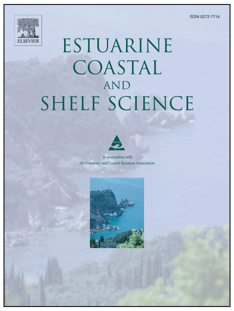

First approach to the growth and age corroboration of Northeast Atlantic chub mackerel (*Scomber colias*) in Northern Iberian waters

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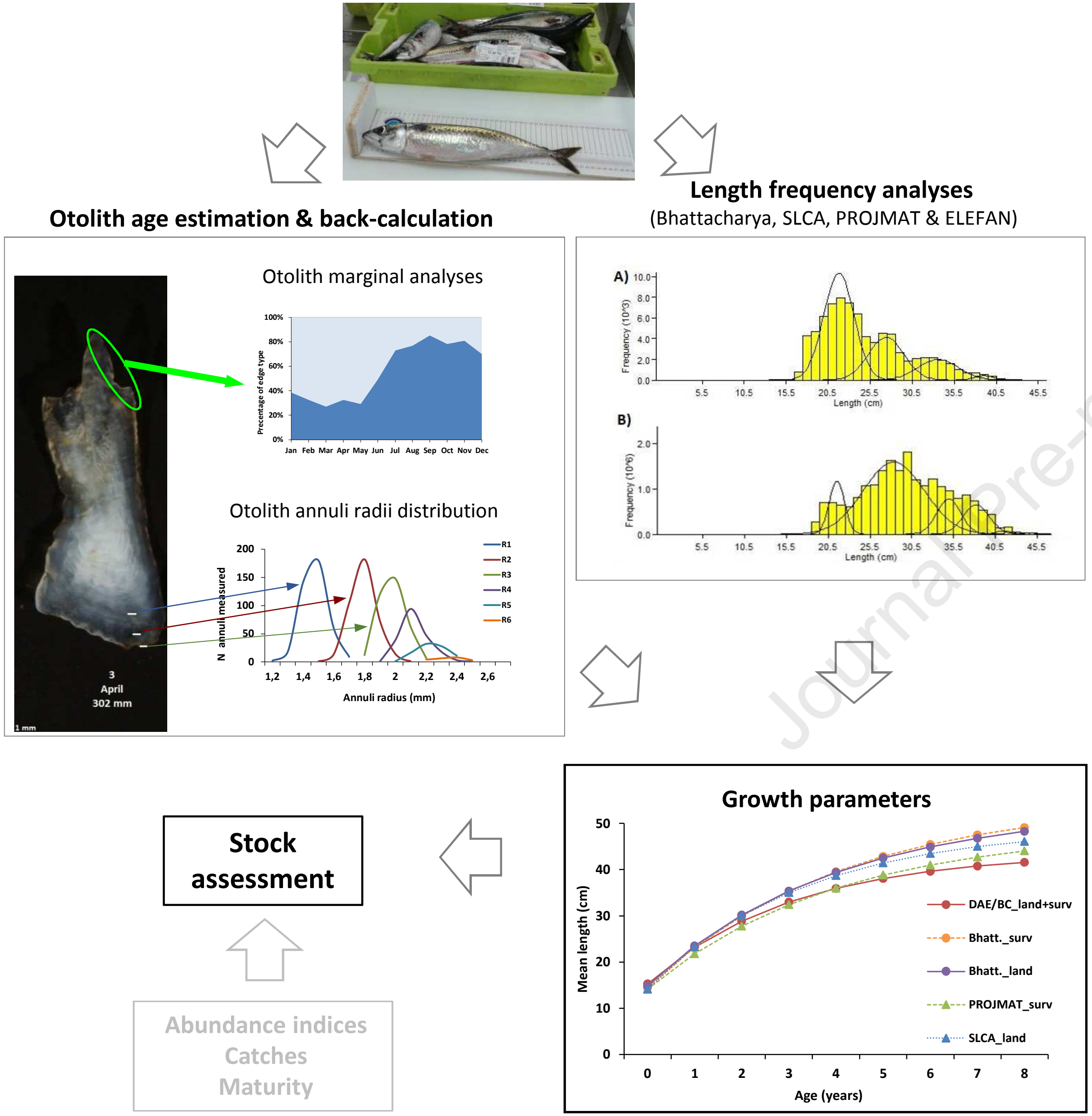

Otolith age estimation & back-calculation

Length frequency analyses

(Bhattacharya, SLCA, PROJMAT & ELEFAN)

Otolith marginal analyses

Otolith annuli radii distribution

Growth parameters

Stock assessment

Abundance indices
Catches
Maturity

FIRST APPROACH TO THE GROWTH AND AGE CORROBORATION OF NORTHEAST ATLANTIC CHUB MACKEREL (*SCOMBER COLIAS*) IN NORTHERN IBERIAN WATERS.

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ABSTRACT

The growth pattern and parameters of Atlantic chub mackerel in Northern Iberian waters were analysed for the first time in this study, using otolith analyses (direct age estimation-DAE, back-calculation-BC and otolith marginal analyses) and length frequency analyses (Bhattacharya, SLCA and PROJMAT methods), on a time series of data from 2011-2017. Two main different growth patterns were obtained, one slower (DAE, BC and PROJMAT) and other faster (Bhattacharya and SLCA). Otolith marginal analyses showed an annual periodicity in the formation of one hyaline and one opaque edge, with a prevalence of the opaque edge from June to December, what in addition to the unimodal distribution of the annuli radii and the obtained back-calculated mean lengths, similar to those obtained by DAE, support the age estimation criteria used here. The growth parameters obtained from DAE (*L_∞: 45.34, k: 0.28, t_0: -1.18*) are proposed for the upcoming stock assessment process.

