlantic oscillation index in Senegal.

The species *S. aurita* inhabits tropical and subtropical regions of the eastern Atlantic Ocean and occurs in high concentrations along the west coast of Africa in three main areas (Roy et al., 1989): between southern Morocco (Western Sahara) and Guinea (10°–26° N), between Ivory Coast and Ghana (7° – 5 °N) and further south between Gabon and southern Angola (0°–18° S) (Froese & Pauly, 2016). *S. aurita* also occurs in the western Atlantic Ocean from Cape Cod (USA) to Argentina, including the Caribbean, West Indies, and Gulf of Mexico (Felder, 2009). It also inhabits the Mediterranean Sea (Boltachev & Karpova, 2014). In all regions, the species preferentially inhabits continental shelves where it prefers saline (between 34 ppt and 36.5 ppt), and warm sea temperatures (between 17° C and 30 °C) (Boëly, 1979). In Senegal, massive reproduction events occur south of the Cap-Vert peninsula (Dakar) to the delta of Saloum at the border with The Gambia (Conand, 1977; Boëly, 1982). In terms of exploitation, *S. aurita* has already been intensively exploited by artisanal fleets in Senegal (Thiao, 2009) and in Mauritania by foreign fishing fleets under fisheries agreements (e.g. Union European and Russian Federation) and Morocco with a small artisanal fleet fishing near the coast (Isselmou & Baye, 2009). Due to the increasing demand for *S. aurita* for human consumption, the fishing effort of artisanal fleets in Senegal and Mauritania has steadily increased in recent years.

Growth characteristics and breeding season of *S. aurita* populations vary among areas. For example, in the eastern Atlantic (e.g., off Senegal), *S. aurita* possesses an asymptotic length of 36.5 cm total length (TL) (Boëly et al., 1982) and a breeding season that extends from February to May and from October to November (Boëly, 1982). In western Atlantic Ocean (off Venezuela), the species possesses an asymptotic length of 32.6 cm (TL) and a breeding period from January to March and from October to December (Gassman et al., 2008). In the Mediterranean (off Greece), *S. aurita* reaches an asymptotic length of 21.4 cm (TL) (Tsikliras et al., 2005) and a rather limited breeding period between May and June (Tsikliras & Antonopoulou, 2006). Biological characteristics of *S. aurita*, such as growth and reproduction, have been shown to be strongly influenced by environmental conditions (e.g., upwelling intensity and sea surface temperature) in both the Mediterranean (Tsikliras et al., 2005; Tsikliras & Antonopoulou, 2006) and the West Atlantic (Fréon et al. 1997). Such findings suggest that growth and reproductive periods of *S. aurita* in the eastern Atlantic (off Senegal) might also be influenced by upwelling intensity and sea surface temperature.

To determine how environmental conditions might be affecting *S. aurita* populations and their biology, we analysed landing data available for coastal Senegal from 1995 to 2014. The data collections included reproductive condition (age of sexual maturity, length-frequency distributions, and condition factor) and growth parameters. The results of this study were compared and discussed in relation to relevant past studies in various north tropical Atlantic (Eastern and Western) and Mediterranean Sea areas.

2. MATERIAL AND METHODS

2.1. Biological data

Data on the growth of *S. aurita* were obtained from fish that landed at the seven main artisanal fishing harbours along the Senegal coast from July 2013 to June 2014 (Fig. 1). Three harbours (Kayar, Saint-Louis and Yoff) are located in the northern part of the coast (from 16° 04’ N to 14° 36’ N) where the continental shelf is narrow. The other harbours (Hann, Mbour, Joal and Kafountine) are located along the southern coast (from 14° 36’ N to 13° 36’ N and from 13° 04’ N to 12 °20’ N) where the continental shelf is wider than the northern part. Length frequency data were collected randomly at about 5 days per week. This study sampled only specimens caught using purse seine nets to have the same fishing gear selectivity for monthly comparisons of the length distribution.

Total length (TL in cm) of fish sampled (n = 32 346 individuals) was measured to the nearest 1 mm, while the body weight (W) was determined to the nearest 0.01 g. Sampled individuals were grouped into 1-cm-interval size classes to calculate size-frequency distributions and to estimate growth parameters.

Length-weight relationship (Le Cren, 1951) was determined for both males and females:

$$W = a \times TL^b \qquad (1)$$

Where W is the weight and TL is the Total Length, and a and b allometric coefficients.

The data we used for our study of *S. aurita* reproduction were collected by other surveys of the artisanal fisheries along the southern Senegal coast from 1995 to 2011, including surveys by the Fishery Research Vessel (FRV) Fridtjof Nansen (Charouki et al., 2011) and by the Centre de Recherches Océanographiques de Dakar-Thiaroye (CRODT in French) covering Senegal (i.e., Senegal Fisheries Research Centre). These fish surveys were conducted regularly from November through December with a few surveys covering the June-to-July period. In Senegal, massive reproduction events occur south of the Cap-Vert peninsula (Dakar) to the delta of Saloum at the border with The Gambia (Conand, 1977; Boëly, 1982) (Fig.1). A total of 4397 fish samples were recorded during the surveys (Table I). The FRV Fridtjof Nansen stopped collecting samples in 2006, at the end of its research project, but technicians involved in the surveys from the CRODT continued to collect seasonal samples until 2011. Weight of gonads (0.1 g) and sex were determined for 4397 fish. Stages of maturity were determined macroscopically using the Fontana (1969) maturity scale (Table II).

The von Bertalanffy (1938) growth parameters [coefficient of growth rate (K), asymptotic length (L_∞), time "t" when the fish length is zero (t_0)] were estimated from monthly length-frequency data using the 'TropFishR' (Tropical Fisheries Analysis with R) package (Mildenberger et al., 2017), while natural mortality was estimated using the McQuinn et al. (1990) method:

$$M = 3/t_{max} \qquad (2)$$

Where t_{max} is the longevity of the species that is by definition the age corresponding to the size average maximum (L_{max}= 95% L_∞) that a fish can reach and estimated by the following equation of Pauly (1983):

$$t_{max} = (3/K) + t_0 \qquad (3)$$

The growth performance index (φ') was used to compare growth rates among *S. aurita* and evaluate growth performance potential under different environmental constraints (Tsikliras et al., 2005). Growth parameters of *S. aurita* from the different Mediterranean, Central Atlantic stocks were used to construct an auximetric double logarithmic plot of an individual's coefficient of growth rate (K) against an estimate of its asymptotic length (L_∞).

The spawning period of *S. aurita* was determined using two approaches: (1) a qualitative approach based on monitoring monthly fluctuations in the percentage of different stages of gonad development and (2) a quantitative approach based on the monthly change in the gonado-somatic index (GSI; in %). GSI was calculated for each sampled individual based on Le Bec, (1983):

$$GSI = \frac{W_g}{W_{ev}} \times 100 \qquad (4)$$

Where W_g is gonad weight and W_{ev} is eviscerated fish weight.

We used the equation proposed by Le Cren (1951) to calculate each individual's condition factor (Kn):

$$Kn = \frac{W_T}{W_{th}} \qquad (5)$$

W_T: total individual fish weight and W_{th}: the theoretical total weight calculated from Eq. 1. This relationship (Eq. 5) indicates that the bigger the fish, the better the environment. The study of this factor makes it possible to see which cycle, seasonal and annual, obeys weight gain of individuals.

Mean length at first sexual maturity (L_{50}; in cm) was estimated using only fish collected during reproductive periods (February to June and October to November*)* (Boëly, 1982; Cury & Fontana, 1988) from 1995 to 2011. A logistic function with an inflection point at 0.5 ($L_{50\%}$) was used to model the relationship between the percent of mature females (M ≥ Stage III) and total length TL. The following equation was used, where b is a constant of the model:

$$M = \frac{1}{1+e^{-b(TL_t - L_{50\%})}} \times 100 \qquad (6)$$

For comparison with the results of this study, growth and reproductive parameters from various north tropical Atlantic (Eastern and Western) and Mediterranean areas are shown in Appendix, as well as the data sources.

2.2. Landing data

The data set was total landing of *S. aurita* by the Senegal artisanal fishery from 1995 to 2014 by the type of fishing gear used (purse seine) and landing port (Kayar, Saint-Louis and Yoff, Hann, Mbour, Joal, and Kafountine).These data set was extracted from the CRODT database (Figure 1). The number of trips per fishing gear was recorded on a daily basis, whereas landing data were collected randomly at about 5 days per week. After sorting the data by port, gear type and period (fortnightly intervals), total landings per port were estimated by multiplying the mean number of fish landed for the sampled trips by the total number of fishing trips made (Chaboud et al., 2015). The landings were summed by month for each landing port (Chaboud et al., 2015). Growth (July 2013 to June 2014) and reproduction (1995 to 2011) data by size, sex, maturity stages and landing sites were extrapolated with landing data from 1995 to 2014..

