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Major changes in sardine growth and body condition in the Bay of Biscay between 2003 and 2016: Temporal trends and drivers

Veron Matthieu ^{1,*}, Duhamel Erwan ¹, Bertignac Michel ², Pawlowski Lionel ¹, Huret Martin ²

¹ Ifremer, Laboratoire de Biologie et Technologies Halieutique, 8 rue François Toullec, 56 100 Lorient, France

² Ifremer, Laboratoire de Biologie Halieutique, 1625 route de Sainte-Anne, 29 280 Plouzané, France

* Corresponding author : Matthieu Véron, email address : matthieu.veron@ifremer.fr

Abstract :

In the Bay of Biscay, mean body length and weight of sardines (*Sardina pilchardus*) have been decreasing since the early 2000s and could severely impact the fishing and seafood industry sector. These trends have no apparent link with fishing pressure, although the latter has been increasing since the late 2000s. As part of an effort to develop suitable assessment and management tools for this stock, we investigated the life-history traits of sardine and analyze its seasonal and inter-annual variations. Based on 14 years of morphometric data from both scientific surveys and professional samples, we analyzed the variability in sardine body condition and its responses to environmental changes. Generalized Additive Models revealed an age-sex specific decreasing trend in body length over the study period, with most of the variability explained by the age class. Linear Mixed Effect Models applied to the body condition evidenced its strong seasonality and an age class specific decreasing trend. Regardless of age class, maximal body condition is reached at the end summer, after the spawning and plankton productive periods. Overall, annual trends in body condition-at-age showed remarkable coherence, with a significant decrease since 2007 for all age classes, suggesting that factors influencing body condition operate at population level. The shift in sardine body condition towards lower values could be broken down into three periods, with a high dependence on surface Chlorophyll-a and sea surface temperature. However, this study highlights that the period supporting the main decrease in body condition is characterized by high Chlorophyll-a, the available proxy for food, which is counterintuitive. Such a result suggests more complex trophic responses involving secondary production, with potential shift in the timing of the production and/or the quality of the food. At the population level, those changes may have a long-term negative effect, with a decrease in body length and important changes in phenology (length at first maturity, reproductive phenology) and potential consequences on sardine population dynamics in the Bay of Biscay.

Highlights

► Strong dependence on age of both seasonal and inter-annual variability in body condition. ► Sardine body condition strongly declined between 2007 and 2011. ► Increase of temperature and changes in Chlorophyll-*a* may explain the decreasing trend in body condition. ► High levels of Chlorophyll-*a* during the critical phase (2007-2011) suggest that food quality rather than quantity is involved.

Keywords : Body condition, Growth, Decadal trends, Environmental effect, Life history traits, *Sardina pilchardus*, Bay of Biscay

1. Introduction

Fishing pressure and climate change are currently the main factors affecting ecosystem dynamics at large scale (Crozier and Hutchings, 2014; Hoegh-Guldberg and Bruno, 2010). These perturbations affect the productivity of marine stocks at all biological levels, whether directly (e.g., by regulating metabolic factors such as growth rates, reproduction and phenology (Edwards and Richardson, 2004), or indirectly (e.g., by modifying trophic interactions through the alteration of food resources, Lloret et al., 2013) resulting, *inter alia*, in spatio-temporal changes in the abundance of exploited fish (Drinkwater et al., 2010) and their population dynamics.

Length and weight and their relationship have gained increasing attention in stock assessment and fisheries management (Lloret et al., 2012; Punt et al., 2013; Taylor and Methot, 2013; Young et al., 2006). As they correspond to the underlying determinants for population responses to fishing impacts, climate and ocean changes (King and McFarlane, 2003), these parameters are commonly used as indicators in fisheries ecology to follow the health of a given population. They make it possible to evaluate individual growth patterns, as well as reproductive potential and the ability to store reserves, which are both vital functions at individual and population levels. Many studies have employed condition indices to understand fish population health and variability (Brosset et al., 2015b; Lloret et al., 2012; Thorson, 2015). Based on morphometric data, body condition is a way to measure the amount of stored energy in the body and reflects a set of biotic (e.g., food availability, parasitic infections, physiology) and abiotic (e.g., physical conditions) factors experienced by individuals over a period of their life (Lloret et al., 2002; Vila-Gispert, 2001). Moreover, as condition largely influences other life-history traits such as growth, reproduction, phenology and mortality, it is a particularly important property of fishes also informing on their future population success (Brosset et al., 2016; Huret et al., 2019; Lloret et al., 2013, 2002; Rosa et al., 2010).

Within marine ecosystems, small pelagic fish populations represent both an important biomass as forage fishes at mid-trophic levels (Cury et al., 2000) and an important target for fisheries (Beckley and van der Lingen, 1999). Their relatively short lifespan and high sensitivity to environmental variability (Cushing and Dickson, 1977; Chavez et al., 2003) make them important indicators of climate-driven environmental changes in marine ecosystems (Drinkwater et al., 2010). An increasing number of studies have brought to light the close relationship between pelagic fish condition variability and the current shift of environmental conditions observed in most ocean systems. For instance, European anchovies in the Strait of Sicily (Basilone et al., 2006), Gulf of Lions (Brosset et al., 2015a, 2015b) and Adriatic (Zorica et al., 2013) are in better condition when the food availability in the surrounding water is high. In the Gulf of Lions, sardines showed a general decrease in growth and condition that could be due to bottom-up processes arising from changes in planktonic productivity or quality (Brosset et al., 2015b). Such variability in condition and growth may have important consequences for stock productivity, ecosystem dynamics and fisheries yields (Jacob et al., 1996; Adams, 1999, Shulman and Love, 1999; Marshall et al., 1999, Lloret et al., 2012).

In the Bay of Biscay, sardine (*Sardina pilchardus*) is an important commercial species in terms of catches and is assessed and managed as a single-stock unit. According to the assessment of the International Council for the Exploration of the Seas (ICES) the fishing pressure on this stock remains low, as only roughly 10% of the biomass is harvested yearly (ICES, 2016). However, the strong decline in abundance of sardine in the Iberian waters since the end of the 2000s resulted in the transfer of Spanish fishing effort from this area towards the Bay of Biscay stock, leading to an increase in Spanish catches in the southern part of the Bay of Biscay (from 640 t in 2010 to 14948 t in 2012). Furthermore, Doray et al (2018) recently highlighted a decreasing trend in mean body length of sardine over time with no clear explanation. Even if fishing is known as an important factor shaping fish population dynamics,

it must be considered within a broader set of multiple factors. Indeed, climate change also impact many of the same individual and/or population traits as fisheries (Grift et al., 2003; Marty et al., 2015), supporting the idea that none of these factors act independently of the others.

From both ecological and management perspectives, this is key to make a detailed description of the evolution of sardine traits in the Bay of Biscay, as well as to understand their underlying processes. In this study, using a unique dataset of morphometric (length and weight) and biological variables over the period 2003-2016, we first described decadal changes in Atlantic sardine body length in order to investigate its temporal variations. Second, we analyzed the dependence of sardine body condition (a less integrative biological parameter than the body length) on endogenous and exogenous factors with two specific objectives. We began by (1) quantifying both seasonal and inter-annual variability in body condition and assessed the degree of coherence among age and sex within the population. Then, (2) we quantified the relative effects of environmental factors and catch levels on the inter-annual variability of body condition. Finally, multivariate relationships among sardine body condition and exogenous factors were described to characterize the state of the population and its global environment over the period 2003-2016.

2. Material and methods

2.1 Study area

The Bay of Biscay (Fig. 1) is an oceanic bay widely open to the Atlantic Ocean and extending from the point of Penmarc'h (north-west France – Offshore of Brittany, 48.5°N) to the Cape Finisterre (north-west of Spain - Galicia, 43°N). Within this area, the sardine population habitat extends over the continental shelf (bathymetry < 330m in this manuscript), where this species completes its entire life cycle and is targeted by the fishery. Sardines are mainly caught by an extensive French fishery concentrated in the northern part of the bay and a Spanish fishery operating predominantly in the southern part. Since this study does not

investigate the spatial dimension of the sardine population dynamics, both environmental variables and catches were averaged over this area (Fig. 1, zone highlighted in grey).

2.2 Data on biological traits

2.2.1 Biometric data

Morphometric sardine data were obtained from both scientific surveys (pelagic and demersal trawlers) and commercial landings (predominantly from purse seiners) within the European Data Collection Framework (DCF) over the period 2003-2016. Each fish sample was randomly selected (within a subsample of size sampling allowing to get a uniform distribution over the whole size range) regardless of the data origin or the sampling period. All morphometric analyses were conducted following the same method so that data were comparable. A summary of fish sample sizes, temporal coverage, month, age, length and weight ranges for each sampling source is given in Table 1.

The *Pélagiques Gascogne* survey (PelGas, Doray et al., 2017), conducted by IFREMER since 2000 onboard the R/V *Thalassa*, monitors the structure and the dynamics of the pelagic ecosystem during spring. Over the period 2003-2016, an average of 27 trawl hauls per cruise made it possible to collect individual sardines. Additional samples were also obtained from the EVHOE demersal survey (*Evaluation des ressources Halieutique de l'Ouest de l'Europe*; Duhamel et al., 2014), the Sentinelle (2009) survey and JUVAGA (2005) survey. Since these surveys were not dedicated to monitor the pelagic ecosystem of the Bay of Biscay, data collection was made in an opportunistic way depending on the occurrence of sardine in the trawl hauls. In the same way, samples collected during the national CAPTAIN project were also included when available. Commercial sardine samples were collected at the fish markets of the six leading French fishing harbours (once or twice a month, depending on landings) over the study period (2003 – 2016, Table 1).