KEY WORDS

Scomber colias, Atlantic Ocean, length frequency analysis, Bhattacharya, direct age estimation, back-calculation, growth curve, otolith edge analysis

1. INTRODUCTION

Atlantic chub mackerel, *Scomber colias* (Gmelin, 1789), is a migratory middle-sized pelagic fish distributed in warm and temperate waters on the two sides of the Atlantic Ocean (Castro and Santana, 2000). In the Eastern Atlantic, *S. colias* is distributed from North West African coastal waters, including the Macaronesian Archipelagos, to the southern Atlantic European waters (i.e., Atlantic coast of the Iberian Peninsula) and the Mediterranean Sea (Whitehead *et al*., 1984; Collette *et al.*, 2011) (Fig. 1.A). Although it was first considered the same species than the Indo-Pacific chub mackerel (*Scomber japonicus*, Houttuyn, 1789), morphologic and genetic studies demonstrated that they are two different species (Scoles *et al*., 1998; Collette, 1999; Infante *et al*., 2007; Catanese *et al*., 2010; Cheng *et al.*, 2011). Atlantic chub mackerel is an important species of the pelagic ecosystem (Wahbi *et al.*, 2015; Albo-Puigserver *et al.*, 2017), which is expanding northwards (Martins *et al.*, 2013; ICES, 2020a).

The 90% of the *S. colias* global catches between 1950 and 2018 in Eastern Atlantic were taken in Atlantic African waters (FAO, 2020), with an average value of 379 thousand tons in 2014-2018 (FAO, 2019). However, in the Iberian Peninsula (Atlantic European waters), landings have increased significantly in the most recent years (ICES, 2020a) (Appendix, Fig. A1). This is likely associated to the increase of its abundance and expansion northwards (Punzón et *al.*, 2016; ICES, 2020a), probably related to an increment of the sea temperature (González-Pola *et al.*, 2012; Costoya *et al.*, 2015; Jurado-Ruzafa *et al.*, 2019) influenced by the Climate Change (Tasker, 2008; Reid and Valdés, 2011). In this context, Atlantic chub mackerel is increasing its importance as target species for the Portuguese and Spanish purse seiner fleets (ICES, 2017). The International Council for the Exploration of the Sea (ICES), as responsible of providing scientific advice for fisheries management in the European Union, is promoting the assessment of *S. colias* in European waters (ICES, 2020a). Currently, the stock identity, dynamics and status of *S. colias* in East Atlantic waters (including

European and African waters) are still unknown (ICES, 2020a). Thus, filling knowledge gaps on biology and ecology of this expanding species is mandatory.

To determinate the age structure of an exploited population is an essential feature in fish stock assessment to estimate the natural mortality and growth rates (Hilborn and Waters, 1992; Haddon, 2001). Accurate age and growth information (e.g., parameters, age-length keys) and validated/corroborated age estimation criteria are necessary to provide unbiased data for the analytical assessment models (ICES, 2020b). The individual age estimation criteria based on otoliths of Atlantic chub mackerel were internationally standardized in 2015 (ICES, 2016) and ICES international calibration exercises among European otolith age readers were performed in 2012, 2015 and 2017 (Martins *et al.*, 2014; Navarro *et al.*, 2015; Silva and Navarro, 2018). However, few age validation or corroboration studies to support them were then available (Villamor *et al*., 2019; ICES, 2020c). Previous works on *S. colias* in the NE Atlantic have estimated growth parameters mainly from direct otolith age estimation and/or back-calculation (Martins *et al.*, 1983; Lorenzo, 1992; Martins, 1996; Carvalho *et al*., 2002; Vasconcelos, 2006; Velasco *et al.*, 2011; Jurado-Ruzafa *et al.*, 2017). Only two studies presented growth parameters also estimated by alternative methods to the otolith age estimation, such as length frequency analyses, using Bhattacharya (Lorenzo, 1992) and ELEFAN (Vasconcelos, 2006) in the Canary Islands and Madeira, respectively. Most of these works were performed during the 80s and early 2000s, being the studies in the West of the Iberian Peninsula (Martins *et al.*, 1983; Martins, 1996) performed before (80s-90s). Therefore, updated age and growth information is required for assessing this expanding population.

Moreover, having updated and detailed information on the demographic structure of this population of *S. colias* will additionally contribute to a deeper understanding of the Iberian pelagic ecosystem, in which this species is occupying an increasingly relevant position and may compete with other important commercial pelagic species like Atlantic mackerel (*Scomber scombrus*, Linnaeus 1758), horse mackerel (*Trachurus trachurus*, Linnaeus 1758), sardine (*Sardina pilchardus*, Walbaum 1792) or anchovy (*Engraulis encrasicolus*, Linnaeus 1758) (Castro, 1993; Martins *et al.*, 2013; Bachiller and Irigoien, 2015; Garrido *et al.*, 2015; Gushchin and Corten, 2017; Veiga-Malta *et al.*, 2019).

The aim of this study is to analyse the growth pattern and estimate growth parameters of Atlantic chub mackerel in Northern Iberian Atlantic waters through different approaches: i) methods related with the direct age estimation in otoliths, including back-calculation and marginal increment analysis; and ii) length frequency distribution analyses. Finally, the obtained results were analysed to assess whether these methods support the current age estimation criteria for this species.

2. MATERIAL & METHODS

2.1. Study area, data acquisition and biological sampling

The study area included the North (N) and Northwest (NW) of the Iberian Peninsula (ICES Div. 27.8.c and 27.9.a N, respectively) (Fig. 1.B), corresponding to temperate latitudes and belonging to the Bay of Biscay and Iberian Atlantic ecoregions. Hydrography in this area is conditioned by a subtropical gyre (anti-cyclonic) and a subpolar gyre (cyclonic), resulting into a subtropical/boreal transition area, where species of warm and cold waters coexist (González-Pola *et al.*, 2005; Lavín *et al.*, 2006).