2.3. Environmental data

We used local environmental indices [Coastal Upwelling Index (CUI) and coastal sea surface temperature (SST)] for the period from 1995 to 2011 to analyse the effect of the environmental conditions on seasonal and inter-annual variability of key biological parameters (mainly reproduction) of *S. aurita*. Both data sets were obtained from the Southern Senegal coast (Fig. 1). The SST (°C) data (averaged on a monthly basis) were obtained from advanced, very-high-resolution radiometer (AVHRR) satellite images (5 km resolution) from Southern Senegal coast to the 200 m isobath, where upwelling-induced SST anomalies are generally maximal (Thiaw et al., 2017). The CUI (m^3 s^{-1} m^{-1}) was deduced from wind speed data obtained from the U.S. NOAA Environmental Research Division website (ERD, Upwelling and Environmental Index Products, http://www.pfeg.noaa.gov; Upwelling and Environmental Index Products, last visited: 20/11/2017). In order to calculate the CUI in the Southern Senegal, we used the method of Ekman's theory (Ekman, 1905) of the transportation of masses of surface water by wind in the north or north-east direction, coupled with the rotation of the earth:

$$CUI = \frac{\tau}{\rho_{\omega} f} \qquad (7)$$

Where τ is the along shore component of wind stress within 270 km of the coastline (positive southward), ρ is the seawater density (1025 kg m^{-3}) and f is the Coriolis parameter (= 2 Ω sin (θ), with Ω and θ equal to the Earth's angular velocity and latitude, respectively).

2.4. Statistical analysis

All fork length (FL) measurements were converted to total length (TL) according to the relationship (Sylla et al., 2016):

$$FL\ (mm) = 10.8264 + 0.8066 TL\ (mm) \quad \text{<-->} \quad TL = (FL - 10.8264)/0.8066 \quad (8)$$

All statistical analyses were performed using the "stats", "mgcv" and "Hmisc" R packages (De Mendiburu, 2014; Harrell Jr, 2017; Wood & Wood, 2017), with a significance level of $\alpha < 0.05$.

Condition factor (Kn) was assessed over annual and interannual temporal scales to test whether environmental parameters affected *S. aurita* reproduction. The Generalized Additive Model (GAM) (Hastie & Tibshirani, 1986; Diankha et al., 2018) was used: (i) to quantify the contribution of the environmental variables (CUI, SST); and (ii) to investigate ranges of each environmental variable associated with condition factor. This model does not require any prior assumption on the functional link between each variable and the condition factor. The explanatory variables included in the model were: SST, CUI. We used the smooth function "s", estimated from the data. This function is used to define smooth terms in the GAM model formulas. The function does not evaluate a smooth (spline), but exists only to help configure a model using spline-based smoothing (Wood & Wood, 2017). Multi-collinearity of explanatory variables was tested using the variance inflation factor (VIF) on SST, CUI (Tiedemann & Brehmer, 2017). The variance inflation factors (VIFs) were calculated for all environmental variables to detect possible high dimensional collinearities (Zuur et al., 2010; Tiedemann & Brehmer, 2017; Diankha et al., 2018). A VIF <2 for all tested explanatory variables was considered adequate (Zuur et al., 2010). Because recruitment was estimated by season [to focus on species biology (the seasonal influence on fecundity)] (Boëly, 1982), season was the temporal unit used to evaluate the effect of environmental variables. The seasonal and interannual means of these three variables were also computed.

$$Model\ <- gam(Kn \sim s(CUI) + s(SST), data = Input\ data) \quad (9)$$

The χ^2-test was used to compare sex ratios and proportion of individual in each stage, which made it possible to determine whether the variables observed for the Petite côte and the Northern part of *S. aurita* were independent. The Petite côte (from 14° 36' N to 13°36' N) extends from the south of the peninsula of Cap Vert (Dakar) to the delta of Saloum at the border with The Gambia, and includes a 130 km long and 10 km wide continental shelf (Fig. 1). We used analyses of variance (ANOVAs) to compare reproductive parameters between males and females and the growth performance index (φ') of different oceanic regions (Mediterranean, Western and Eastern Central Atlantic), followed by Kruskal-Wallis tests. The growth performance index (φ ') was used to compare growth rates and to assess the potential for growth under various environmental stresses.

2.5. Ethics statement

No specific authorization was required for any activities undertaken during this work at any of the sites visited. The study was conducted in the waters of the Senegalese State. The activities carried out were in collaboration with the Local Fishing Committee (CLP in French) and the local fishermen. Threatened or protected species have not been involved in any part of the field studies.. No approval was required from the Institutional Animal Care and Use Committee, and no field license was required during any part of the experiment.

3. RESULTS

3.1. Size spectra and length-weight relationships

The length-frequency distributions between coastal areas (northern and southern part) showed that *S. aurita* off the northern part are larger (mode: 32 ± 2 cm) than fish caught off the southern coast (two modes: 13 ± 1 and 24 ± 3 cm) (Fig. 2). The size distribution of the southern population exhibited a higher peak at a smaller size (24 cm) relative to the northern individuals (peak at 32 cm).

The relationship between the total weight and total length was allometric [a= 0.008 ± 0.001; b = 3.02 ± 0.01, and r = 0.93 (n = 4397)]. Fig. 3 indicates fish growth in length to be faster than gaining weight when it is young and the older the fish the less the fish is growing in length but is gaining in weight. Only in a very short period, it seems that the fish is relatively seen gaining weight and length at the same rate.

3.2. Temporal variability of condition factor and environmental parameters

The condition factor (Kn) varied seasonally (X^2 = 22.01, df = 11, p = 0.001) with maximum values in May and September (Fig. 4a). The increase in Kn from February to May corresponds to a period of high upwelling intensity (CUI) and low sea surface temperature (SST) along the "Petite côte" (Fig.1) in March–April. Thereafter, Kn declined until August as the CUI declined. A maximum Kn in September was again followed by a decline in CUI and an accelerated decline in SST. The seasonal cycle of declining SST coincides with an increase in CUI because strong offshore, wind-induced upwelling in winter brings cold water to the surface. The relationship between Kn and CUI and SST showed wider amplitude on an annual basis than did seasonal variations (0.88 to 1.14, Fig. 4b). The condition factor for *S. aurita* remained fairly stable over the study 17-year period, except for two peaks, one in 1998 (1.2) and the other in 2003 (1.1). Over the period 1995-2011, SST and CUI varied inter-annually. Mean sea surface temperatures increased in 1998, 2001, 2005, 2008 and 2010, but decreased in 1999 and 2009. The most striking feature during this period was the slight drop in the upwelling index in1997 at 0.84 $m^3 s^{-1} m^{-1}$. However, as a result of this slight weakening of the CUI, the CUI showed a rapid and considerable increase in 2004 and 2009. Although both condition factor and environmental phenomena varied seasonally, the variation in Kn was related to CUI (F-stat= 6.186; p = 0.0143) and not for the SST (F-stat = 3.238; p = 0.0745). The model explains 5.19 % of the observed variability with R-sq. (adj) = 0.03. During the study period (1995-2011), the condition factor reached its maximum at CUI ≈ 1 $m^3 s^{-1} m^{-1}$ in 1995, 2003 and 2006 (Fig. 5).

3.3. Growth parameters

Based on the length frequency data, L_∞, K and φ' for July 2014 to June 2015 were estimated to be 35.4 cm, 0.26 $year^{-1}$ and 2.51 respectively. *Sardinella aurita* grows quickly during its first year, while subsequent growth rates decline gradually with age. No statistical differences between the growth performance index (φ') of historical data collected off the Senegal coast and data collected from other areas of the Eastern Central Atlantic was found (ANOVA: F value = 2.371, p = 0.139) (Appendix, Table I). However, we did find a significant difference between φ' data from the Senegal coast and other regions (West Atlantic, East Atlantic, and Mediterranean) (ANOVA: F value = 10.81, p= 0.001) (Appendix, Table I). The Eastern Central Atlantic and Western Central Atlantic did not differ statistically (Tukey: df = 0.15, p = 0.171), while the Eastern Central Atlantic and the Mediterranean differed significantly (Tukey: df = 0.33, p = 0.001). The growth parameters (L_∞, K and φ') of *S. aurita* in the Eastern Central Atlantic were higher than Western Central Atlantic and Mediterranean Sea (Fig. 6) and decline over time (from 1932 to the present study), while in the West Atlantic, there was an increasing of L_∞. Asymptotic length (L_∞) was lower in the Western Central Atlantic than in the Eastern Central Atlantic (Tukey: df = 0.15, p = 0.001). *Sardinella aurita* inhabiting these two coastal systems (Eastern and Western Central Atlantic) are characterized by higher lifespans (t_{max}), higher maximum lengths (L_{max}) and longer asymptotic lengths (L_∞) than those inhabiting the Mediterranean (Tukey: df = 0.15, p = 0.001) (Appendix, Table I). However, growth parameters seem to have remained constant in the Mediterranean over the period examined (from 1932 to 2012; Fig. 6).

3.4. Maturity

Sex ratio (SR) for *S. aurita* was in balance with around 51% females. The cumulative frequency curve of individuals that had reached or passed maturity Stage 3 indicated that 50% (L_{50}) of males were mature at 24.8 ± 1.0 cm, while 50 % of females were mature at 25.7 ± 1.8 cm. We found significant differences between maturity stages (proportions of fish in each stage) for the period investigated (1995–2011) (Table III). This sentence is linked with the results showed in the Fig. 7 and 8.

Two main reproductive periods were determined from our analysis of sexual maturity stages and GSI. For this study, the reproductive period was defined as the period between gonad maturation (Stage ≥3) to spawning. The first reproductive period occurred from February to May off Senegal. Within this period, gonad maturation occurred in February, April and May. Our analysis of sexual maturity showed that individuals in Stages V were present in January, March, and April and from October to December after the first reproductive period. A second reproductive period, with continuous spawning (more intense than during the first period), occurred from October to the end of December.