In this paper, analyses were performed without elevation to the population level, due to

the lack of monthly biomass data for the commercial samples. Total individual body length (L, cm) and body mass (M, g) were rounded to the lower half centimeter and to the lower gram, respectively. Individual sex (female, male) and macroscopic maturity stages were determined following ICES guidelines (ICES, 2008) with visual examination of the gonads based on a six-stages key as follows: stages 1 & 2 indicate immature and developing individuals, stages 3-5 indicate three steps of increasing gonad development and the spawning period (stage 3: partial pre-spawning; stage 4: spawning (hydrated); stage 5: partial post-spawning) and stage 6 features the final post-spawning period. Stage 1 includes both virgin (individuals of age 1) and immature (individuals above 1 year old) fishes. Fishes characterized by maturity stages 3, 4 or 5 are considered as being in an active reproductive period.

Otoliths were extracted from each sample, cleaned and mounted in black plastic plates using a synthetic resin. Age reading (in years) was then carried out visually by binocular microscopy by experienced readers at the “Laboratory of technology and biology fisheries” of IFREMER (Lorient, France), following ICES guidelines (ICES, 2011). For each sample, the Julian date (D, day since the beginning of the year on which the fish was caught) was also recorded.

For this study, we used a dataset including morphometric (i.e., length and weight) and physiological (i.e., sex, age, maturity) characteristics from more than 20,000 individuals collected over the period 2003-2016. The sample sizes (total number of individuals collected) were globally similar between years with an average of 1,418 fishes (min: 893, max: 1,892) collected annually.

2.2.2 The relative condition index

The relative condition index (K_n , Le Cren, 1951) was used as a proxy of sardine body condition. This index is considered as the best morphometric indicator of fish condition in marine ecosystems (ICES, 2017) and applies here under the realistic assumption of an overall

positive allometric growth pattern for sardines (Van Beveren et al., 2014). As it corresponds to the weight of each individual normalized to the weight of a reference fish of the same length (coming from a weight-length relationship, denoted below as WLR), this index is centered on 1, with higher and lower values indicating good or poor body condition, respectively.

In order to account for differences between the sexes (tested as an interaction with fish length in linear models, e.g., $\ln W = \ln L \times \text{sex}$), a distinction was made between males and females in the calculation of the WLRs. Furthermore, in order to have enough individuals and avoid any bias in the calculation of the WLRs coefficients, the quarter was used as the highest resolved time unit. The presence of both smallest and largest individuals was verified to avoid potential bias in the estimation of the coefficients of the weight-length relationships. For each sex s , we therefore fit the following $\hat{W} = \alpha_s * L^{\beta_s}$ equation across length and weight data by quarter to obtain estimates of α_s and β_s for each quarter of each year. The resulting WLRs were then considered when the number of individuals was greater than to 29. The sample size for each sex and quarter by year used in the estimation of α_s and β_s is described in the Appendix A (Table A.1). We tested for consistency among all the WLRs obtained for each quarter with a regression analysis of $\log \alpha_s$ over β_s to detect any questionable WLRs and verified that the estimates of these coefficients were unbiased (Froese, 2006, Fig. A.1). These coefficients were then averaged by sex s using a geometric mean (“m” subscript in the following coefficients) to obtain the overall α_{m_s} and β_{m_s} estimates, then used to compute the individual relative condition index. The advantage of using a single weight-length relationship to compute the relative condition index is to get a common basis to compare both seasonal and inter-annual differences in sardine body condition. Based on the whole set of individuals, the following values were obtained: $\alpha_{m_F} = 8.79 \times 10^{-3} \pm 8.26 \times 10^{-3}$; $\beta_{m_F} = 2.99 \pm 2.10 \times 10^{-1}$ for the females and $\alpha_{m_M} = 7.59 \times 10^{-3} \pm 1.36 \times 10^{-2}$; $\beta_{m_M} = 3.03 \pm 2.52 \times 10^{-1}$ for the males. Finally, the relative condition index (hereafter named “body condition”, Eq.1) was calculated as follows:

$$K_{n_{i,s}} = \frac{W_{i,s}}{\hat{W}_{i,s}}, \quad \hat{W}_{i,s} = \alpha_{m_s} * L_{i,s}^{\beta_{m_s}} \quad (\text{Eq.1})$$

Where $\hat{W}_{i,s}$ corresponds to the predicted weight of an individual i , of a given total length $L_{i,s}$ obtained from a sex-specific weight-length relationship for the sex s and $W_{i,s}$ is the weight of this individual of sex s .

2.2.3 Data pre-processing

Data were filtered by a 2-level process. First, length and weight ranges were kept as large as possible to avoid any bias and to retain the complete variability of the age distributions (Table 2). Serious potential outliers in the dataset were identified and removed in two stages combining the Cleveland dotplot as a graphical tool (Zuur et al., 2010) and a regression of log weight against log length using a least square linear model. Records with an absolute Studentized residual value > 4 were discarded. By this way, unrealistic combinations of length and weight resulting from sampling biases or from erroneous records in the dataset were filtered out. The second filter was applied by excluding fishes for which age was missing and/or for which the sampling date was unknown. Individuals younger than 1 year old were removed from the analyses due to the low number of samples. In order to avoid any biases in the analyses due to very low numbers of older individuals, fishes were divided into seven age classes with all individuals older than 6 years pooled in the oldest age class (7+ group).

2.3 Exogenous variables

Environmental variables and sardine catches were considered as potential factors that might impact both sardine body condition and length in the Bay of Biscay. Environmental variables considered relevant for their potential impact on sardine body condition were extracted from the Copernicus Marine Service (CCMS, <http://marine.copernicus.eu/>). Monthly sea surface temperature (SST , °C), surface salinity (Sal , PSU), Eddy kinetic energy (Eke , measuring turbulence in $\text{cm}^2 \cdot \text{s}^{-2}$), ocean mixed layer depth (MLD , m) and net primary

production (NPP , $\text{mg}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$) came from the Atlantic Iberian Biscay Irish (IBI) model (which is based on the NEMO v3.6 ocean circulation model and assimilates *in-situ* temperature, satellite sea surface temperature and vertical salinity profiles) whereas sea surface Chlorophyll-*a* ($Chl-a$, $\text{mg}\cdot\text{m}^{-3}$) was derived from satellite data. Oxygen was also included in the analysis since it can impact body condition and growth. The Eddy kinetic energy (Eq.2) was computed as follows:

$$Eke = \frac{u^2 + v^2}{2} \quad (\text{Eq.2})$$

where u and v correspond to the eastward and northward sea water velocity, respectively (Gent, 2011). All environmental data were monthly averaged over the continental shelf of the Bay of Biscay (bathymetry < 330m, Fig. 1).

Estimates of yearly total catches of sardine were deduced from the estimations of the Working Group assessing the sardine Bay of Biscay stock (WGHANSA). Outputs of monthly sardine catches from the IFREMER SACROIS algorithm (Demanèche et al., 2010) were used to disaggregate quarterly French catches in monthly catches while Spanish catches were disaggregated using scientific expert knowledge. Monthly total catches were finally obtained by adding both French and Spanish monthly catches at the level of the Bay of Biscay.

2.4 Statistical analyses

Temporal variations of two biological parameters (body length and condition) were analyzed using two distinct methodologies. Since fish body length partly reflects the consequences of a set of environmental conditions experienced by individuals throughout their life, it represents a more integrative parameter than body condition, which mainly reflects recent and current environmental conditions and strongly varies according to individuals' state. Investigating the existence of instantaneous relationship between body length and its drivers (either endogenous or exogenous factors) is therefore meaningless. We used generalized

additive models to describe long term variability of sardine body length and highlight the existence of potential differences among group of individuals of a given population. We used Linear Mixed effect models to assess if variability in body condition was associated with changes in endogenous factors, current environmental conditions, and catch levels.

2.4.1 Characterizing the decreasing trend in sardine body length

The decreasing trend in sardine body length was investigated at the population level by the mean of Generalized Additive Models (GAM) as implemented in the R-package *mgcv*, 1.8-17 (Wood, 2011). As growth patterns are known to potentially differ within fish populations (Fig. A.2), length was modeled as a function of age class, sex (introduced as categorical effects) and year, considered as a continuous variable in the non-parametric smooth trend. The existence of specific trends within the population was tested by considering a set of nested models without a time trend, or with an identical time trend for each age class and sex. Nested models were first built by adding successively the categorical effects (age class and sex). Then, depending on their significance, their interaction was included in order to account for potential differences between sexes in mean length at age. Finally, the smooth time trend was considered either as independent of age and sex or in a dependent way (Eq.3). Model structures (Ms) tested are detailed in Table 3. The most complex model considered was:

$$L_{Y,A,S,i} = A \times S + s(Y, A \times S) + \varepsilon_i \quad (\text{Eq.3})$$

where $L_{Y,A,S,i}$ is the body length for any fish i of age A and of sex S , caught in year Y , $A \times S$ is the age by sex interaction, $s(Y, A \times S)$ is the age by sex specific smooth time trend and ε_i are independent and identically distributed residuals. Since auto-correlation can cause violation in the assumption of independence of error terms, we also checked for temporal correlation in sardine body length time-series, and autocorrelation was insignificant. Model selection was performed using the Akaike Information Criterion (AIC) and the explained deviance was also used to determine the relative importance of the covariates in explaining data

variability and to identify the best model. Selected GAM was validated by examining the residuals distributions (i.e. normal distribution and verification of normality, homogeneity and independence). Relative rate of change over the study period was also considered to quantify the intensity of changes in mean body length. Results from this analysis support those highlighted by the GAM and are provided in supplementary materials (Appendix B.1).

2.4.2 Sardine body condition and its dependence upon various factors

We analyzed the characteristics of sardine body condition over time. First we focused on both the seasonal and inter-annual variability of sardine body condition taking into account the impact of endogenous factors (age, sex and reproductive stage). Second, we investigated the relationship between sardine body condition and both the environmental conditions and catch levels to better understand fluctuations in sardine body condition. In this last analysis, we mainly focused on the inter-annual variability of sardine body condition in order to investigate if environmental factors can explain it.