A total of 10403 individuals of *Scomber colias* were collected between 2011 and 2017, 8272 specimens came from commercial landings collected in the fish markets of Santander, A Coruña and Vigo, and 2131 specimens came from scientific acoustic surveys “PELACUS” (Massé *et al*., 2018; ICES, 2020d) carried out by the Spanish Institute of Oceanography (IEO) on board of the R/V Miguel Oliver during March-April (Fig. 1.B). Total length (TL) to the lower cm, total and gutted weight (1 g) and gonad and liver weight (0.1 g) were recorded, sex and maturity were determinate according to the Walsh maturity key (Walsh *et al.*, 1990), and the otoliths were removed and preserved for further analyses.

In addition, length samplings by quarter from commercial landings were performed in the fish markets from six harbours of the N and NW Iberian Peninsula (Santoña, Gijón, Avilés, A Coruña, Santa Eugenia de Riveira and Vigo) (Fig. 1.B), during the same period (2011-2017). Likewise, length distributions from the scientific surveys PELACUS, for six years (2011, 2013-2017) were also obtained.

2.2. Age estimation procedures

For the age estimation, whole otoliths were mounted on black plastic slides, concave side up, covered with transparent resin and observed using a binocular microscope (Nikon SMZ 1500) under reflected light (Villamor *et al.*, 2015). Each pair of otoliths was examined twice by the same reader, and a third examination was performed for those otoliths in which the two age estimates disagree. Age was estimated following standardized criteria (ICES, 2016) (Appendix, Fig. A2.A).

Biannual Age-Length Keys (ALK) were obtained by year and applied to each biannual length distribution (LD) for the commercial landings and the scientific PELACUS surveys catches. These mean lengths (ML) at age from the Direct Age Estimation (DAE) were averaged for the monitored time period to be compared to ML at age estimated from back-calculation and length frequency analyses (see subsections 2.3.2 and 2.3.3).

2.3. Age corroboration studies

The age estimation method and the obtained otolith growth pattern were assessed with complementary studies: back-calculation (BC), frequency distribution of annuli radii, otolith marginal and length frequency analyses (LFA). The two first methods are more focused on the precision and consistency of the age, and the others on age corroboration (ICES, 2020c).

2.3.1 Otolith marginal analyses

Two otolith marginal analyses were performed. On the one hand, the nature of the edge (opaque/hyaline) was identified in 8852 otoliths. The proportion of individuals with hyaline (H) and opaque (O) edge was determined monthly to find out the annual formation pattern, and also by age, to check possible ontogenic differences in the time of the opaque edge formation (Holden and Raitt, 1974). On the other hand, a marginal distance analysis was performed. The absolute marginal distance (AMD: distance between the end of the last hyaline annulus and the edge) and the distance between the last two hyaline annuli ($D_{i,i-1}$) were measured to estimate the relative marginal distance (RMD: ratio of the AMD and $D_{i,i-1}$) (Panfili *et al.*, 2002) (Appendix, Fig. A2.B). Only whole otoliths were selected, and measures (in microns, µm) were obtained by using a microscope (Nikon SMZ 1500) and the image analyser NIS-Element D 3.0. The otolith selection included at least 20 otoliths by month (except for July, with only 5 valid otoliths available), amounting to a total of 423 otoliths from January 2011 to December 2012, with representative samples of the whole length range.

2.3.2. Back-calculation and frequency distribution of annuli distance analyses

The same otoliths than those considered for the marginal distance analysis were used for the back-calculation analyses. Total otolith and annuli radii (OR and AR respectively) (Appendix, Fig. A2.B) were measured, and their frequency distributions were plotted and analysed by using a Kolmorogov-Smirnov normality test, to check the regularity of the growth pattern (Panfili *et al.*, 2002) and to corroborate the formation of one annulus per year.

After checking that TL-OR relationship fitted to a power equation (tested by an ANOVA associated to regression) back-calculated lengths were obtained using the Fraser-Lee equation and Body Proportional Hypothesis (BPH) equation (Ricker, 1992):

1) Fraser-Lee equation: $\ln L_i = \frac{\ln R_i}{\ln R_t}(\ln L_t - \ln a) + \ln a$
2) Body Proportional Hypothesis (BPH): $\ln L_i = \frac{\ln L_t(\ln a + b \ln R_i)}{\ln a + b \ln R_t}$

where, L_i is the TL when the OR was R_i (cm); L_t the TL when the specimen was caught (cm); R_i the OR of the annulus i (mm); R_t the OR when the specimen was caught (mm); a and b are the parameters of the power regression.

2.3.3. Length frequency analyses

Length frequencies from surveys data offer less biased information about juvenile length distributions than the commercial landing data. However, *S. colias* is not the main target species of the pelagic survey series PELACUS, focused on other more economically important species, mainly Atlantic mackerel (*S. scombrus*), horse mackerel (*T. trachurus*), sardine (*S. pilchardus*) and anchovy (*E. encrasicolus*) (Massé *et al.*, 2018; ICES, 2020d). In addition, the commercial landings cover a wider length range, especially of larger specimens. Thus, both datasets were analysed as they provided complementary information. Nevertheless, the different magnitude between the length compositions obtained from surveys and commercial landings (thousands vs millions of specimens, respectively), did not allow to analyse both data combined as a whole. For this reason, these sources were analysed separately, considering, on one hand, the length frequencies from the surveys (from March-April), and, on the other hand, the length frequencies from the first semester of the commercial landings (which are, therefore, seasonally comparable with the data from the surveys).