The monthly record of sexual maturity stages showed that females in stage VI and VII were more abundant from January to February and from July to December. The proportion of females at stages > IV peaked in January to April, and September to December (Fig. 7a). Stage III females were mainly present in June. Stage V males were present in February-March and from August to December. Stage III and IV males were found throughout the year mostly from May to November (Fig. 7b).

Monthly changes in GSI followed sexual maturity Stages IV and V (Fig. 8). There were two spawning peaks in April and October. In October, there was a higher presence of Stage IV and V individuals and higher GSI values relative to September and November for males and females. A resting period between spawning occurred in June and August.

4. DISCUSSION

4.1. Growth strategy of *Sardinella aurita*

Three main size classes exist among *S. aurita* inhabiting Senegal coastal waters, suggesting that the adults mainly inhabit more northern coastal waters, while juveniles and young breeders (<25 cm) are concentrated off the southern coast. The highest concentration of juveniles and young breeders off the “Petite côte” of Senegal has been linked to a nursery area located there (Roy et al., 1989; Tiedemann & Brehmer, 2017). Roy et al. (1989) assumed that the concentration of juveniles and young breeders in Senegal’s southern coastal waters may be due to differential functioning, whereas the northern waters, northward the Cap Vert peninsula (Dakar), where physical properties differ significantly, i.e., mesoscale activity, Ekman coastal divergence and upwelling patterns (Ndoye et al., 2017), which play a role in system productivity and retention processes mean (e.g., larval retention). Indeed, the “Petite côte” of Senegal is characterised by high phytoplankton biomass (Auger et al., 2016) and high chlorophyll content during upwelling events (Auger et al., 2016), which are conditions optimal for providing a suitable nursery (Tiedemann & Brehmer, 2017). Tiedemann & Brehmer (2017) suggested that the retention of ichthyoplankton over the shelf was related to food availability, and is important for the reproduction of many pelagic species during the planktonic stages. Indeed, they are able to detect variations in temperature and can follow masses of water whose behavior or quality (nutritive, calorific) suits them (Chikhi, 1995). Thus, temperature and food availability is generally the most important condition for habitat selection.

Growth parameters (L_∞, K and φ') for *S. aurita* in the Eastern Central Atlantic differ from patterns in the Mediterranean Sea, but no significant differences were found between the Eastern and Western Central Atlantic. Differences in *S. aurita* growth between the central Atlantic and Mediterranean may be related to differences in food abundance or environmental conditions (Wootton, 1998). The growth parameter and asymptotic length for a same short life species are higher in the most productive area (Fig. 6). The availability of food and temperature in Mediterranean is much lower than the Eastern Central Atlantic (Stergiou, 2000). Indeed, the instability of primary production and hydrographic conditions (Puerta et al., 2015) could make the Mediterranean less suitable for *S. aurita* populations. The complex mesoscale eddy complexes of the western Mediterranean resulting from the influx of Atlantic waters have different implications for feeding, transport and larval survival. This has important consequences for the productivity and functioning of the Mediterranean pelagic ecosystem (Puerta et al., 2015). According to Bakun (2013), some mid-scale vorticity features provide improved feeding and retention conditions for pelagic larvae. While in the Californian Current, a significant delay in the spring transition (Barth et al., 2007) might change the ecosystem, affecting primary production (Thomas & Brickley, 2006), zooplankton (Mackas et al., 2006), and fish (Brodeur et al., 2018). For example, the growth of Atlantic herring *Clupea harengus harengusis* related in part to the temperature of summer water (Anthony & Fogarty, 1985) while in Pacific herring *Clupea harengus pallasi*, Haist and Stocker (1985) found that SST of 12 ° - 13 ° C was optimal for juvenile growth. In the Eastern Central Atlantic, the seasonal variability of wind forcing is the main driver of seasonal variability in surface chlorophyll (Auger et al., 2016) and affects the distribution and abundance of fish populations, and their associated fisheries, over a large range of timescales (Thiaw et al., 2017). The environmental processes responsible for changes in growth rates between different regions are not always clearly identified, but in most of the examples given, they seem to be related to temperature and abundance of food.

In addition to environmental factors, high rates of fishing mortality can alter population structure and growth rates. For example, in the Mediterranean Sea (Greece), it increased from 32 cm in 1952 (Ananiades, 1952) to 21 cm in 2005 (Tsikliras et al., 2005) (Δ = - 11 cm). On the contrary, there is an increase in asymptotic length in the western central Atlantic of Venezuela (Mendoza et al., 1994) estimated at 26 cm (in 1994) and recently, the study of Barrios et al. (Barrios et al., 2010) showed a slight increase in asymptotic length to 27 cm (Δ = + 1 cm). In Atlantic Eastern Central, we observe a decrease of asymptotic length L_∞ of *S. aurita*, particularly in Senegal, from 42 cm in 1950 (Postel, 1955) to 35.4 cm in this study (2013-2014) (Δ = - 7 cm). In Greece, the commercial exploitation of *S. aurita* has steadily increased since the early 1990’s (National Statistical Service of Hellas, 1990-2002) due to a high fish market demand drive by the canning industry as bait for the profitable tuna and swordfish fisheries. Total landings increased from 69 t in 1990 to 2 733 t in 2002 (Tsikliras, 2004). At the same time, in the west-central Atlantic area, *S. aurita* has not yet reached the state of overexploitation. In addition, a drastic reduction in catches was reported in 2009 (WECAFC, 2014). *Sardinella aurita* has been overexploited off West Africa for a decade (FAO, 2016) and Thiaw et al. (2017) assumed that increased fishing presence could have a strong influence on the decline in *S. aurita* growth in Senegal. As concluding remark, the environmental characteristics and the level of fishing pressure on a small pelagic fish species had a balanced impact on their growth parameters and asymptotic length at least for *S. aurita*, and thus should be considered as phenotypic parameters.

4.2. Reproductive strategy of *Sardinella aurita*

A sex ratio biased slightly toward females (51.1%) agrees with results of several authors studying the *S. aurita* population off Senegal (Conand, 1977; Boëly, 1982), Mauritania (Wague & Mbodj, 2002) and the Mediterranean. Boëly (1979) noted there was a slight predominance of females (55%) among younger and older individuals off the Senegal coast. This slight difference in sex ratio could be attributed to differences in reproductive growth [(more females are produced) (Boëly, 1982)], differential mortality or differences in the energy cost of reproduction between sexes (Tsikliras & Antonopoulou, 2006). Size at first sexual maturity for males and females was 24.8 and 25.7 cm, respectively in our present study. Conand (1977), Boëly (1982), and Fréon (1988) found smaller size at first sexual maturity than present study while Goudiaby et al. (2008) and Samba (2011) found larger sizes at first sexual maturity than present study (see Appendix, Table II) for both males and females. According to Boëly (1982), size of *S. aurita* at first sexual maturity may vary from one year to another or within the same year. In the Mediterranean, the size at first maturity of *S. aurita* varies from 15 cm to 16.8 cm for females and from 14 cm to 15.8 cm for males, whereas in the Western Central Atlantic (where most studies have focused on females), the size at first sexual maturity ranged from 18 cm to 20 cm. We can therefore assume that the size at first sexual maturity for *S. aurita* also varies throughout its distribution. Size at first maturity depends on environmental and genetic factors (Wootton, 1998), but may also be influenced by other factors, such as long-term fishing pressure (Thiaw et al., 2017). Adaptive phenotypic plasticity is often the only way for populations to react quickly to environmental change and thus ensure their survival. A change in size at first maturity for an *S. aurita* population is probably one of the best indicators of its response to changes and/or stress in its environment. The length-weight relationship parameters calculated for *S. aurita* caught in the Eastern Central Atlantic (Mauritania and Senegal) are similar in values to those calculated for fish in the Western Central Atlantic (off Venezuela). However, lower values have been calculated for fish caught in the Mediterranean (Koutrakis & Tsikliras, 2003). Many factors (*e.g.*, morphology, proportion of fatty acids, sex, sexual stage, egg density, condition of the digestive tract, etc.) can lead to fluctuations in the weight of an individual fish (Wootton, 1998). Weight is determined by the condition factor (Kn). Variations in Kn suggest that males and females adopt a similar energy intake strategy during gonad maturation and spawning in that Kn reaches its maximum value the month before the beginning of spawning (May or September). According to Boëly (1982) and Fréon (1988), the weight of *S. aurita* seems to be intimately related to upwelling intensity and agrees with the results obtained in present study..