Since fish body condition depends on fish length (Le Cren, 1951), one could wonder whether change of body condition at age only results from the decrease of body length-at-age. In order to ensure it does not, we first analyzed the pattern of body condition with length class by year using Generalized Additive Models. Results of this analysis are presented in the supplementary materials (Appendix B.2) and confirm a length specific decrease in body condition over time.

2.4.2.1. Statistical approach and model selection

Independent Linear Mixed Effect models (LMEs, Eq.4) were used to take into account the properties of time-series datasets and introduce an auto-correlation term to avoid violation of the independence assumption. We used an autoregressive variance-covariance matrix (cor AR1 in R, R development core team 2009), which represents the first-order autocorrelation structure and makes it possible to model serial correlation among observations (Zuur, 2009).

To account for potential violation of the independence assumption caused by biological and ecological similarity of individuals collected within the same trawl haul (intra-haul correlation), the biological station (corresponding to the haul) was treated as a random effect (Zuur, 2009).

The Linear Mixed effect model structure was defined as follows:

$$K_{n_i} = X_i \times \beta + Z_i \times b_i + \varepsilon_i \quad (\text{Eq.4})$$

where K_{n_i} contains the sardine body condition values for station i , $X_i \times \beta$ corresponds to the fixed term (i.e. predictor variables: year, quarter and endogenous factors in section 2.4.2.2 and quarter, environmental parameters and catches in section 2.4.2.3, see details below), $Z_i \times b_i$ is the random term and ε_i is the error vector (with an AR-1 correlation structure). X_i and Z_i are design matrices of dimensions $n_i \times p$ and $n_i \times q$, where n_i is the number of observations in K_{n_i} (the number of observation per station), p the number of predictor variables in X_i and q the number of explanatory variables in Z_i . β and b_i are the vectors of fixed and random effects of dimension $(p \times 1)$ and $(q \times 1)$, respectively. b_i is normally distributed with zero mean and a variance $\sigma^2_{station}$, which depends on the station.

Model selection was made using the likelihood ratio test, based on maximum likelihood (ML), starting from a full model with fixed effects only retained if they improved the fit ($p < 0.05$, Zuur, 2009). Differences in goodness of fit and model complexity among model structures were then analyzed using the Akaike Information Criterion (AIC; Burnham et al., 2002; Zuur, 2009). Finally, the optimal model was fitted with the Restricted Maximum Likelihood Estimation (REML) method. Model validation was performed through visual inspection of diagnostic plots (QQnorm and residuals distribution) to verify assumptions of normality, homogeneity, and independence (Zuur, 2009; Zuur et al., 2007). The magnitudes of estimated marginal and conditional R^2 values, which describe the proportion of variance in the data explained by the fixed factors alone and by both fixed and random factors combined,

respectively, were also used to assess the fits of LME model.

2.4.2.2. Variability of sardine body condition and endogenous factors

With a Le Cren condition index value (body condition) for each fish in our dataset, a Linear Mixed Effect model was applied to estimate and analyze the variability of sardine body condition at age and the impact of sex and maturity stage. Sardine body condition is known to highly fluctuate seasonally (Fig. A.3), as a result of both the environmental variability and the reproductive cycle (Gatti et al., 2018; Rosa et al., 2010) which may lead to different levels of energy and weight along the year. In order to take into account such property, and due to lack of sufficient data at the monthly scale, the quarter was used as unit of time to analyze the seasonal variation in sardine body condition. Body condition was therefore modeled at the level of individuals, considering a set of five fixed categorical effects [predictor variables: year, quarter and three endogenous factors: age, sex and description of the reproductive status (immature, mature, mature and spawning)]. Moreover, as we wanted to test for potential differences in body condition within the population, the interaction between age and all the other covariates was included in the full parameterization.

Otherwise, given seasonal variations in sardine body condition, a supplemental analysis was implemented in order to identify which season(s) support(s) the observed trend in sardine body condition. Results from this analysis are presented in supplementary materials and highlight the particular involvement of two seasons in the observed trend in sardine body condition (Appendix B.3).

2.4.2.3. Investigating the impact of exogenous factors on sardine body condition

To assess potential drivers of variability in sardine body condition in addition to seasonality and endogenous factors, the impact of exogenous factors (environmental variables and catch levels) on the trend of body condition was analyzed using de-seasonalized time series. Monthly mean values of exogenous parameters corresponding to the time of sampling were

considered. Thus, all biological stations sampled in a given month were linked to the same monthly environmental parameters and catches averaged over the continental shelf of the Bay of Biscay. As the magnitude of the residual variability in sardine body condition anomalies can vary at both seasonal and inter-annual scales and since we wanted to investigate if environmental factors can explain some of the observed inter-annual variability in sardine body condition, the quarter was added as categorical variable in the model. This inclusion allowed us to assess the respective part of the seasonal and inter-annual variations in sardine body condition anomalies. Finally, as we were interested in detecting the impact of both the environment and catch levels, body condition was modeled without interaction terms between variables.

Before variable selection (investigation of co-linearity among explanatory variables, detailed below), the full set of predictor variables was composed by: sea surface temperature (*SST*), surface salinity (*Sal*), Eddy kinetic energy (*Eke*), ocean mixed layer depth (*MLD*), net primary production (*NPP*), Oxygen (*O*), seas surface Chlorophyll-*a* (*Chl-a*) and catches. The non-co-linearity between continuous variables was verified using Pearson correlation (coef < 0.5) and the variance inflation factors with a stepwise selection (VIF, release threshold of VIF > 2) (Zuur et al., 2010). Moreover, to obtain an initial idea of the shape of relationships between the response variable (sardine body condition) and the predictor variables (exogenous parameters), we first considered a full Generalized Additive Mixed Model (GAMM, R software package *mgcv*, function *gamm*; Wood, 2011) with all covariates included. Based on the GAMM outcomes (not shown), we then fitted a Linear Mixed Effect model (LME) where sardine body condition was expressed as a function of the explanatory variables and both their quadratic and cubic terms when necessary. We also considered a sex effect nested within age effect within the station as random effect to account for both inter-individual variability and potential differences in the variance around the mean of the response (body condition) between age

classes and sexes. All explanatory variables were standardized (centered and scaled) to facilitate model convergence and enable comparison of their respective contribution (using their corresponding slope coefficients).

2.4.3 Characterizing changes in sardine body condition

A Principal Component Analysis (PCA) was implemented to describe the multivariate relationships among annual values of sardine biological parameters (body condition and maximum size (estimated for each year by computing the 90% quantile of fish size distribution) and exogenous factors (environmental factors (*SST*, *SSal*, *Eke*, *MLD* and *Chl-a*) and sardine catches; the descriptors) over the years (the objects) of the study period. This analysis summarizes into a few dimensions the variability of both biological parameters and exogenous parameters over the study period, so that we could comprehensively consider the state of the population according to environmental conditions and catches in the Bay of Biscay between 2003 and 2016.

3. Results

3.1 Long-term variability in sardine body length

Selected GAM model analyzing the temporal trends of body length explained 80% of the variability in the data (Table 3, Fig. 2).

Overall, the non-linear smoothed temporal trends show a decrease in mean body length for all age classes (Fig. 2). Sardine body length was best explained by a GAM including both an average interaction term and a smoothed temporal trend for the 2003-2016 period, indicating a general decrease over time specific to age-sex combination. The average age-class term had the greatest effect on mean length (70.16% of deviance explained). The strongest difference appeared between age classes 1 and 2, which corresponds to the most critical period for individual growth during the life cycle. Comparatively, the sex effect explains a smaller part of

the deviance with the females appearing longer overall than the males over the time series for each age-sex combination. As expected, the smoothed time trend explains a much smaller part of the total deviance but remained important with a contribution of 7.32% to the total explained variability. The variability of the trend over the study period appears substantial for all age classes, as indicated by the effective degrees of freedom (edf) (i.e., edf higher than 1, except for males of age 7+).

This analysis highlights negative average rates of change which depends upon both age class and sex. Those changes have proven to be more important for individuals of age 1 (Fig. 2, Appendix B.1).

3.2 Sardine body condition times-series and endogenous factors

Visual examinations of diagnostic plots (allowing assessment of normality, homogeneity and model fit, Fig. A.4) confirmed the ability of the linear mixed effects model to reproduce the individual variability of the mean sardine body condition-at-age. The most parsimonious LME model describing body condition included the following fixed effects: year, quarter, age, sex, reproductive status and the interactions between age and all the other covariates (Table 4). The additional variation explained by including the station as a random factor was 20.8%. This sizable gain in variation explained by just the random factor suggests that variation in body condition is much greater between samples than within samples. The significance of the interaction between age class and all covariates strongly supports the hypothesis of different responses of body condition within the population.

Our model shows a major negative effect of year on sardine body condition-at-age (decreasing trends, Fig. 3.a). Mean body condition-at-age was relatively stable during the first four years of the period 2003-2006 [mean $Kn = 1.03 \pm 2.3 \cdot 10^{-3}(\text{SE})$] before declining gradually until 2011 [mean $Kn = 0.93 \pm 1.4 \cdot 10^{-3}(\text{SE})$] when it stabilized (Fig. 3.a). Although sardine body condition showed high inter-annual variability for all age classes, the dynamic process of

change in body condition breaks down into three successive periods: P1: 2003-2006; P2: 2007-2011 and P3: 2012-2016 (Fig. 3.a). The period between 2007 and 2011 supports major changes at the population level since a decrease in body condition is observed for all age classes. These results were also supported by a breakpoint analysis presented in the Appendix B.4.

The inclusion of the quarter effect in the LME highlights important seasonal variations in body condition for all age classes (Fig. 3.b). Relative to the winter period, the whole population displayed an increase in body condition towards a peak in summer followed by a decrease in autumn. The most pronounced seasonal increase in body condition was for individuals of age 1. A systematic decline in body condition between winter and spring was observed for individuals of age 3 and older, while individuals of 1 to 2 years old showed an increase in body condition between these two periods of the year (particularly for one year old individuals).