Several approaches to the length frequencies time-series compilation were tested (grouping data by area, quarter, semester, etc.), but only the data from the two areas as a whole (ICES Div. 27.8.c and 27.9.a.N) and grouped by semester showed clear multimodal length distributions, and allowed the use of the two types of length frequency analysis (LFA) methods: i) Modal class Progression Analysis (MPA), by the Bhattacharya's method (Bhattacharya, 1967) included in the FISAT II program (Gayanilo *et al.*, 2005); and ii) three methods of length frequency analysis included in the software package Length Frequency Distribution Analysis (LFDA) (MRAG, 2001): Shepherd's Length Composition Analysis (SLCA), Projection Matrix Method (PROJMAT) and Electronic Length Frequency Analysis (ELEFAN). The MPA analyses were finally performed on a combined LD of the six annual LD of surveys and another combined LD of the seven annual LD of the first semester of commercial landings. However, the LFDA methods do not work on a single LD, but on a series of LD with temporal succession, and were finally applied to a LD series of the six annual LD of surveys and to a LD series of the seven annual LD of the first semester of commercial landings.

2.4. Annual growth pattern and growth parameters estimation

The growth parameters of *S. colias* were estimated by sex and for both sexes combined, according to the von Bertalanffy equation: $L_t = L_\infty(1 - e^{-k(t-t_0)})$

where L_t is the TL at age t; L_∞ is the mean asymptotic fish length; k is the instantaneous growth coefficient; t is the age; and t_0 is the hypothetical age at which the TL is 0.

The growth parameters were calculated using SPSS software (IBM Corp., 2017) from DAE and BC data, and using the ML at age from MPA. In the case of the length-frequency analysis, the growth parameters were provided directly by the LFDA program.

Growth curves for both sexes and each method were compared using the Kimura's likelihood ratio test (Kimura, 1980) and the Chen test (Chen *et al.*, 1992). The von Bertalanffy curve is strongly influenced by the estimates of L_∞ and t_0, usually associated to higher uncertainty because of the lack of data of the youngest (in the case of commercial landings) and oldest (in the case of scientific surveys) age groups (Haddon, 2001). Thus, to compare growth curves it is important to conduct tests only over similar and well represented (in number) length ranges. Because of this, the Kimura's likelihood ratio test was applied only to the range of ages for which datasets were comparable (Haddon, 2001), and the growth parameters had to be re-estimated according to the age range of the pair of methods compared in each test. These parameters were re-estimated using ML at age in SPSS (IBM Corp., 2017).

The growth performance index ($\phi'=\log_{10}K+2\log_{10}L_\infty$, Pauly and Munro, 1984) was calculated to compare our growth parameter values with previous studies of *S. colias*.

3. RESULTS

3.1. Direct age estimation (DAE)

Age was estimated in a subset of 6867 otoliths (5029 from commercial landings and 1838 from surveys), and 546 otoliths were rejected (161 for differences between age estimations and 385 for being illegible). Fish ranged from 14 to 50 cm of total length, and estimated ages from 1 to 14 years (Appendix, Table A1). Overall mean values of the biannual ML at age of the total commercial landings are presented in Table 1. The ML in the most abundant age groups in the landings (1 to 5) ranged between ~24 and 37.5 cm in the first semester, and between ~27 and 38 cm in the second one, i.e., ML increased between 0.7 and 3 cm (depending on the age group) from the first to the second semester. The ML at age from surveys (March-April) presented similar (or slightly lower) values than those estimated in the first semester from commercial landings (Table 1).

3.2. Age corroboration studies

3.2.1. Otolith marginal analyses

The analysis of the nature of the edge showed a prevalence of otoliths with opaque edge higher than 50% from June to December, with a maximum in September. On the contrary, the prevalence of otoliths with hyaline edge reached values higher than 50% from January to May, with a maximum in March (Fig. 2.A).

Analysing the edge type by age group, it was observed that younger individuals (ages 1 and 2) formed the opaque edge earlier than the older ones, starting this formation in March for 1 year-old individuals, in May for 2 years-old, and in June for 3 years-old and older (Fig. 2.B).

The mean values of AMD and RMD increased progressively from January to December, in agreement with the aforementioned prevalence of the opaque edge. The highest AMD mean value was reached in December (126.95 µm) and the lowest in February (32.64 µm), while the highest RMD mean values were obtained in July (0.61) and December (0.60) with the lowest one occurring in February (0.23) (Fig. 2.C). A yearly sinusoidal pattern was observed, although the relatively high mean values of AMD and RMD in July must be considered with caution because only 5 otoliths were measured. Likewise, mean values of AMD and RMD observed in April were probably affected by the high number of one-year-old individuals collected during the scientific surveys, because the earlier formation of the opaque edge in youngest individuals.

3.2.2. Back-calculation and frequency distribution of annuli distance analyses

The relationship between total fish length (TL) and otolith radius (OR) was $TL=13.29OR^{1.283}$ ($r^2=0.87$, $p<0.005$) (Fig. 3.A).

The frequency distribution of annuli radii (AR) presented a unimodal distribution in each age group (Fig. 3.B). The first and second annuli presented quite well separated distributions, nevertheless, the AR frequency of age 3 and older overlapped considerably. Length range, ML and standard deviation of each annuli are presented in Table 2. However, the Kolmorogov-Smirnov test did not prove that they statistically fit a normal distribution.

A total of 1341 back-calculated lengths were obtained. The mean back-calculated lengths at age were estimated by the two BC methods (Fraser-Lee and BPH) and resulted very similar between them and close to the values of the ML at age obtained from DAE both, commercial landings and surveys catches, in the most abundant age groups (up to age 5) (Table 1).