Studies of *S. aurita* populations sampled off the coast of Senegal have shown that sexual activity occurs over most of the year and that number and magnitude of spawning peaks change from year to year and from one area to another (see Appendix, Table II). The spawning pattern we found in our study corresponds to the patterns identified by Cury and Fontana (1988) in Senegal. However, the pattern differed from those identified by Conand (1977), Boëly (1982), Goudiaby et al (2008) and Samba (2011) for Senegal and by Wague and Bodj (2002) for Mauritania. Spawning seems to be correlate with periods of high zooplankton abundance. In West Africa, breeding strategies are associated with local environmental conditions (Fréon, 1988; Roy et al., 1989). In places where spawning occurs in twice annually, *S. aurita* is better able to exploit its environment and maintain its population. A single peak of reproduction over a two-month (Tsikliras & Antonopoulou, 2006), three-month (Gaamour et al., 2001), or four-month period (Ananiades, 1952) occurs in the Mediterranean, whereas a more extended breeding season occurs in the Western Central Atlantic (October to April), which supports our results for those coastal areas. We observed in present study that peak spawning corresponds to periods of low sea surface temperature (February or March, depending on the year). This may be due to temperature having a direct effect on the flow of energy through an ecosystem and population dynamics (Thiaw et al., 2017; Diankha et al., 2018). Species-specific differences in fish tolerance to abiotic factors (e.g., temperature, food availability, and other abiotic factors) show species-specific changes in population fecundity. In patients, embryonic stage duration and larval survival are treated with physical processes, at water temperature and food availability, which affect recruitment in upwelling systems (Tiedemann & Brehmer, 2017). Repetitive breeding tends to have a longer spawning season than recruited spawners; thus increasing the likelihood that their offspring will encounter favourable environmental conditions for growth and survival. The many environments studied, it is generally accepted that changes in SST alter ecological stability. Ben-Tuvia (1960) found a positive relationship between the SST in March (pre-spawning period) and the strength of the year-round sardinella age classes in Israel (Mediterranean). In Southern California (Eastern Central Atlantic), warm temperatures allow larval development and successful breeding of sardines (MacCall, 2009). Thus, water temperatures and food availability can affect abundance (Thiaw et al., 2017), recruitment (Diankha et al., 2018), stages of egg and larvae (Tiedemann & Brehmer, 2017), distribution (Sarré et al., 2018) and productivity (Auger et al., 2016) pelagic fish. Any modification at the level of temperature and upwelling might cause a mismatch between *S. aurita* reproduction and occurrence of their food and other organisms, leading to recruitment failures.

Sardinella aurita adopts a specific growth and reproductive strategy that is a reaction to specific environmental cues. We observed significant differences in the Eastern Atlantic Ocean *vs* the Mediterranean Sea. The primary spawning period for *S. aurita* occurs in times of high zooplankton abundance (during upwelling) and in places that is generally the most favourable for early life stage development. This strategy allows *S. aurita* to adapt its abundance to fluctuations in food availability. Surprisingly, even under the effect of multiple stressors (mainly environmental changes), the size at spawning for *S. aurita* does not vary in the Canary Current LME. Such result should be considered in management purposes particularly in the context of climate change, and suggest that such parameters must be regularly updated for accurate fisheries management.

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Formal analysis: BSB KB JK.

Methodology: BSB KB.

Project administration: BSB PB.

Resources: FNS.

Software: BSB KB.

Validation: PB, WE.

Supervision: MF MD.

Visualization: BSB.

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Writing – review & editing: PB WE JK KB.

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COMPETING INTERESTS

The authors have declared that no competing interests exist.

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Figures captions

FIG. 1: Map of the study area with the localization of sampling stations corresponding to the main landing ports along the Senegal coast. The northern section includes Saint-Louis, Kayar, and Yoff; the southern section includes the “Petite côte” (Hann, Mbour, and Joal) and Casamance (Kafountine). Gambian EEZ was not taking into account in the study, neither were Mauritanian EEZ and Bissau Guinean EEZ.

FIG. 2: Size frequency distributions for *Sardinella aurita* caught off the Senegal coast from July 2013 to June 2014. Total length was used. Three modes exist in the frequency data: one for fish located off the northern coast (black) (32 cm, n = 10.109) and two for fish caught off the southern coast (grey) (13 and 24 cm, n = 22.237).

FIG. 3: Length-weight relationships for *Sardinella aurita* caught off the coast of Senegal (data: 1995 to 2011; n = 4397). The black line is the exponential regression curve fitted to all measurements.

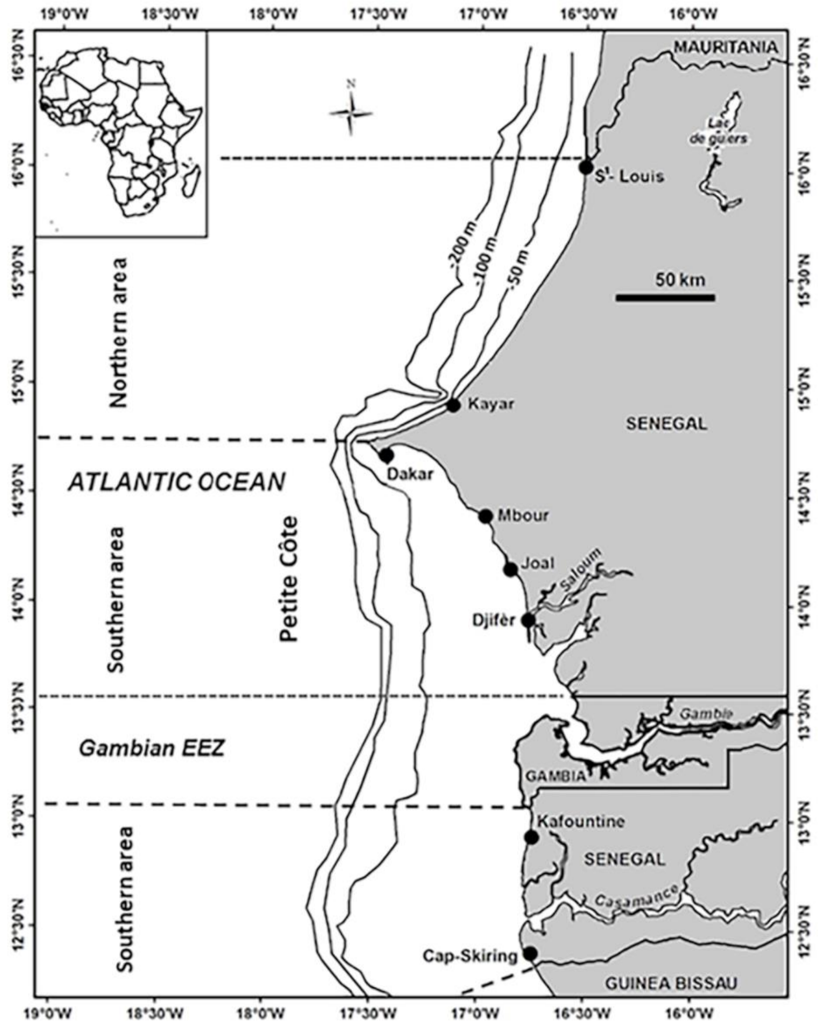
FIG. 4: *Sardinella aurita* condition factor (Kn) data (black line), combined to seasonal environmental components for Senegal coastal waters (1995 to 2011): coastal Sea Surface Temperature (dashed line) (Modis AVHRR) and Coastal Upwelling Index (grey line). (a) Monthly and (b) annual mean data.

FIG. 5: Condition factor (Kn) of *Sardinella aurita* as a function of Coastal Upwelling Index (CUI) throughout the study (1995-2011).

FIG. 6: Auximetric plot (double logarithmic plot of parameters K and L_∞) for *Sardinella aurita* populations for four coastal areas. Data from this study in Senegal (square) and from a literature review of Eastern Central Atlantic (circles), Mediterranean Sea (triangles) and Western Central Atlantic (plus signs). Abbreviations: L_∞: (asymptotic length, in cm) and K: [coefficient of growth rate (by year)].

FIG. 7: Monthly sexual maturity stages (*sensu* Fontana 1969) for *Sardinella aurita* off the Senegal coast (1995 to 2011). (a) female (n = 2131) and (b) male (n = 2266)

FIG. 8: Gonado-somatic index (GSI) for *Sardinella aurita* in Senegal coastal waters (1995 to 2011). (a) female (n = 2131) and (b) male (n = 2266). Means are represented by the horizontal line inside the box plots. Standard errors are represented by circles.


19°0'W
18°30'W
18°0'W
17°30'W
17°0'W
16°30'W
16°0'W
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13°30'N
13°0'N
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N
MAURITANIA
Lac de guiers
Sᵗ- Louis
-200 m
-100 m
-50 m
50 km
Northern area
Kayar
SENEGAL
Dakar
ATLANTIC OCEAN
Mbour
Southern area
Petite Côte
Joal
Saloum
Djifèr
Gambie
Gambian EEZ
GAMBIA
Kafountine
SENEGAL
Southern area
Casamance
Cap-Skiring
GUINEA BISSAU