Overall, sardine body condition shows a quadratic age effect, with body condition improving from ages 1 to 3 and then subsequently declining (Fig. 3.d, Fisher test highly significant). Both ages 2 and 3 display the best body condition of the whole population. Regarding the sex covariates (Fig. 3.d), differences in body condition between the sexes vary across age classes, with males in better body condition than females among individuals of 1 to 3 years while older females showed better body condition than males.

Our results also suggest a correlation between fish body condition and the reproductive cycle, as shown by the significance of the interaction between age and maturity stages (Fig. 3.c). Relative to the immature individuals, an increase in body condition during the spawning period (Active individuals) was only observed for individuals of age 1, while all the other age classes showed a decline in body condition between immature stage and spawning stage. The most important decline in body condition between these two stages was observed for individuals of age 5 and older.

3.3 Influence of exogenous factors on the trend in sardine body condition

The detection of co-linearity among environmental covariates through the computation of variance inflation factors (VIFs) led us to remove the variable “oxygen” (VIF = 3.8 >2). All the other variables displayed a maximum VIF of 1.31 and were kept in the analysis. Similarly to the previous analysis using linear mixed effect model, the diagnostic plots of the final model were satisfactory and residuals were mostly normally distributed (not shown). Linear, second-order and/or third-order polynomial smoothing was fitted to the data depending on whether the relationship with the response variable was linear, quadratic or cubic (based on GAMM outcomes, not shown). The inclusion of the nested age effect within the station as a random effect clearly improved the proportion of variance explained in the data while the nested sex effect was not retained in the selection process. This result suggests that body condition responses to environmental variations differ among age classes while they appear the same between sexes.

Overall, model selection procedure, using the top-down strategy as recommended by Diggle et al. (2002), retained quarter (as categorical variable) and Chlorophyll-*a* (*Chl-a*), Mixed Layer Depth (*MLD*) and Sea surface temperature (*SST*) in their linear form and both a quadratic and cubic terms on Eddy kinetic energy (*Eke*) and sea surface salinity (*Ssal*), respectively (Table 5).

The inclusion of polynomial forms particularly highlights the complexity and non-linearity of the relationship between the body condition and environmental variables. The model selection procedure reveals that both net primary production and catches levels were not significant. The final model explains 41.7% of the variability in data as shown by the estimated conditional R^2 value (Table 5).

Overall, sardine body condition increased significantly with Chlorophyll-*a*, while it significantly decreases with sea surface temperature and mixed layer depth (all p-values <0.018, Table 5, Fig. A.5). A negative quadratic effect of Eddy kinetic energy on body condition was

highlighted by the LME and reflected higher values of body condition for extreme values of Eke. Regarding the sea surface salinity, an optimal range of salinity ($34.74 \pm 0.15 \leq \text{Salinity} \leq 35.26 \pm 0.15$) was highlighted by our model and a decrease of body condition was observed for highest salinity values. Looking at the absolute value of estimated coefficients, sea surface temperature had the largest effect (in its linear form) on sardine body condition (higher estimated slope between standardized covariates).

Furthermore, our results emphasize predominance of the inter-annual variations in the anomaly of sardine body condition over seasonal variations (Fig. 4, Fig. A.5). While sardine body condition anomalies vary in a small range of values between seasons (maximum change in sardine body condition anomalies: 0.23, Fig. 4), our results highlight larger changes in its anomalies over the whole range of environmental values (which corresponds to the inter-annual variability once the influence of quarter has been accounted for).

Changes in sardine body condition anomalies vary between 0.37 and 1.04 depending on the environmental factor considered (Fig. 4) supporting the fact that environmental factors explain some of the observed inter-annual variability in body condition.

3.4 Decadal covariation between biological parameters and exogenous factors in the Bay of Biscay

In the PCA performed on sardine biological parameters (sardine body condition and maximum size) and exogenous factors (environmental parameters and catch levels) over the study period, the first two components (PC 1 and PC 2) encompassed 59.9% of the total variance (40.9% and 19%, respectively, Fig. 5). Positive values on the first axis of the PCA (PC 1) represent years with high mean body condition and maximum size which were negatively correlated to high mean sea surface temperature and catches. Axis 2 of the PCA was characterized by both the Mixed Layer Depth and Chlorophyll-*a* with high annual mean values for positive values on this axis.

The period was super-imposed for each year and the projection of the barycenters showed a clear segregation between periods, especially on the first axis. This notably undermines that the PCA reproduces well the decline in both sardine body condition and size. Even if inter-annual variability within period was important, points of the same period were closer to each other than those from other periods, indicating a similarity between years of the same period much higher than the similarity between periods. While the first two periods (2003-2006 and 2007-2011) appeared quite similar in terms of sea surface temperature (with average lower values), the third one (2012-2016) was clearly associated with higher sea surface temperatures and higher sardine catches (Fig. 5). This notably reflects the current ocean warming and the increasing trend of sardine catches since Spanish fleets have transferred their effort from the Iberian waters towards the south Bay of Biscay. We also mention that according to the combination of these two axes, period 2 was strongly correlated to higher values of *Chl-a* while this latter corresponds to the critical phase of decrease in sardine body condition (Fig. 5).

4. Discussion

4.1 Evidence for changes in phenotypic traits at the population level

Changes in life history traits, particularly the decreasing trends in both body size and weight have been reported in many marine fish species all over the world (Cheung et al., 2013). This study highlights a significant decrease in both sardine body length and condition between 2003 and 2016. We emphasize a common response at the population level for all ages which is linked to the variability of environmental conditions in the Bay of Biscay. Such changes have already been highlighted in small pelagic fish species in other European regions (Mediterranean Sea (Brosset et al., 2017, 2015b; Van Beveren et al., 2014), Iberian and Mediterranean waters (Silva et al., 2008) and in other part of the world (northern Chile (Canales et al., 2018) with a specific focus on their relationships with environmental conditions (in particular food quality and availability).

The decrease in sardine body condition breaks down into three successive periods. The breakpoint analysis presented in Appendix B.4 emphasizes common breakpoints for young individuals at the beginning (2006-2008) of the critical period (2007-2011), while older individuals exhibited synchronous breakpoints at the end of this period (2010). Despite the geographical separation, this decline occurred synchronously with a drop in sardine body condition in four areas of the Mediterranean Sea (Brosset et al., 2017). Those temporal similarities across distant ecosystems suggest the existence of broad-scale processes impacting marine ecosystems at large scales.

The strength of the decrease in mean body length is age dependent and differs between sexes for younger ages (Appendix B.1). This age-specific decrease was not so clear in sardine body condition suggesting that even if both biological parameters can be impacted by the same factors, the strength of their response remains parameter-specific. Such hypothesis might be explained by the differences in their properties and has been corroborated with a supplemental analysis (Appendix B.2) underlining that the decreasing trend in sardine body condition did not result only from the decrease in body length.

Several processes can be involved in the decreasing trends observed in both biological parameters. Density-dependent factors, such as competition for food, may greatly impact fish growth as suggested by Doray et al. (2018) to explain the observed decrease in sardine mean body length at age one in the Bay of Biscay. Such processes could be, *inter alia*, more important for young individuals within nursery grounds where other species inhabit and compete for food. Otherwise, sardine nursery grounds in the Bay of Biscay are mainly distributed over coastal areas, where both the hydrological structure and primary production have been shown to be highly influenced by the plumes of the Gironde and Loire rivers (Dupuy et al., 2011; Pasquaud et al., 2012; Planque et al., 2004). Moreover, river discharges are known to potentially impact fish body condition (Brosset et al., 2017). Therefore, the mesozooplankton variability in these

coastal areas could also explain the observed trend in sardine body condition.

It is worth noting that the period of low body condition values (2012-2016) coincides with a strong increase of catches as the result of the increase in fishing effort from the Spanish fleets moving from the Iberian waters to the south of the Bay of Biscay. Even if both biological parameters (body length and condition) can be affected by changes in environmental conditions and/or fishing pressure, an impact of fishing on body condition through a decrease in food availability appears unlikely due to the fact that sardine essentially feed on planktonic resources (Bode et al., 2004; Rosa et al., 2010) that are not exploited in this area. This could explain the non-significance of catches in our LME model. However, it should be noted that catchability, which is size and condition-dependent, might explain the observed trend in body length-at-age. Fisheries-induced selection is commonly known to significantly impact biological traits of exploited populations such as changes in population demography, decreases in size-at-age or earlier maturation (Ernande et al., 2004; Grift et al., 2003; Marty et al., 2015; Mollet et al., 2016). One of the reasons for the age-dependent decrease in body length could therefore be the result of the fishery becoming more and more size-selective to ensure an appropriate supply to both the canning industry and consumers. This study also reveals a synchrony between the increase in sardine catches and the decline in sardine maximum size (Appendix B.4) suggesting that an evolutionary response might be involved in the decreasing trend in sardine body length.

Apart from the fishery, predation could also act as a top-down control which may increase mortality in fish populations and impact life history traits. In the Bay of Biscay, small pelagic fish species constitute a key prey group of the top predators (Spitz et al., 2013), which mainly feed on energy-rich schooling fish (Spitz et al., 2018). Although the existence of such processes has been dropped to explain the current situation of both anchovy and sardine in the Gulf of Lions (Saraux et al., 2019), the strength of their impacts in the Bay of Biscay remain unquantified. An increase in predation from those top-predators, which is size-selective, may

explain higher mortality rates in sardine population and changes in its size distribution. Such a process might result in a sardine evolutionary response in order to limit predation risk (Spitz et al., 2010).