3.2.3. Length frequency analyses

Data of the commercial landings showed a clearer multimodal length distribution than in the case of surveys, both being also seasonally comparable (Fig. 4). The 99% of the *S. colias* caught in surveys were between 17 and 33 cm, while the 99% of the commercial landing specimens were between 20 and 40 cm (Fig. 4). Noticeable catches of Atlantic chub mackerels were obtained in the surveys in 2016 and 2017, with modal lengths of 21 and 18 cm, respectively (Fig. 4). The predominance of young specimens was as well observed during the second semester of 2017 in the commercial landings, with specimens between 20-25 cm (mode 22 cm) representing the 82% of the total catch of that year, while these specimens represented the 0.2-30% of the catch in the rest of years.

3.2.3.1. Modal Progression Analysis (MPA)

Due to the interannual variability in the abundance of PELACUS surveys catches (Fig. 4), the MPA analysis was performed by sum of percentages of the combined LD for the six surveys, to eliminate abundance influence in the ML estimation (Fig. 5). This interannual variability in the abundance did not appear in commercial landings (Fig. 4), and MPA analysis of the combined LD of the first semester of the seven years of commercial landings was performed using absolute values (Fig.5). ML for both analyses resulted in similar values, presenting 5 age groups within the length range ~21-40 cm (the most abundant in the landings), which implies a faster growth than that obtained by DAE/BC, where 7 age groups were estimated within the same length range (Table 1).

3.2.3.2. Length Frequency Distribution Analysis (LFDA).

The LFDA analyses were performed for the LD series of the six annual surveys (a series of six LD, relative values), and for the LD series of the seven annual LD of the first semester of commercial landings (a series of seven LD, absolute values). The optimal growth parameters offered by the program, according to the maximization of a goodness-of-fit function through iterations, were those obtained by the PROJMAT method for the survey data (Score: -0.983), and the SLCA method for the commercial landings data (Score: 6472) (Table 3). ML at age were estimated from these growth parameters, resulting in 5 age groups by SLCA in the length range ~21-40 cm (as by MPA), and 6 age groups by PROJMAT (Table 1).

3.3. Annual growth pattern and growth parameters estimation

The growth parameters estimated by the different methods are presented in Table 3, with DAE and BC methods offering lower L_∞ values (42.63-45.34 cm), than those estimated by LFA (48.74-55.00 cm). Additionally, the von Bertalanffy growth parameters obtained by sex using DAE were: L_∞: 43.33, K: 0.345, t_0: -0.663 for males; L_∞: 42.81, K: 0.361, t_0: -0.615 for females. Kimura's likelihood ratio and Chen tests did not detect differences between sexes in the growth curves from DAE (Table 4) and the growth curve of combined sexes was considered instead for the rest of the study. In the same way, as the growth curves of the two BC methods did not differ between them, only BPH method was considered for the rest of the study. The growth parameters from DAE and BC methods allowed to include together information from surveys and commercial landings, as they are based on pairs of length and estimated age values from both sources that could be jointly analysed, providing more information. MPA (Bhattacharya) and LFDA methods estimated growth parameters independently for surveys and commercial landings (from the first semester of the year and therefore comparable) (Table 3; Fig. 6).

No differences between DAE and BC growth curves were observed according to the Kimura's likelihood ratio test and Chen test (Table 4), and new growth parameters obtained from the combined DAE and BC data were estimated (Table 3) and used to be compared with those from the other methods. The Kimura's likelihood ratio test did not detect differences between the growth curves of Bhattacharya and SLCA, both from commercial landings, but significant differences were obtained when comparing the growth curves of the other methods (Table 4). The Chen test showed no significant differences between Bhattacharya growth curves obtained for surveys and commercial landings but presented significant differences between DAE/BC and these Bhattacharya growth curves (surveys and commercial landings) (Table 4). No comparison involving the growth curves from LFDA methods (PROJMAT and SLCA) could be performed by the Chen test. This test is an analysis of the residual sum of squares and because the ML of the LFDA methods were estimated from the given growth parameters, the value of their residual sum of squares was zero. Hence, here, it was not possible to perform the Chen test. In the Kimura's likelihood ratio test, the selected length range for the comparisons was 20-40 cm (99% of the commercial landings), that corresponded to ages 1 to 7 for DAE and BC methods, 1 to 6 for PROJMAT method (surveys), and 1 to 5 for Bhattacharya (surveys and commercial landings) and SLCA (commercial landings) methods. Thus, the re-estimated growth parameters were slightly different of those originally estimated by each method but showing similar ϕ' values to the original ones.

The ϕ' values obtained from DAE, BC and DAE-BC, were similar (2.76-2.79). The ϕ' values obtained by Bhattacharya method, for surveys and commercial landings, and by LFDA in commercial landings (SLCA) were 2.86, while the ϕ' obtained by LFDA in surveys (PROJMAT) was 2.77 (Table 3).

4. DISCUSSION

Our results represent a great contribution to the knowledge of important aspects of the life-history of *Scomber colias,* a highly distributed species in the Atlantic Ocean. The growth parameters here estimated are available to be used in the stock assessment process using age-structured models, contributing to a future better management of this fishing resource.

The ML at age and growth progression by semester from DAE presented a coherent pattern, supporting the reliability of the age estimation criteria applied in this study, in the same way as the rest of the analyses carried out here with otoliths.

Regarding the periodicity in the formation of one annulus composed by one hyaline and one opaque band in *S. colias* from the N and NW Iberian Peninsula the annual formation on one annulus is supported by the analysis of their monthly prevalence from the 7-years' time-series.