FIG. 1

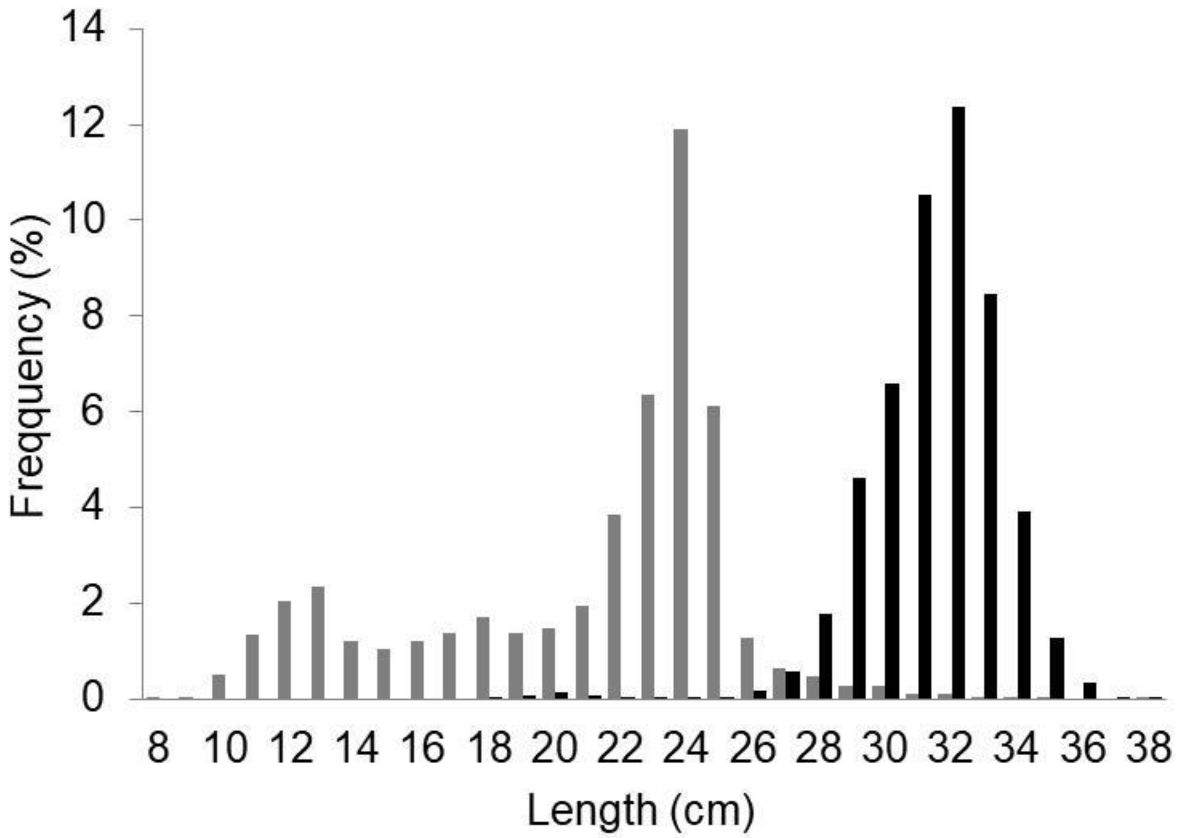

14
12
10
8
6
4
2
0
Freqquency (%)
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
Length (cm)

FIG. 2

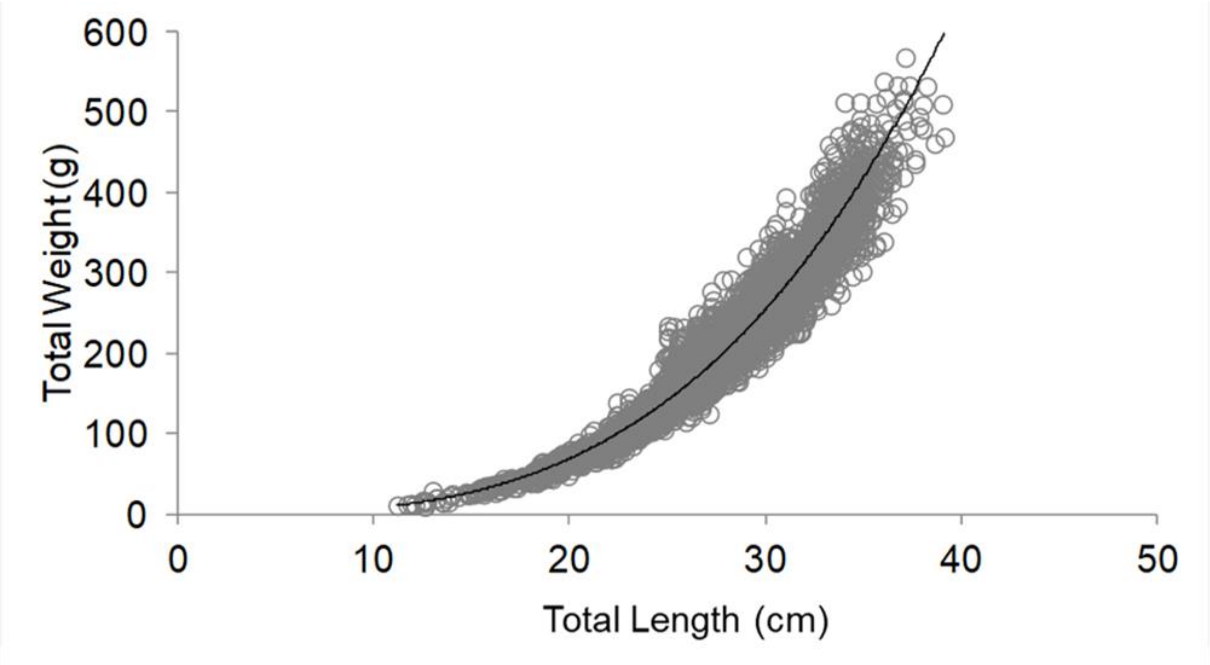
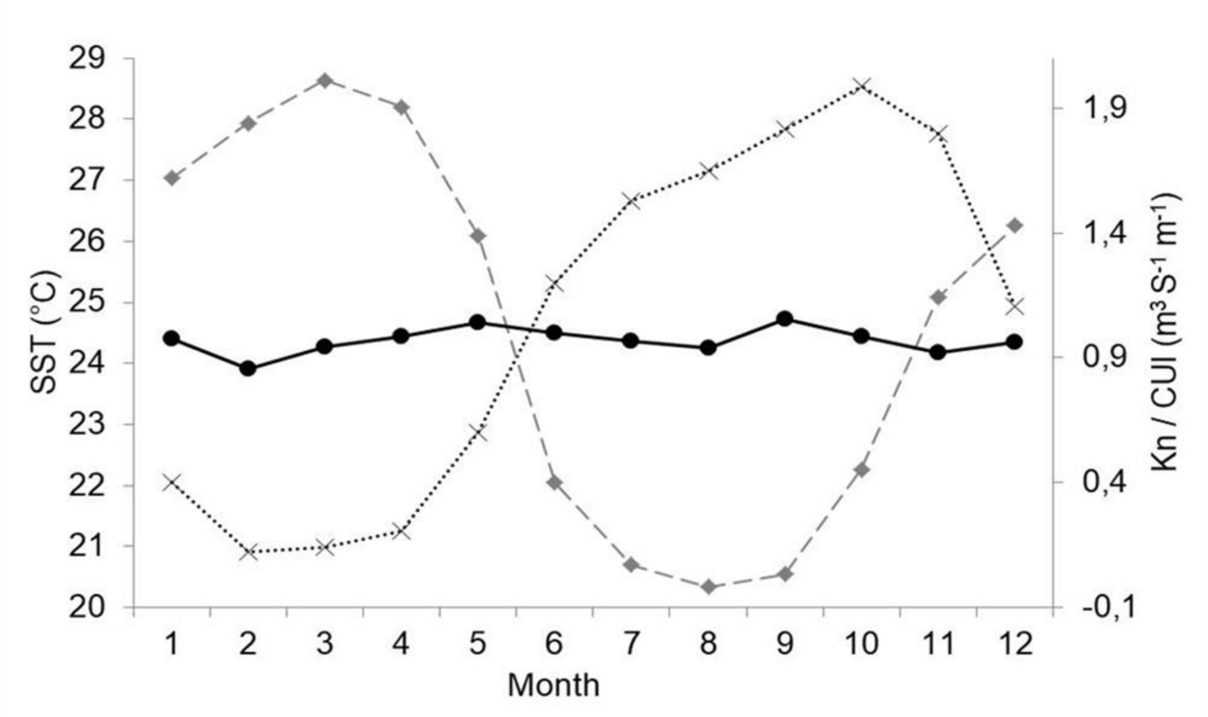
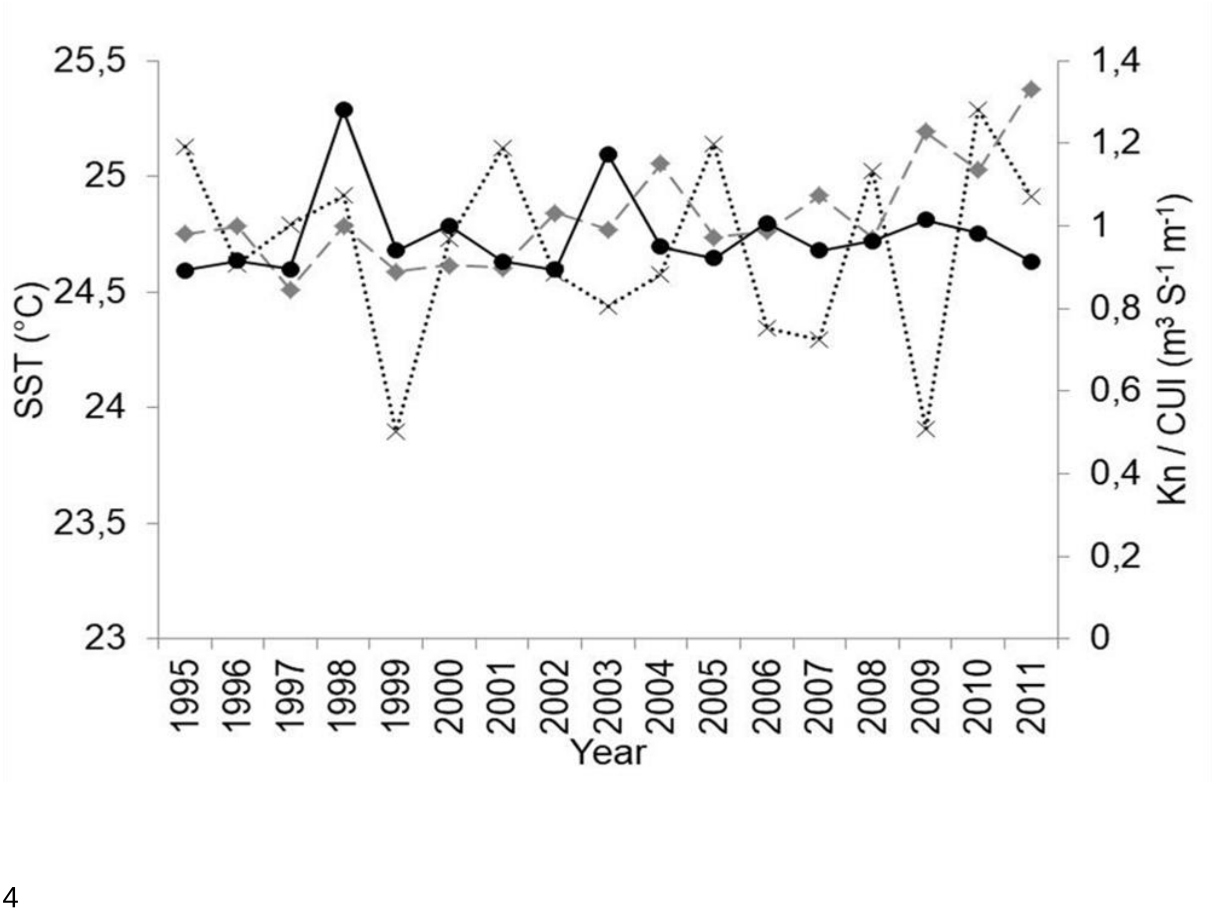