4.2 Dependence of sardine body condition upon endogenous factors

Sardine body condition appears highly dependent upon age class. Within the whole population, both 2- and 3- years-old individuals show the maximum body condition among all age classes. This pattern agrees with other studies (Brosset et al., 2015b; Gatti et al., 2018), highlighting a strong increase in body condition between ages 1 and 2, a maximum reached between ages 2 and 4 and finally a decrease for older individuals. These authors suggested that changes towards a decrease in energy acquisition and/or an increase in energetic cost for older individuals may be the cause of their declines in body condition.

The differences in sardine body condition-at-age may also be partly explained by different energy allocation strategies towards growth and reproduction between age and/or length and sex, as underlined in several studies (Caponio et al., 2004; Jørgensen and Fiksen, 2006; Nunes, 2011). Indeed, differences in growth between sexes have already been described for sardines in the Mediterranean Sea, highlighting the fact that, at the same age, females are longer than males (Caponio et al., 2004; Sinovcic et al., 2004). Here, we hypothesize that a higher energy investment in growth for females during their first years might explain their lower body condition relative to males at these stages, resulting in females being longer than males at the same age (Fig. A.2). The ability to assimilate energy and the duration of the reproductive season may differ between sexes (Coleman and Jones, 2011; McBride et al., 2015), which may be another source of body condition variability (Nunes, 2011).

4.3 Seasonal cycle of body condition, food availability and reproduction

The strong seasonality highlighted by our LME model supports the fact that body condition relies on seasonal cycles such as those of prey availability and reproductive cycle and

therefore reflects the balance between gain and cost of energy at seasonal scale.

Our results showed maxima of body condition during summer and minima during both winter and spring. Monthly variations in sardine body condition displayed a minimum in March/April and a peak in August/September (Fig. A.3), as already described in other studies using energy density analyses (Gatti et al., 2018; Rosa et al., 2010). The strong seasonal variation in body condition between autumn and the end of winter is in agreement with those found by Gatti et al. (2018) and reveals the negative energy balance during this period. In the Bay of Biscay, spring and summer are characterized by high plankton production and therefore constitute the main growth and energy storage seasons for sardines (McBride et al., 2015), preparing them for a potential autumn spawning but mostly for overwintering through the low production season.

This study also shows differences in the energy allocation between age classes during the first two quarters of the year (Fig. 3 b). Taking into account that young fish spend more energy on growth than reproductive investment (Lambert et al., 2003) and since young sardines may allocate energy differently than adults (Caponio et al., 2004), we hypothesize that these individuals may favour both reserve storage and energetic allocation to growth during spring to the detriment of reproductive activity to ensure their survival. Our results suggest a trade-off between energy storage and spawning activity that appear age class dependent. Such dependence may explain the differences in energy reserves between young and old individuals, with small individuals investing more energy in spawning activity than older (increase in energy costs) (Nunes, 2011; Zwolinski et al., 2001).

4.4 Environmental changes in the Bay of Biscay

Habitat characteristics are important drivers of the level of condition of the populations (Lloret et al., 2002; Rätz and Lloret, 2003; Vila-Gispert, 2001). This study supports the strong link between small pelagic fish and environmental conditions and emphasizes that the residual

variability in sardine body condition anomalies is more driven by changes in environmental condition on an inter-annual scale than on a seasonal scale. We showed a positive effect of *Chl-a*, a positive effect of both surface salinity and eddy kinetic energy in a specified ranges of values and a negative effect of both sea surface temperature and mixed layer depth on body condition. The non-significance of the net primary production could be explained by the fact that these data originate from the IBI model, which might not be accurate enough in its biological processes to capture a potential trend, as compared to satellite-derived *Chl-a* data.

Our results highlight that lower sardine body condition in the Bay of Biscay is linked to the recent increase in sea surface temperature which is known to impact both year-to-year fluctuations and long-term trends in fish populations (Garrido et al., 2017). Indeed, water temperature may affect fish physiology directly (by increasing the rate of metabolic processes) or indirectly through changes in ecosystem production and food availability (Brosset et al., 2015b). Garrido et al. (2017) suggested that an increase in temperature may lead to changes in the timing, duration and density of plankton blooms. Moreover, several studies have shown that temporal variations in mesozooplankton abundance and composition may be directly related to year-to-year variations in water temperature and salinity (Chouvelon et al., 2015). The differences in patterns observed in sea surface temperature and surface salinity could therefore correspond to differences in food availability and quality resulting in the observed trend in sardine body condition. In particular, the much lower sea salinity observed during the third period (2012-2016, not shown) may suggest an increase in planktonic production due to an increase in river discharge and might explain the new phase of stability in sardine body condition since 2012.

Results from the PCA reveal that the period of major changes in sardine body condition (2007-2011) towards lower levels was closely linked to *Chl-a*. Although sardines preferentially feed on zooplankton (Basilone et al., 2006; Bode et al., 2004; Rosa et al., 2010), *Chl-a* also

plays an important role as the species also feeds on dinoflagellates and diatoms (Garrido et al., 2008; Nikolioudakis et al., 2014). Deeper analyses of environmental factors during this period (not shown) revealed a longer and later peak of the Chl-*a* (pattern mainly supported by data from 2007 and 2008) compared with the two other periods (2003-2006; 2012-2016). Such a result could therefore suggest that despite a high level of Chl-*a*, other factors such as zooplankton quality and quantity may negatively impact body condition and growth, leading to their decrease. Analyzing temporal trends in the mesozooplankton and copepod communities Dessier et al. (2018) highlighted three temporal phases of adult copepod dominance. The periods 2003-2006 and 2010-2013 were characterized by higher abundance values in copepods than the mean decadal abundance in spring, while a lower abundance was found during the period 2007-2009. Moreover, these authors also emphasized a change in taxonomic composition in the Bay of Biscay over this period, with a major change recorded in 2006. Therefore, taking into account that changes in nutritional intake may have negative effects on fish growth and survival (Beaugrand, 2003; Brosset et al., 2017, 2015b; Canales et al., 2018; Huret et al., 2019), the observed decline in sardine body condition between 2006 and 2011, together with the decline in individual length-at-age, may be closely related to these phenomena (i.e., lower plankton abundance and/or quality).

4.5 What potential impacts of sardine body condition on population dynamics?

At the population level, even though body condition and size mostly varied in parallel, our analyses reveal that this was not totally the case (Appendix B.4), as suggested by Sinovčić et al. (2008). This pattern also agrees with results found in the Mediterranean Gulf of Lions for anchovy and sardine, where both species showed a decrease in body condition before a decrease in growth (Van Beveren et al., 2014). Such an early decrease in body condition may be partly explained by the fact that body condition index responds more quickly than length to environmental variations because it depends on weight, which is directly affected by food intake.

Furthermore, it is widely established that energy reserves or individual's body condition are keys elements in growth, reproduction and survival in various fish species (Cox et al., 2010; Jensen, 1996; Lambert and Dutil, 2000). Energy allocation to these functions may vary across the life cycle and depend upon various factors such as an individual's age, body size, energy reserves and environmental conditions (Caponio et al., 2004; Garrido et al., 2008; Jørgensen and Fiksen, 2006; McBride et al., 2015). Moreover, it is commonly known that the cost of the reproduction impacts energy allocation towards both growth and maintenance, leading individuals to make trade-offs and preventing them from simultaneously maximizing all of their life history traits (Stearns and Koella, 1986). Therefore, the decreasing trend in sardine body condition and potential food limitation may imply a lower supply of energy towards individual growth, resulting in a decrease in both the mean length-at-age and maximum size.

Over the study period, the magnitude of the decline in sardine body condition appears different among age classes and depends upon year. Despite the effect of overwintering which leads to lower body condition approaching a basal level every year at the beginning of spring, one can wonder if body condition at age one may impact subsequent individual growth trajectories. This process could result from the modification of growth rate and thus length-at-age, leading to an inability to catch up a potential retarded growth. Such hypothesis has been corroborated by an analysis of the relationship by cohort between the mean body condition at age one and the maximum size (Fig. A.6; Table A.2). This relationship was also tested by year and revealed a non-significant relationship between both variables. Those results therefore support the hypothesis of a cohort effect in the Bay of Biscay sardine population with a lower growth rate at age 0 and 1 implying such a phenomenon. Moreover, taking into account the specific geographic distribution of sardines through their life cycle, both the year and variable environmental conditions (food quality and/or quantity, temperature, salinity, etc.) experienced by young sardines within their nursery grounds may also contribute to explaining this specific

cohort effect and growth.

This potential deterministic growth may also result from maternal effect. Indeed, it has been established that fatty acid reserves of adult sardines transferred to their progeny depend on their lipid composition and therefore on their feeding ecology (Garrido et al., 2017). Lower body condition of adult sardines might therefore lead to i) lower growth rate of the upcoming individuals and ii) higher mortality of eggs produced due to their low energy, both hypotheses having potentially huge repercussions on population dynamics.

Our analysis also reveals that, at the end of the overwintering period, sardines emerge with a low body condition, corresponding to a limited amount of reserves. Furthermore, the decreasing trend in body condition over the study period seems to be mainly supported by both the third and the fourth quarters (Appendix B.3). The substantial decline in body condition observed in recent years during both the third and the fourth quarter suggests that sardines enter the overwintering period with lower body condition and thus a smaller amount of energy reserves than at the beginning of the time series. Considering that winter corresponds to a period of low energy intake, we suggest that a decrease in the pre-winter value, which for part of the population is probably lower than a threshold value allowing overwintering, may cause an increase in winter mortality rate. This mortality process would affect preferentially the oldest (and biggest), whose condition is lower than age 2 or 3 individuals. This can in turn modify the age structure of the sardine population in the Bay of Biscay and could partly explain the scarcity of older individuals recently observed in the population. Moreover, as no change in the proportion of active spawners among old individuals across the time series has been observed, a decrease in body condition in parallel to an investment towards reproduction kept constant, could be an additional factor explaining their lower survival (Jørgensen et al., 2006).