Most otolith edge studies in *S. colias* from the NE Atlantic indicate that the opaque edge predominates mainly from April/May to the end of summer/autumn. The occurrence of opaque edge in its distribution area seems to follow an overall latitudinal gradient from South to North, starting its deposition in the Gulf of Cadiz from March/April to September/October (Rodríguez-Roda, 1982; Velasco *et al*., 2011), then Portugal from May to August (Martins *et al*., 1983), finishing in the NW and N Iberian Peninsula, from June to December (present work). In the Atlantic archipelagos, the South to North gradient is also observed from the Canary Islands and Madeira between April and August (Lorenzo, 1992; Vasconcelos, 2006) to Azores, from May to September/October (Carvalho *et al*., 2002). However, this gradient should be taken with caution due to the temporal differences among studies and the lack of information for the whole annual period in some of them (Rodríguez-Roda, 1982; Martins *et al.*, 1983). Additionally, Lucio (1997) reported the occurrence of opaque edge during November in the N Iberian Peninsula, but he analysed otoliths only from two months (November 1989 and May 1997). The formation of the opaque or hyaline bands has been attributed to various factors, such as seasonal sea temperature cycles, light conditions, fish feeding and reproductive cycles (Beckman and Wilson, 1995). Geographical differences of all these factors and their timing probably explain geographical variability of hyaline/opaque band formation time.

The seasonal formation of the marginal increment of Atlantic chub mackerel's otoliths differs among age groups. This is the first study in which was observed a progressive delay in the opaque edge formation with the age of *S. colias*. These differences have been reported in other pelagic species such as Baltic herring (*Clupea harengus*, Linnaeus, 1758), Baltic sprat (*Sprattus sprattus,* Linnaeus, 1758), Atlantic sardine (*S. pilchardus*) and anchovy (*E. encrasicolus*) (ICES, 2008ab; ICES, 2011; Uriarte *et al*., 2016).

Regarding RMD, Vasconcelos (2006) reported the highest values in May, September, October and December in Madeira coinciding with our results. However, these highest RMD values in Vasconcelos (2006) did not match with the highest opaque edge prevalence described in the same work (April-August).

In conclusion, our results of the otolith marginal analyses support the consistency of the age estimation criteria used.

The regularity of the increment formation and the unimodal radii distributions support the regularity of the growth pattern in otoliths and the formation of one annulus by year, despite the Kolmorogov-Smirnov test did not prove that our annuli radii distribution statistically fit a normal distribution.

In most studies, the fish length-otolith radius (TL-OR) relationship in *S. colias* fitted to a power model (Lorenzo, 1992; Velasco *et al.*, 2011; Jurado-Ruzafa *et al.*, 2017 and present work; in the Canary Islands, Gulf of Cadiz, Mauritanian and northern Iberian waters, respectively). In Martins *et al*. (1983) and Vasconcelos (2006), in the Portuguese coast and the Azores, respectively, only the linear model was tested and therefore considered. Lorenzo (1992) obtained a good fit to both, power and exponential model, although this may be explained by the small length range analysed (14-25 cm of the 95% of the samples).

In our study, the back-calculated ML at age 1 (~22 cm) agrees with that obtained by DAE from surveys, although it is smaller than that obtained from commercial landings (~24 cm and ~27 cm in the first and second semester respectively). Differences may be related to the fishing gear selectivity (pelagic trawl gear in surveys and mostly purse seine gear in commercial landings), allowing the catch of smaller specimens (of 1 year old) in surveys. The estimation of the ML at age 1 can be more reliable in the BC method as it is less influenced by the sampling bias. Discrepancies between BC and DAE in the ML at age 1, related with biased sampling and affecting to the ML at age 1 estimated by DAE, has as well been observed in other species, such as golden shiners (*Notemigonus crysoleucas*, Mitchill 1814) (Pierce *et al*., 1996). Back-calculated lengths are useful for reducing the effect of size-selective sampling bias on the lengths estimates for the youngest fish in the sample (Campana, 2001). In addition, the low presence of old individuals (> 5 years) could influence the ML at old age groups estimated by the two methods (BC and DAE). In any case, the unimodal annuli radii frequencies in addition to the back-calculation results, also supports the consistency of the age estimation criteria used. Additionally, the increase from the first to the second semester in the ML at age estimated by DAE corroborates too the consistency of the growth pattern throughout the year. Finally, the similarity between DAE and BC results testify the coherence in the application of the age scheme and age criteria.

Our results of the BC analysis are similar to previous studies in Mauritanian waters (Jurado-Ruzafa *et al.,* 2017), but higher than the back-calculated ML obtained by Lorenzo (1992) and Vasconcelos (2006) in the Canary Islands and Madeira, respectively. Likely due to geographical and temporal variations in the growth parameters, and also to differences in the length ranges sampled and the BC method used.

The match in the ML at the first age group here estimated by various methods (~22 cm in the first semester), could allow the first winter increment in the otoliths in this work to be more robustly considered as the first true annulus. The mean first annulus radius (1.5 mm) obtained may be used as a reference for forthcoming age and growth works in this area, at least until validated by daily growth studies.

Regarding the analyses of length frequencies, the different number of modal lengths observed in the length distributions of each year analysed was a challenge in the application of MPA in this study, in addition to the subjectivity of this method. This difference in number of modal lengths by year is probably linked to the presence of low-abundant cohorts (with modes in the length distribution masked by the most abundant cohorts). Despite this, a general consistency was observed in the mean values estimated in both MPA analyses (surveys and commercial landings).

ML estimated by MPA in Lorenzo (1992) were smaller than in our results, but similar to those estimated in the same study using DAE/BC methods. As pointed out in growth studies of other pelagic species, like the congener *S. scombrus* (Villamor *et al.*, 2004) and several tuna species (Murua *et al.*, 2017), geographical and temporal differences may explain these different ML values of MPA between these works. However, the different sampling methodology used, like the different amplitude of time series, number of samples and length range of the data used in the two studies (e.g., the 95% of the specimens studied had 14-25 cm in Lorenzo (1992) and 20-40 cm in the present study) should be considered as well (Villamor *et al.*, 2004; Murua *et al.*, 2017). Fish growth varies temporarily and geographically, and different growth patterns could be obtained for the same population if the samples come from different areas or periods (Panfili *et al*., 2002), or if they have a different degree of representativeness (length range and sample size) of the actual population (Haddon, 2001).