Total Weight (g)
600
500
400
300
200
100
0
0
10
20
30
40
50
Total Length (cm)

FIG. 3


SST (°C)
29
28
27
26
25
24
23
22
21
20
Kn / CUI ($m^3 S^{-1} m^{-1}$)
1,9
1,4
0,9
0,4
-0,1
1
2
3
4
5
6
7
8
9
10
11
12
Month

a)


SST (°C)
25,5
25
24,5
24
23,5
23
Kn / CUI ($m^3 S^{-1} m^{-1}$)
1,4
1,2
1
0,8
0,6
0,4
0,2
0
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year

b)

FIG. 4

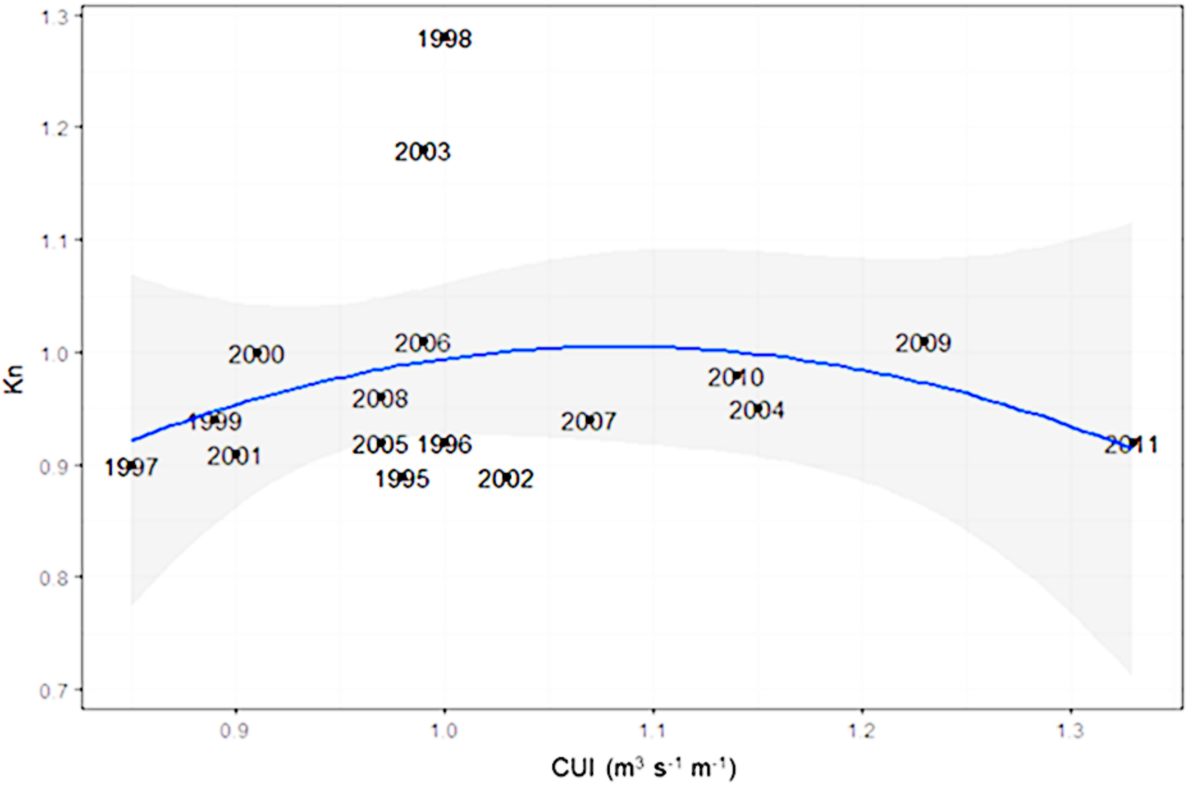

1.3
1.2
1.1
1.0
0.9
0.8
0.7
Kn
0.9
1.0
1.1
1.2
1.3
CUI (m³ s⁻¹ m⁻¹)
1998
2003
2000
2006
2009
2010
2008
2004
1999
2007
2005
1996
2011
1997
2001
1995
2002