4.6 Implications for stock assessment and fisheries management

Our study highlights an important change in the body condition of the Bay of Biscay

sardine population. These changes may greatly impact population dynamics through the modification of growth rate (intra- and/or intergenerational effect), increase in natural mortality or modification of reproductive capacities and phenology. Several studies have already pointed out the potential effect of fish energy reserves (condition) on key parameters in population dynamics (Brosset et al., 2016; Lloret et al., 2012; Rätz and Lloret, 2003; Stevenson and Woods, 2006). Unfortunately, although both condition indicators (such as morphometric and gonadosomatic indices) and environmental factors act as key components of population dynamics, their use in stock assessment models and fisheries management remains very limited (Lloret et al., 2012; Methot and Wetzel, 2013) despite the great improvements they could offer.

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Appendix A. Supplementary materials

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Supplemental figure A.4: Diagnostic plot of the Linear Mixed Effects model used to predict sardine body condition at age according to endogenous factors.

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retained with the model selection procedure. Confidence intervals are plotted around the mean value.

Supplemental figure A.6: Regression analysis of the estimated maximum size (taking into account 4- and 5-years old individuals) against mean body condition at age one by cohort.

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Supplemental table A.1

Supplemental figure A.1

Supplemental figure A.2

Supplemental figure A.3

Supplemental figure A.4

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Supplemental figure A.6

Supplemental table A.2

This analysis was also realized by considering the mean body condition-at-age one and the maximum size estimated for each year of the study period (not shown). Results revealed a non-significant relationship between both variables (p -value = 0.071) and therefore support the potential effect of mean body condition-at-age one on the resulted maximum size by cohort.

Appendix B. Additional analyses

Supplemental Analysis B.1: Consideration of the relative rate of change in both biological parameters to quantify the intensity of changes between age and sex over the study period.

Supplemental figure B.1: Relative rate of change (mean and 95% confidence interval) in body length and condition over the period 2003 - 2016.

Supplemental Analysis B.2: Pattern of body condition with size

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Table B.2: Statistics of the GAM model describing the pattern of body condition with length class by year.

Supplemental Analysis B.3: Evolution of seasonal sardine body condition across time

Table B.3: GAM summary: estimates, associated standard errors, effective degree of freedom (edf) and significance (p-value). Quarter X refers to the season.

Figure B.3: Panel a) shows the predicted sardine body condition values by quarter across the study period (2003-2016) from the GAM model. Continuous lines indicate the model fit for each quarter and the shadow corresponds to the average ± 2 standard error of the fit. The relative rate of change (mean and 95% confidence interval) by quarter in sardine body condition over the study period is presented in panel b).

Supplemental Analysis B.4: Breakpoint analysis of environmental parameters and both sardine body condition and maximum size.

Figure B.4: Panel a) show the breakpoints for both biological parameters at the population level while panel b) describes those breakpoints for body condition-at-age. Identified breakpoints for exogenous factors (SST, Salinity, CHL-a, MLD and catches)

are presented in panels c), d), e), f) and g), respectively. Horizontal lines indicate the confidence interval around the detected breakpoint. The orange area specifies the period (2007-2011) of major changes in sardine body condition for the whole population. Due to the relatively large confidence interval for mixed layer depth, time series of exogenous factors are presented with an x-axis covering the period between 2002 and 2018.

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Appendix B.

Supplemental analysis B.1

Material and Methods

The relative rate of change in life-history traits over the study period was investigated to test for potential differences in the intensity of response between the sexes and among the age groups. The average rate of change (in % year⁻¹) was estimated as the slope of a linear model over time. The effects of age class and sex on the rate of change were introduced as categorical effects and the year was considered as a continuous variable.

Results

Consistently with the analyses of non-linear trends (GAM), average rates of change in body length were all negative and dependent upon both age class and sex (according to the model selected) (Fig. B.1.a). The largest rate of change was found for 1-year-old individuals, which also exhibited a significant difference between females and males ($-0.29 \pm 0.006\%$ and $-0.26 \pm 0.005\%$ per year, respectively). Regarding differences between ages, a pair-wise test revealed that the relative rate of change in length was similar for 2- and 3-year-old individuals, for which length declined by an average of 0.18% per year and for individuals older than 4, which declined by 0.08% per year. Although the difference between males and females was only substantial for 1-year-old individuals (tested through a pair-wise comparison test), females showed, on average, a stronger decline in mean length (except for age 5) than males.

In the same way, all rates of change were found to be negative for the body condition-at-age (Fig. B.1.b) and corroborate the results obtained from the LME model. Individuals between 2 and 6 years old showed the greatest rate of change, with an average decline in body condition of 0.0095% per year. Within these age classes, 3-year-old individuals appear to be most affected by this decline, with an average rate of 0.011% per year. The rate of change in body condition

did not differ between individuals of 1 and 7 years old, the fish having lost on average of 0.0061% (age class 1) and 0.005% (age class 7) of their initial body condition each year between 2003 and 2016.

Supplemental Figure B.1

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Supplemental analysis B.2:

Material and Methods

In order to ensure that the observed decreasing trend in sardine body condition did not only result from a decrease in body length, we investigated the pattern of body condition with length by year of the study period using generalized additive model (GAM, library *mgcv*, Wood, 2011). The following equation $Kn \sim year + s(length, by = year)$ describes the model structure and was used to predict body condition using data collected during summer and autumn. The first effect "*year*" is the average value of sardine body condition for each year of the study period on the whole length range. The second effect, $s(length, by = year)$, is the smoothed year specific trend of body condition with length around the previous average. Model validation was realized by analyzing the residuals distribution which did not demonstrate any violation of assumption of normality (not shown).

Results

The GAM model explained 39% of the variability of the data, with all effects being significant. Estimates confirm a year specific variation in body condition with length confirming a decrease in body condition for a given length. Table B.2 summarizes the statistics of the model and figure B.2 shows the prediction of body condition for three length classes over the study period.

Supplemental Figure B.2

Supplemental table B.2

Supplemental analysis B.3:

Material and Methods

Sardine body condition is known to highly fluctuate between seasons, as a result both the seasonal environmental cycle and the reproductive cycle (Gatti et al., 2018; Rosa et al., 2010) which may lead to different levels of energy and weight according to the season considered. In order to identify which season may particularly support the observed trend in sardine body condition, the pattern of body condition with year was quantitatively analyzed by quarter using generalized additive models (GAM, library *mgcv*, Wood, 2011). The following equation: $K_n \sim quarter + s(year, by = quarter)$, in R computation language, describes the structure of the model. The first effect “quarter” is the average body condition value (for the whole population) for each quarter over the study period. The second effect, $s(year, by = quarter)$, corresponds to the smoothed quarter specific variation of body condition with year around the previous average. Moreover, the seasonal relative rate of change in sardine body condition over the study period was investigated to quantify the involvement of each quarter in the observed decreasing trend. The average rate of change (in % year⁻¹) was estimated as the slope of a linear model over time. The effect of quarters on the rate of change was introduced as categorical effect and the year was considered as a continuous variable.

Results

Fig. B.3.a) displays model predictions of the evolution of sardine body condition by quarter across years resulting from the GAM model used to quantitatively identify which season may support the decreasing trend observed in sardine body condition. Selected GAM model explained 36.7% of the total deviance (Table B.3). Most effects were highly significant, apart from the intercepts of both quarters 2 (spring) and 4 (autumn). Therefore, we also tested for common average body condition value for quarters 1 (winter), 2 (spring) and 4 (autumn) (i.e. same intercept), but the best model in terms of AIC was a GAM with separated intercepts (not

shown).

Estimates highlight that sardine body condition is higher on average during summer (Quarter 3) and autumn than during winter and spring periods and therefore confirm previous observations that sardine body condition highlights maxima during the summer period. The large confident interval estimated for the winter period is likely due to the low number of individuals collected during this season. According to the GAM predictions, the decreasing trend observed in sardine body condition between 2003 and 2016 seems to be mainly supported by summer and autumn periods with body condition falling down from $1.18 \pm 5.75e^{-3}$, $1.08 \pm 6.11e^{-3}$ to $1.04 \pm 5.92e^{-3}$ and $0.98 \pm 5.70e^{-3}$ for summer and autumn, respectively.

Supplemental figure B.3

Supplemental table B.3

Consistently with the analyses of non-linear trends (GAM), average rates of change in sardine body condition over the study period were all negative and dependent upon quarter (Fig. B.3.b). The largest rates of change were found for both the summer and autumn periods. Again, the large confident interval estimated for the winter period probably results from the low number of individuals collected during this season.

Supplemental analysis B.4:

Material and Methods

Time series of environmental variables and both sardine body condition and maximum size (estimated for each year by computing the 90% quantile of fish size distribution) were jointly analyzed with a breakpoint analysis (Zeileis et al., 2015) to identify and compare periods of major changes between time series and check if there was synchrony between fluctuations. This method discriminates between two continuous periods of significantly different levels and provides the optimal combination of segments of the time series with confidence intervals. The optimal number of segments used to describe the data was assessed through the Bayesian information criterion (BIC). The synchrony between series was then evaluated using the identified year(s) of statistically significant changes in series and comparing the change direction (increasing or decreasing breakpoint).

Results

Overall, the breakpoint analysis indicates that the period between 2007 and 2011 was a period of major changes in the whole sardine population of the Bay of Biscay. Indeed, both sardine body condition and maximum size strongly decline since 2007. Even if sardine body condition seems to reach a stability phase since 2011, it has to be highlighted that the decrease in maximum size endures over time until to reach a minimum of 20.5 cm in 2015 (Fig. B.3 a).

Regarding sardine body condition, all age-class time series showed one or two decreasing breakpoints occurring between 2007 and 2011 (Fig. B.3 b). Although most of the breakpoints were widely spread in time (not shown in the graph), it is interesting to note that 1- to 3-year-old individuals showed common breakpoints between 2006 (age 2) and 2008 while older individuals showed synchronous breakpoints at the end of this period (2010).