Five age groups were obtained in the length range ~21-40 cm using LFDA for commercial landings (by SLCA), equal to what was previously described from Bhattacharya. However, one more age group (6) for the same length range was obtained using LFDA for surveys (PROJMAT). Considering that LFDA program analyses the progression of the modal lengths throughout the length distributions, the differences between commercial landings and surveys estimations could be explained by the higher interannual variability occurring in the survey length distributions.

In the only other work of LFDA of *S. colias* (Vasconcelos, 2006) based on ELEFAN method, the estimated growth rate was slower than the ones estimated here (PROJMAT and SLCA). As aforementioned for the comparison of the Bhattacharya results between the present study and the one of Lorenzo (1992), geographical and temporal differences, as well as the differences in the time series, number of samples and method used may explain the variability observed in the two studies.

The two different growth patterns here obtained are within the total range of *ϕ´* obtained in previous age and growth works of *S. colias* in the Northeast Atlantic (*ϕ´*: 2.55-2.86) summarized in Table 3. The *ϕ´* values of most of those previous references varied between 2.70 and 2.86, highlighting the slow growth pattern estimated by Martins (1996) in the Portuguese coast (*ϕ´*: 2.55).

Differences between the growth patterns obtained by length frequency analyses and direct age estimation have also been found in other species, such as the Baltic cod (*Gadus morhua*, Linnaeus 1758) (ICES, 2004). Those results confirmed differences in age estimation between countries, and interannual variations in the reader's interpretation of age compositions. In growth studies should be considered as well that the variability of growth patterns found in an area may be influenced by different factors, like the origin of the samples or those related to age interpretation (Carbonara *et al.*, 2019). This poses a serious problem to stock assessment, because even small errors in age determination may result in over- or underestimation that influences the values of fishing mortality and spawning-stock biomass (Reeves, 2003).

The use of methods that analyse the precision and accuracy of the age determination is essential to provide unbiased information for the stock assessment process (Campana, 2001). The combined use of several corroboration methodologies is considered the best practice to clarify the periodicity of otolith growth and the correct age interpretation in small pelagic species (ICES, 2020c). Our results support the consistency of the age interpretation in otoliths of *S. colias* based, furthermore, on ageing standardized criteria. However, our length frequency analyses results do not support the pattern obtained by age estimation and only the first two ML may be corroborated by these methods.

If the faster growth rate hypothesis here obtained by Bhattacharya and SLCA is true, the age interpretation in otoliths could be biased due to e.g., the presence of checks misinterpreted as true annuli. However, this seems to be quite unlikely due to the evident and regular decreasing growth pattern of increment widths observed in *S. colias* otoliths. Moreover, the opposite (true annuli considered as checks) has been observed in the congener NE Atlantic mackerel (*S. scombrus*) during an international otolith exchange from mark-recaptured experiences (ICES, 2019). That led to an underestimation of older ages in *S. scombrus*, identifying as false rings some true annuli (as the mark-recapture experiments proved).

Conversely, if the slow growth hypothesis (DAE/BC) is considered as valid, the possible bias in the growth rate obtained by Bhattacharya and SLCA, with fewer ML values than in DAE/BC, could be related with the length distributions analysed. Despite analysing a 7-year series (2011-2017) may provide clear results from the LFDA, the presence of low-abundant cohorts (low recruitment years) and/or the migratory behaviour of Atlantic chub mackerel (Castro and Santana, 2000) could mask some modal lengths within the full-length distribution (Sparre and Venema, 1998). Moreover, the length range analysed in the present study (~20-40 cm) may not be wide enough, and together with the low presence of large specimens may affect the results of the length frequency analyses, as observed in some tuna species (Murua *et al.*, 2017). Furthermore, the application of length frequency analyses is difficult when increasing age, as the length distribution of older cohorts overlap. In addition, fishing and natural mortality can reduce the absolute size of a particular year class hindering the modes identification in length frequencies in older age classes (Casselman, 1987; Laslett *et al.*, 2004).

In 2017, an extraordinary increase of the abundance of younger specimens (cohort of 2016) was observed in Atlantic Iberian waters and in the NW African coast (ICES, 2020a). A preliminary analysis of the tracking of the abundances in the length distributions of this 2016-cohort in 2018 and 2019 surveys (Landa and Navarro, pers. comm.) seems to confirm the two first modal lengths (~22, ~27 cm) here estimated by DAE/BC, Bhattacharya and PROJMAT analyses. The tracking of that cohort through 2020 and later will help to corroborate the growth pattern in the following older age groups.

Other authors encountered difficulties when trying to estimate growth curves based on length frequencies of migratory pelagic species, like the Indian scad (*Decapterus russelli*, Rüppell 1830) (Sousa, 1988; Sparre and Venema, 1998). Sousa (1998) observed that some modal lengths were missing in the length distribution analysed because the cohort was not present in the sampled area during a determined time period by migration causes. The age -length succession in the migratory routes of some pelagic species, like the congener *S. scombrus* in NE Atlantic, can lead to seasonal differences in the growth parameters (Dawson, 1986). This growth differences in *S. scombrus* have been linked to gradual spatial and temporal changes in lengths at age along the annual migration (Dawson, 1986; Eltink, 1987; Villamor *et al.*, 2004), due to large fish migrate earlier in time (Dawson, 1986) and longer distances than smaller ones (Skagen, 1989). When samples of *S. scombrus* were taken successively in one area along the migration path (Kästner, 1977), or on several positions at one time (Corten and Van de Kamp, 1978) it was possible to fit different growth curves to each sample (Dawson, 1986). Consequently, Atlantic chub mackerel migration behaviour should be studied for a correct interpretation of the growth pattern.