FIG. 5

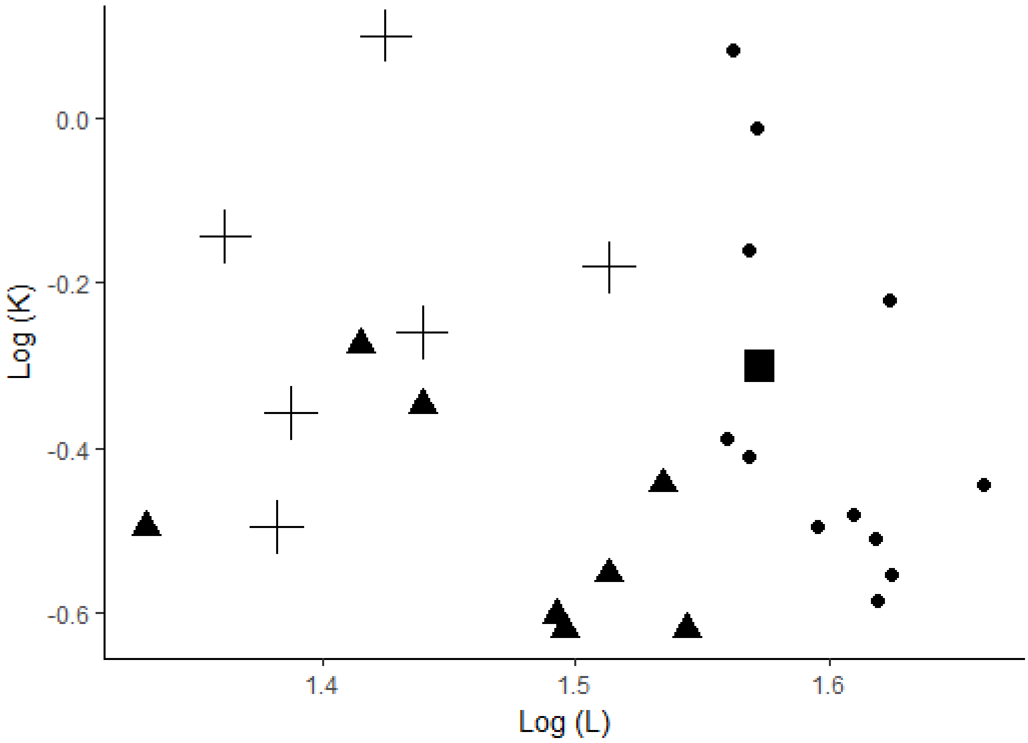
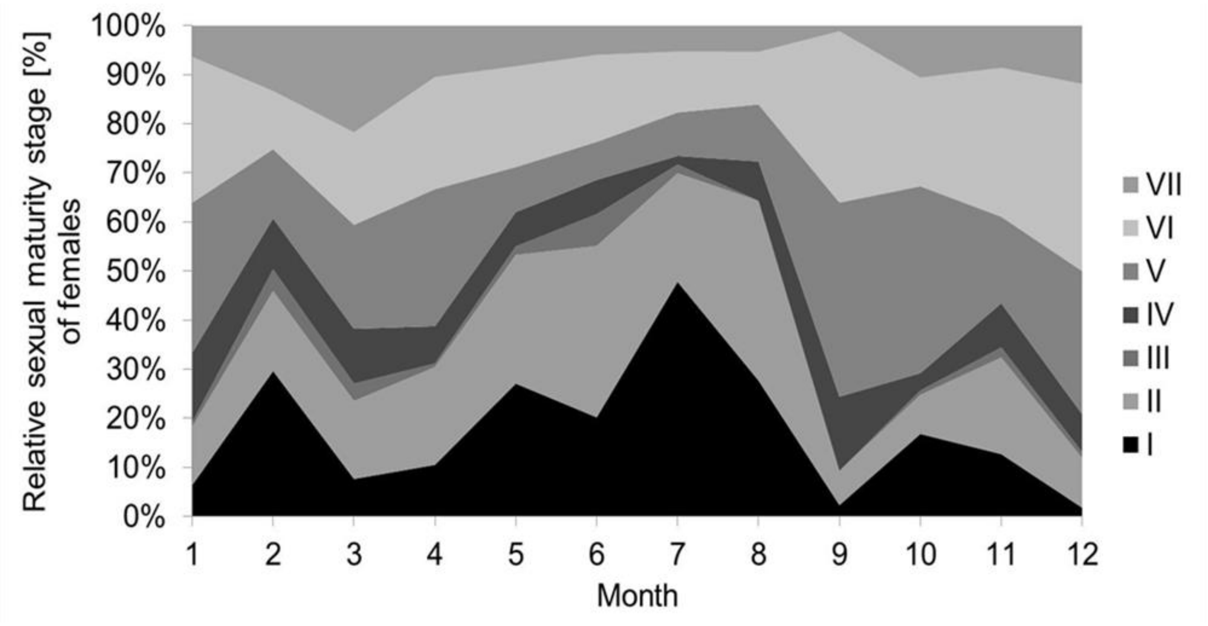
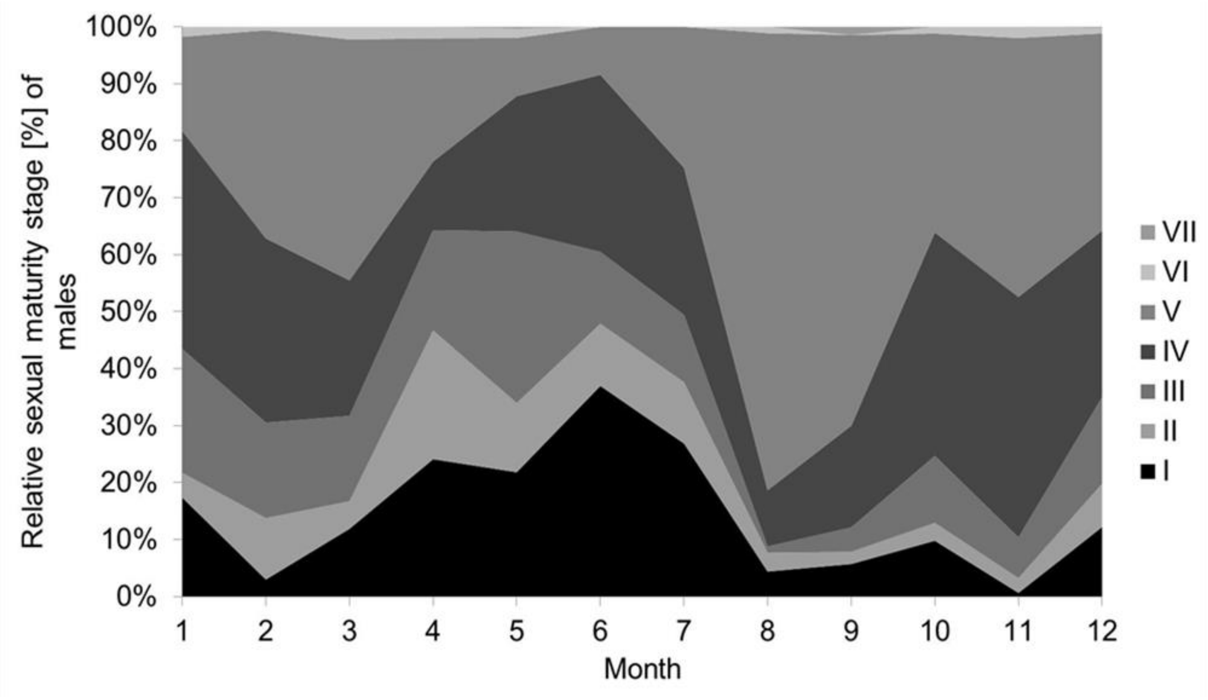


FIG. 6


Relative sexual maturity stage [%] of females
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
2
3
4
5
6
7
8
9
10
11
12
Month
VII
VI
V
IV
III
II
I

a)


Relative sexual maturity stage [%] of males
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1
2
3
4
5
6
7
8
9
10
11
12
Month
VII
VI
V
IV
III
II
I

b)

FIG. 7

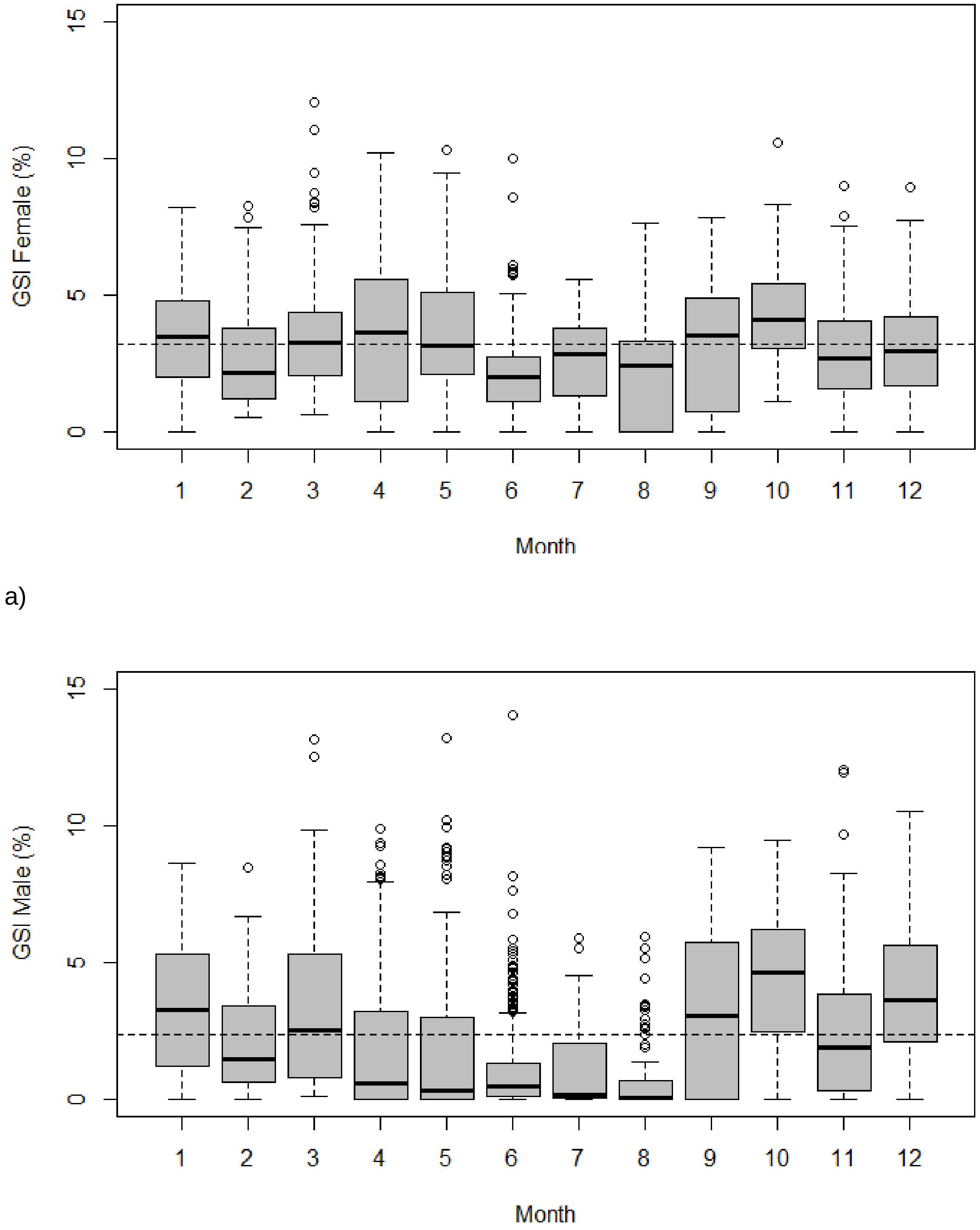

GSI Female (%)
0
5
10
15
1
2
3
4
5
6
7
8
9
10
11
12
Month
a)
GSI Male (%)
0
5
10
15
1
2
3
4
5
6
7
8
9
10
11
12
Month
b)

FIG. 8

TABLE I: *Sardinella aurita*. Number of monthly observations for all variables except weight, by sex and maturity stages.

	Month													
		1	2	3	4	5	6	7	8	9	10	11	12	Total
Sex	F	219	135	170	276	229	401	113	112	86	113	244	168	2266
	M	209	115	167	227	199	362	119	93	91	140	255	154	2131
	Total	428	250	337	503	428	763	232	205	177	253	499	322	4397
Stages	I	22	60	18	56	110	160	98	56	6	27	56	4	673
	II	33	27	45	66	105	184	38	51	9	12	56	21	647
	III	28	31	34	36	39	135	17	11	1	7	35	13	387
	IV	91	58	73	75	40	114	39	33	22	29	122	78	774
	V	175	38	97	173	64	68	20	36	107	139	132	119	1168
	VI	65	18	33	68	51	77	14	12	31	25	77	67	538
	VII	14	18	37	29	19	25	6	6	1	14	21	20	210
	Total	428	250	337	503	428	763	232	205	177	253	499	322	4397

TABLE II: A brief description of the maturity stages of *Sardinella aurita* used in this study according to Fontana (1969).