Regarding environmental factors, no breakpoints were detected in the *Eke* time series.

The four other environmental variables (*Sal*, *SST*, *MLD* and *Chl-a*) showed one to three breakpoints. Chlorophyll *a* showed an increasing breakpoint in 2006, followed by two decreasing breakpoints in 2009 and 2014 (Fig. B.3 e). For the first two breakpoints, it is interesting to note that they occur in the same period of changes in sardine body condition for young age classes. Overall, the increase in *CHL-a* in 2006 co-occur with a decrease in body condition for 2-years old individuals. We also observe a lag of one year between change in chlorophyll *a* and a potential response in sardine body condition for almost all age classes (except ages 1 and 2). Increases in sea surface temperature and sea surface salinity co-occurred in 2010 (Fig. B.3 c,d) and were accompanied by a decrease in body condition for all age classes except for 1 and 2. Sardine catches (Fig. B.3 g) show three breakpoints over the study period with the first two one (increasing trend) occurring during the period of changes in both biological parameters. Interestingly, these two breakpoints occur one year before the decreasing breakpoints identified in maximum size, suggesting a potential response of the population to this increase in fishing effort.

Overall, this breakpoints analysis confirms a general decrease in body condition for all age classes with a period of change between 2007 and 2011 and suggests that other factor may be implied in those changes. The increase in both sardine catches and sea surface temperature could be linked to the decreasing trend observed in maximum size. Moreover, this analysis also confirms a lag between decrease in sardine body condition and maximum size.

Supplemental Figure B.4

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Figure 1. Bay of Biscay with the continental shelf domain (<330m) corresponding to our study area highlighted in grey.

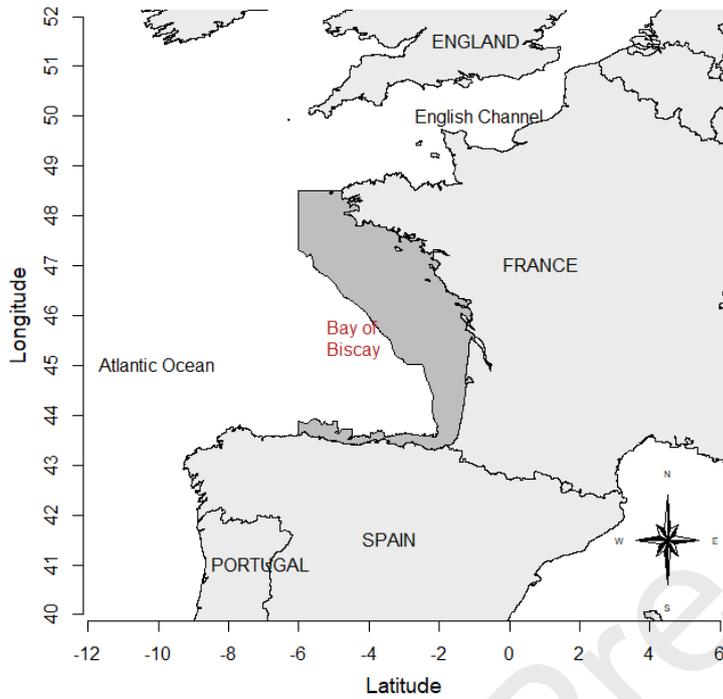


Figure 2. Long-term changes in sardine body length at-age over the study period. Lines correspond to the fit of the GAM model. The shaded bands represent the 95% confidence interval.

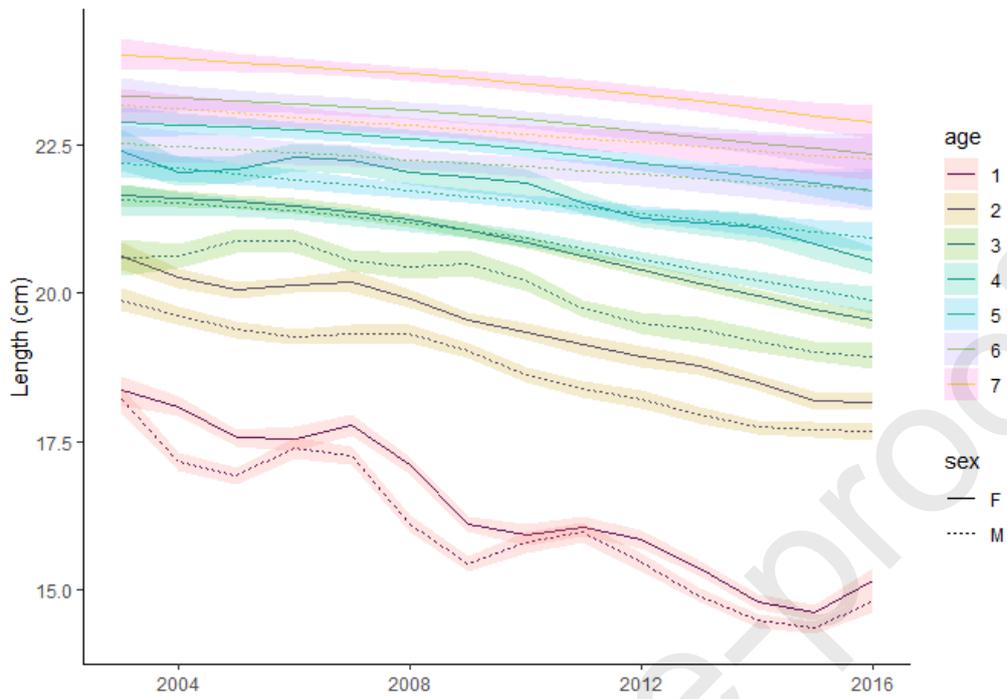


Figure 3. Average prediction of sardine body condition-at-age estimated for each of the fixed-effect covariates: a) year, b) quarter, c) reproductive stage and d) sex, included in the most parsimonious linear mixed effects model. Error bars correspond to the standard error.

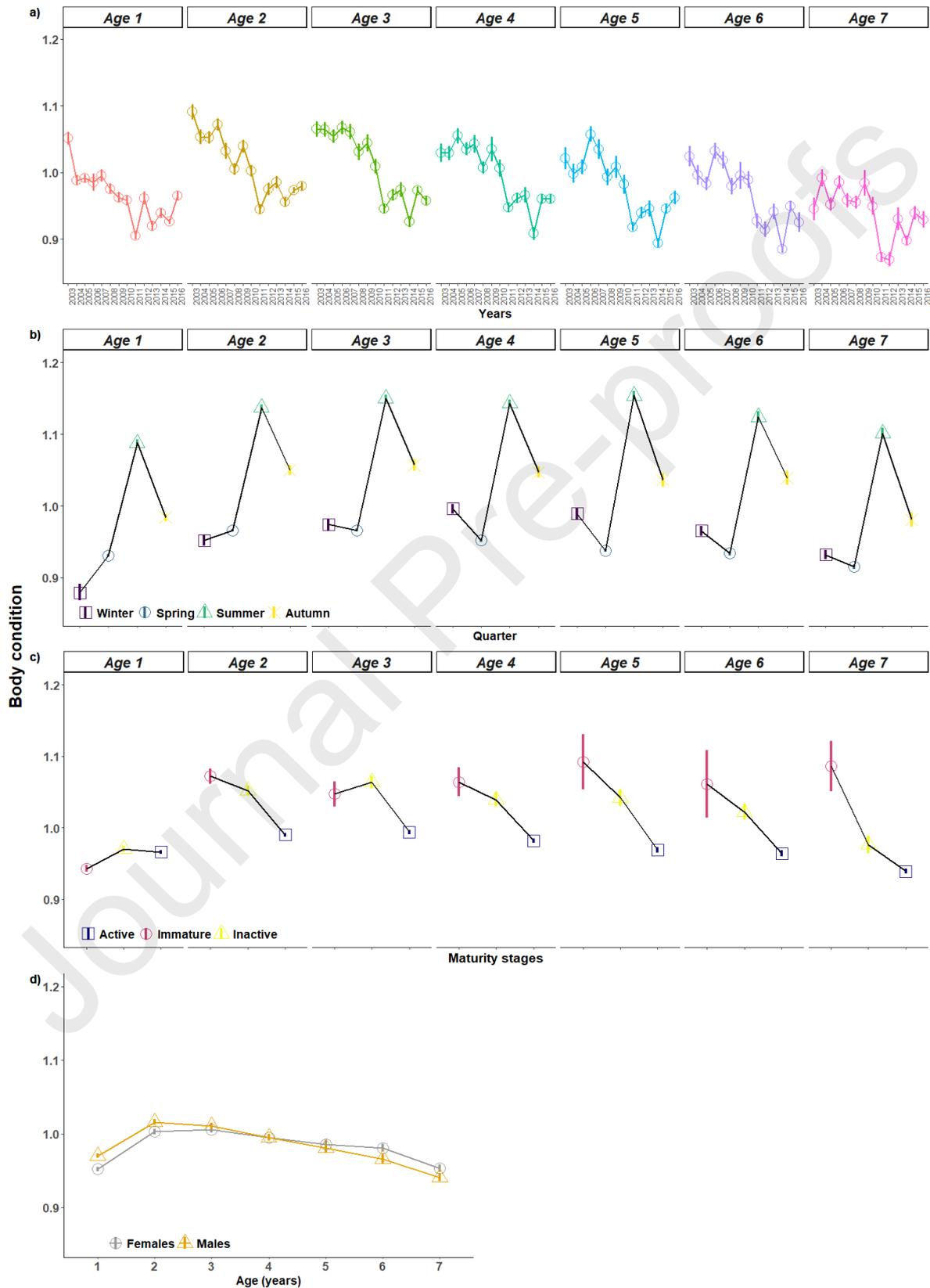


Figure 4. Maximum variability in sardine body condition anomalies for both seasonal and inter-annual scales. This variability was computed as the difference between the maximum and the minimum of sardine body condition anomalies predicted by the LME model for both seasonal and inter-annual scales. Red line corresponds to the maximum variability in sardine body condition anomalies explained by seasonal variations (yellow block) while environmental factors traduce the inter-annual variability.