Stage	State	Description
I	Immature	Female gonad small and firm, transparent or light pink, invisible oocytes. Male gonad white or slightly translucent, very fine.
II	Rest	Characteristics of female and male gonads substantially identical to Stage I.
III	Maturation start	Female gonad, firm and of color varying from pale pink to light orange, some oocytes are sometimes visible through the ovarian membrane. Male gonad whitish firm, no liquid will flow if an incision is made.
IV	Pre-egg / pre-release	Female gonad bigger and less firm usually light orange then dark. Oocytes visible through the ovarian membrane make the surface of the ovary granular Male gonad softer and white. A whitish liquid flows as soon as an incision is made.
V	Sperm laying / Emission	Female gonad very large occupying the entire abdominal cavity. Very fine ovarian membrane. Hyaline and large-sized ovules are perfectly visible and are expelled at the slightest pressure on the abdomen. Large and soft male gonad. The sperm flows at the slightest pressure exerted on the abdomen.
VI	End of spawning / Emission and recovery before subsequent spawning	The female ovary is flask very vascularized. Its color varies from pink salmon to red. Through the ovarian membrane the oocytes of 460 micrometers are perfectly visible. Numerous hyaline spaces / Flaccid male gonad with a very fine vascularization especially in the posterior part.
VII	End of the last laying / Emission and involution of the ovary	Female ovary completely collapsed very flaccid of red color due to a very strong vascularization. At this stage, the ovary has the characteristic appearance of an empty bag. Male gonad very flaccid, exhausted and strongly vascularized.

TABLE III: Proportion of *Sardinella aurita* male and female at the different sexual maturity stages (report to table I) in Senegal (data: 1995 to 2011). χ^2: Chi-square test; + : < 0.05.

Stages	Female (%)	Male (%)	X^2	*p*-value
I	56.8	43.2	2.658E+09	+
II	66.6	33.4	1.0519e+10	+
III	12.6	87.4	2.188e+10	+
IV	20.8	79.2	2.2785e+10	+
V	34.9	65.1	6.424E+09	+
VI	93.2	6.8	2.9401e+10	+
VII	98.9	1.1	1.3085e+10	+

Appendix

TABLE I: Growth parameters and natural mortality of *Sardinella aurita* estimated in Senegal (present study and historical review) and from Eastern and Western Central Atlantic as well as the Mediterranean Sea. The growth parameters have been estimated according to three different methods, *i.e*., scale, otoliths or length frequencies as in the present study (size expressed in cm). TL: Total Length, FL: Fork Length, L_∞: L_t value when the growth rate is zero; K: coefficient of growth rate, t_0: the time “t” when the fish length is zero, φ’: growth performance index, M: natural mortality, t_{max}: the longevity of the species. NR: not reported.

Country	Method	L_∞	L_∞	K	t_0	φ’	t_{max}	M	References
		FL	TL						
Western Central Atlantic									
Brazil	Scales	20.7	24.4	0.44	-0.39	2.42	6.42	0.46	Matsuura (1971)
Brazil	Otoliths	19.6	23.0	0.72	-0.25	2.58	3.91	0. 76	Saccardo et al. (1988)
Brazil	Otoliths	23.2	27.5	0.55	-0. 30	2.62	5.15	0.58	Cergole et al. (2002)
Venezuela	NR	20.5	24.1	0.32	-0.55	2.27	8.82	0.34	Heald & Griffiths (1967)
Venezuela	Length frequencies	22.5	26.6	1.26	-0.13	2.95	2.25	1.33	Mendoza et al. (1994)
Venezuela	Length frequencies	27.3	32.6	0.66	-0.05	2.85	4.48	0.66	Barrios et al. (2010)
Mediterranean									
Algeria	Length frequencies	29.3	35.0	0.24	-0.70	2.47	12.01	0.24	Bouaziz et al. (2001)
Croatia	Length frequencies	28.6	34.2	0.36	-0.94	2.62	7.39	0.40	Mustać and Sinovčić (2012a)
Egypt	NR	22.0	26.0	0.53	0.34	2.55	5.00	0.60	El-Maghraby et al. (1970)
Greece	Scales	27.3	32.6	0.28	-0.57	2.47	10.14	0.29	Ananiades (1952)
Greece	Scales	18.3	21.4	0.32	-0.55	2.17	8.82	0.34	Tsikliras et al. (2005)
Israel	Length frequencies	26.1	31.1	0.25	-1.80	2.38	10.20	0.29	Ben Tuvia (1956)
Spain	Length frequencies	23.2	27.5	0.45	-0.38	2.53	6.28	0.47	Navarro (1932)
Tunisia	Otolith	26.3	31.3	0.24	-2.50	2.37	10.00	0.30	Gaamour et al. (2001)
Eastern Central Atlantic									
Canary Islands	Length frequencies	34.6	41.5	0.31	-0.63	2.71	11.34	0.26	Navarro (1932)
Congo	Length frequencies	31.0	37.0	0.69	-0.56	2.96	5.82	0.51	Rossignol (1955)
Mauritania	Scales	34.6	41.6	0.26	-0.87	2.65	13.11	0.22	Chesheva (1998)
Mauritania	Otoliths	31.0	37.0	0.39	1.46	2.72	9.15	0.32	Pascual-Alayón et al. (2008)
Mauritania	Scales and Otoliths	32.9	39.4	0.32	-1.78	2.69	10.89	0.27	Pascual-Alayón et al. (2008)
Mauritania	Otoliths	30.4	36.3	0.41	-0.94	2.72	6.38	0.47	Iglesias et al. (2009)
Mauritania - Senegal	Scales	34.0	40.7	0.33	-0.60	2.74	10.81	0.27	Thuoc & Szypula (1973)
Mauritania - Senegal	Scales	38.1	45.9	0.36	-0.69	2.87	9.91	0.30	Maxim and Maxim (1988)
Mauritania - Senegal	Length frequencies and Scales	31.2	37.3	0.97	-0.21	3.12	4.58	0.65	Boëly et al.(1979)
Senegal	Length frequencies	35.0	42.0	0.60	-0.24	3.02	4.75	0.63	Postel (1955)
Senegal	Scales	35.0	42.1	0.28	-0.99	2.70	12.22	0.24	Krzeptowski (1982)
Senegal	Length frequencies and Scales	30.6	36.5	1.21	-0.06	3.20	3.97	0.75	Boëly et al. (1982)
Senegal	Length frequencies	29.4	35.4	0.26	- 0.76	2.51	10.77	0.27	Present study

TABLE II: Reproductive parameters in Western Central Atlantic (*i.e.* Brazil and Venezuela), in Mediterranean Sea (*i.e.* Greece, Croatia and Tunisia) and in Eastern Central Atlantic (*i.e.* Senegal and Mauritanian) for *Sardinella aurita*. TL: Total Length (cm); FL: Fork Length (cm); N: Number of individual; SR (%): Sex Ratio; L_{50} (cm) represents the size at which 50% of individuals in a given population reach the maturity; 'a' and 'b': allometric coefficient; (*) Reproduction period; NR: not reported.

Country	Method	N	Month												Male	Female	a	b	SR	References
			1	2	3	4	5	6	7	8	9	10	11	12	L_{50}	L_{50}				
Western Central Atlantic Ocean																				
Brazil	TL	250	*	*	*	*							*	*	NR	18.60	NR	NR	NR	Petermann and Schwingel (2016)
Venezuela	TL	92834	*	*	*								*	*	NR	19.70	1.0377	3.399	NR	Fréon et al. (1997)
Venezuela	TL	3736	*	*	*							*	*	*	NR	20.00	NR	NR	55.5	Gassman et al. (2008)
Mediterranean																				
Greece	TL	NR					*	*	*	*					14.00	15.00	NR	NR	NR	Ananiades (1952)
Croatia	TL	2033						*	*	*					15.80	16.60	NR	NR	NR	Mustać and Sinovčić (2012b)
Greece	TL	19	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0.0087	2.950	NR	Koutrakis and Tsikliras (2003)
Greece	TL	7942					*	*							15.50	16.80	NR	NR	50.5	Tsikliras and Antonopoulou (2006)
Tunisia	TL	918							*	*	*				14.10	15.20	NR	NR	NR	Gaamour et al. (2001)
Eastern Central Atlantic Ocean																				
Mauritania	FL	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0.007940	3.227	NR	Lawal and Mylnikov (1988)
Mauritania	TL	3073						*	*	*	*				34.61	34.61	NR	NR	55.0	Wague and Mbodj (2002)
Senegal	TL	1334					*	*				*	*		NR	23.45	NR	NR	52.0	Conand (1977)
Senegal	FL	2232	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0.000005	3.194	NR	Boëly (1982a)
Senegal	TL	9645		*	*	*	*					*	*		NR	21.59	NR	NR	55.0	Boëly (1982b)
Senegal	FL	2433	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0.006392	3.274	NR	Fréon (1988)
Senegal	NR	NR		*	*	*	*	*			*	*	*		NR	NR	NR	NR	NR	Cury and Fontana (1988)
Senegal	TL	3947				*	*	*				*	*		27.66	30.98	0.000038	3.162	50.5	Goudiaby et al. (2008)
Senegal	TL	NR										*	*		21.10	26.55	0.000007	3.040	NR	Samba (2011)
Senegal	TL	4397		*	*	*	*	*			*	*	*		24.82	25.72	0.008	3.02	51.1	Present study