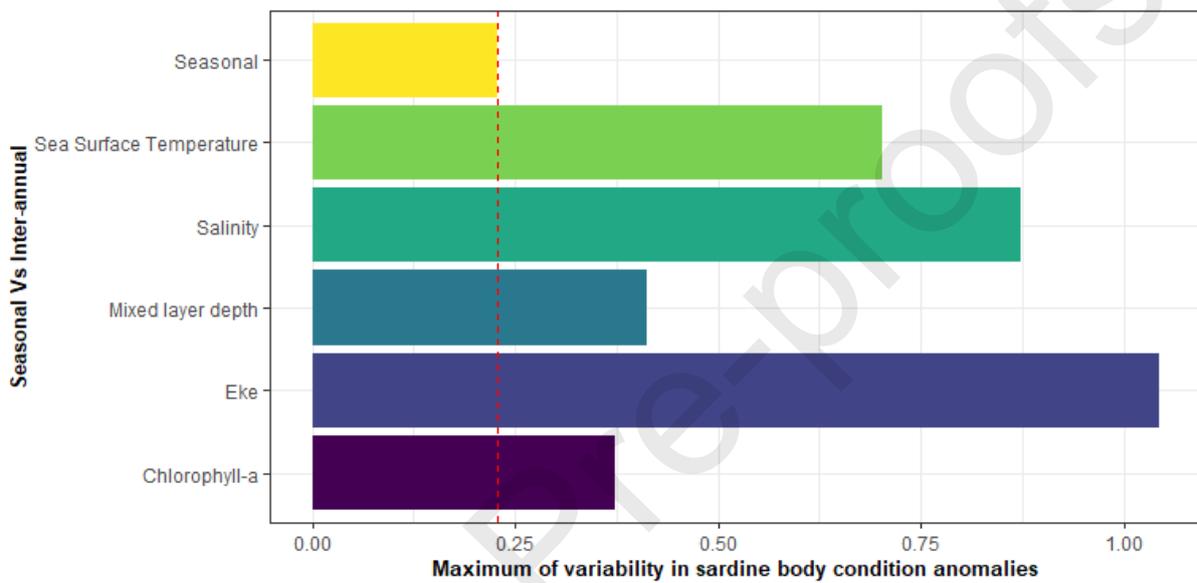


Figure 5. Principal component analysis showing the relative importance of biological parameters and exogenous factors over the study period (2003-2016). The three periods of changes identified in this study were super-imposed and larger symbol reflects the barycenter of each period.

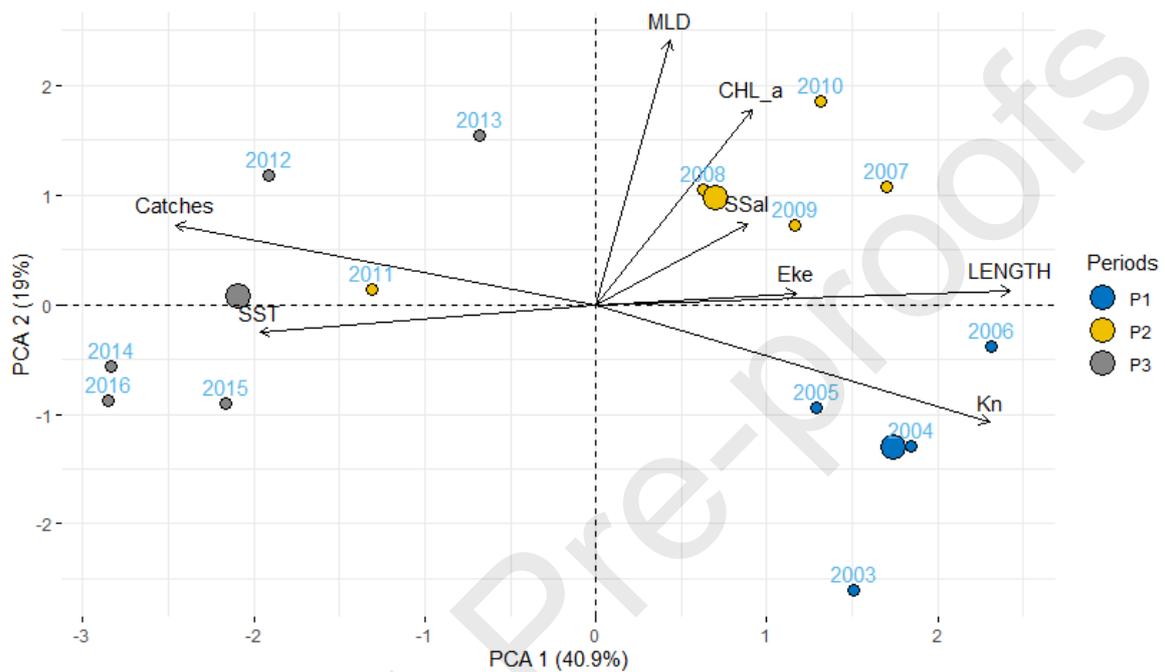


Table 1. Data type, origin, sampling period, sample size (N) and age, length and weight ranges included in the analyses (study period: 2003 – 2016).

Table 2. Summary information of length and weight per age class used in the analyses.

Table 3. Main statistics from GAMs applied to sardine body length as a function of age, sex and year. % of deviance explained and AIC are presented for each tested model. Selected model is denoted by bold characters.

Table 4. The most parsimonious model structure for LME investigating the variability of sardine body condition and its dependence upon endogenous factors. Covariates: Y - year, Q - quarter, A - age, S - sex, Ms - maturity status and the interaction between age and all covariates X (A:X). AIC: Akaike's information criterion, LL: maximum log-likelihood. Marginal R^2 value provides information on the proportion of variance explained by the fixed factors, while conditional R^2 incorporates both fixed and random factors.

Table 5. Results of the selected linear mixed effect model describing the relationship between the sardine relative condition index and environmental variables. A nested age effect within station was included in the model as a random effect. Explanatory variables were standardized to allow comparison of their slope coefficients. $I(Y,Z)$ corresponds to the Z order polynomial effect of the Y covariate. AIC: Akaike's information criterion, LL: maximum log-likelihood. For quarter variable that was coded as factor in the model, coefficients are given in reference to the first quarter (winter).

Table 9. The most parsimonious model structure for LME investigating the variability of sardine body condition and its dependence upon endogenous factors. Covariates: Y - year, Q - quarter, A - age, S - sex, Ms - maturity status and the interaction between age and all covariates X (A:X). AIC: Akaike's information criterion, LL: maximum log-likelihood. Marginal R² value provides information on the proportion of variance explained by the fixed factors, while conditional R² incorporates both fixed and random factors.

Model	Kn ~ Y + Q + A + S + Ms + A:Y + A:Q + A:S + A:Ms				
AIC	LL	Observations (n)	Marginal R ² (%)	Conditional R ² (%)	
	-47,782	24,034	20,145	40.69	61.51
Random effect	1 Station				
	Intercept	Residual			
Std dev:	0.05112537	0.0695083			
	F-value	p-value			
Intercept	200,521.53	<.0001			
Year	20.78	<.0001			
Quarter	149.01	<.0001			
Age	291.21	<.0001			
Sex	104.19	<.0001			
Maturity	142.01	<.0001			
Age : Year	2.91	<.0001			
Age : Quarter	6.65	<.0001			
Age : Sex	12.24	<.0001			
Age : Maturity	3.53	<.0001			

Table 10. Results of the selected linear mixed effect model describing the relationship between the sardine relative condition index and environmental variables. A nested age effect within station was included in the model as a random effect. Explanatory variables were standardized to allow comparison of their slope coefficients. $I(Y,Z)$ corresponds to the Z order polynomial effect of the Y covariate. AIC: Akaike's information criterion, LL: maximum log-likelihood. For quarter variable that was coded as factor in the model, coefficients are given in reference to the first quarter (winter).

Model	Kn ~ Quarter + Chl-a + MLD + SST + Eke + I(Eke,2) + Ssal + I(Ssal,2) + I(Ssal,3)				
AIC	LL	Observations (n)	Conditional R ² (%)		
	48,961	-24,465	20,145	41.7	
Random effects					
	Intercept	Residual			
	1 Station				
Std dev	0.5295967				
	1 Age %in% Station				
Std dev	0.2900521	0.7723823			
	Value	Std. Error	DF	t-value	p-value
Intercept	-0.16902187	0.14308391	17,267	-1.181278	0.2375
Spring	0.06120377	0.14421970	592	0.424379	0.6714
Summer	0.07854486	0.15458721	17,267	0.508094	0.6114
Autumn	-0.14945273	0.15475007	17,267	-0.965768	0.3342
Chlorophyll α	0.07463748	0.02700617	17,267	2.763720	0.0057
Mixed Layer Depth	-0.08250494	0.02952849	17,267	-2.794079	0.0052
Sea Surface Temperature	-0.14042005	0.02895085	17,267	-4.850291	0.0000
Eddy kinetic energy	-0.07834172	0.03308790	17,267	-2.367685	0.0179
(Eddy kinetic energy) ²	0.14082574	0.02198327	17,267	6.406043	0.0000
Sea Surface Salinity	0.25455956	0.05263021	17,267	4.836758	0.0000
(Sea Surface Salinity) ³	-0.05265323	0.02090196	17,267	-2.519057	0.0118

Highlights

- Strong dependence on age of both seasonal and inter-annual variability in body condition
- Sardine body condition strongly declined between 2007 and 2011
- Increase of temperature and decrease in Chlorophyll-*a* may explain the decreasing trend in body condition
- High levels of Chlorophyll-*a* during the critical phase (2007-2011) suggest that food quality rather than quantity is involved

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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