Taking into account all the aforementioned, we recommend the use of the growth parameters from DAE (L_∞*: 45.34, k: 0.28,* t_0*: -1.18*) for the upcoming stock assessment process, at least until a definitive direct validation of age estimation is achieved. However, given the changing environmental conditions and the migratory behaviour of the species, keeping the monitoring system updating the time series is crucial, and a greater certainty on the modal lengths will be reached by LFAs. In addition, further works focused on the probable different bathymetrical distribution and migration behaviour of the chub mackerel by sized would put light on the growth pattern of the oldest age groups. Finally, addressing the growth of *S. colias* using holistic approaches in other regions, would help to describe the population structure of the species in the East Atlantic, including its possible latitudinal variation.

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Table 1. Mean length at age (cm), obtained from direct age estimation (DAE), back-calculation (BC), Bhattacharya, PROJMAT and SLCA methods of surveys (surv) and commercial landings (land) of *S. colias* in N and NW Iberian waters. Sem1: first semester; Sem2: second semester.

	DAE			BC	Bhattacharya		PROJMAT	SLCA
Age group (years)	surv	land		surv + land	surv	land	surv	land
	Sem1	Sem1	Sem2	Sem1	Sem1	Sem1	Sem1	Sem1
1	21.3	23.8	26.7	21.9	21.8	21.5	21.8	23.3
2	26.4	27.7	29.3	28.3	27.4	28.4	27.8	30.0
3	31.8	31.0	33.1	32.1	33.6	34.9	32.4	35.0
4	34.4	35.1	36.5	35.7	39.0	38.2	36.0	38.7
5	36.8	37.6	38.3	37.5	42.5	41.5	38.8	41.5
6	39.3	38.4	40.8	38.5		44.5	41.0	43.5
7	39.9	39.7	39.9	40.3		46.5	42.7	45.0
8	40.5	41.3	41.1	43.7			44.1	46.1

Table 2. Measurements of annuli of *S. colias* otoliths from N and NW Iberian waters: Mean, Standard Deviation (SD), Minimum (Min), Maximum (Max) and Number of measurements (N).

Annulus	Radius (mm)				
	Mean	SD	Min	Max	N
1	1.5	0.09	1.2	1.7	409
2	1.8	0.09	1.5	2.1	389
3	2.0	0.08	1.8	2.2	350
4	2.1	0.10	1.9	2.5	203
5	2.2	0.10	2.0	2.6	89
6	2.3	0.10	2.2	2.5	21
7	2.5	0.13	2.3	2.7	9
8	2.6	0.10	2.5	2.7	4

Table 4. Results of the comparison among the growth parameters obtained by each method performed in this study, by the Kimura's Likelihood ratio and Chen tests. No significant: n.s. (p>0.05); significant: * (p<0.05); ** (p<0.01); *** (p<0.001). M: Male; F: Female; I: Indeterminate; DAE: Direct Age Estimation; BC: Back-calculation; Bhatt: Bhattacharya; surv: surveys; land: commercial landings. Comparison between methods by the Kimura's Likelihood test was limited to overlapping age range in each test.

Method 1	Method 2	Kimura's Likelihood ratio test				Chen test
		Age range	L_∞ *p*	*k p*	t_0 *p*	*p*
DAE_M+I	DAE_F+I	0-7	n.s.	n.s.	n.s.	n.s.
DAE	BC	1-7	n.s.	n.s.	**	n.s.
DAE/BC	Bhatt_surv	1-5	***	***	***	***
DAE/BC	Bhatt_land	1-5	***	n.s.	n.s.	***
Bhatt_surv	Bhatt_land	1-5	**	**	*	n.s.
DAE/BC	PROJMAT_surv	1-5	***	***	***	-
DAE/BC	SLCA_land	1-5	***	*	***	-
PROJMAT_surv	SLCA_land	1-5	***	***	***	-
Bhatt_surv	PROJMAT_surv	1-5	***	**	**	-
Bhatt_land	SLCA_land	1-5	n.s.	n.s.	n.s.	-

Table 3. Growth parameters (*L∞, k and t0*) and growth performance index (ϕ') obtained by different methods in the present and previous studies of *S. colias* in the NE Atlantic. DAE: Direct Age Estimation; BC: Back-calculation; Bhatt: Bhattacharya; surv: surveys; land: commercial landings.

Author	**Present study**							Martins et al., 1983	Martins, 1996	Velasco et al., 2011	Carvalho et al., 2002	Vasconcelos, 2006		Lorenzo, 1992			Jurado-Ruzafa et al., 2017
Area	**N & NW Iberian Peninsula**							Portuguese coast	Portuguese coast	Gulf of Cadiz	The Azores	Madeira		The Canary Islands			Mauritanian waters
Years	**2011-2012**	**2011-2017**						1981-1982	1986-1995	Oct. 2003-Sept. 2004	1996-2002	2002-2003		1988-1990			2005-2011
Method	**BC**	**DAE**	**DAE-BC**	**Bhatt**		**PROJMAT**	**SLCA**	BC	DAE	DAE-BC	DAE	DAE	ELEFAN	DAE	BC	Bhatt	BC
	surv + land	**surv + land**	**surv + land**	**surv**	**land**	**surv**	**land**										
L_{∞} (cm)	**42.63**	**45.34**	**43.70**	**55.00**	**53.26**	**48.74**	**49.30**	53.83	58.52	43.00	57.52	50.08	38.00	50.69	49.22	49.22	48.40
K	**0.33**	**0.28**	**0.32**	**0.24**	**0.26**	**0.25**	**0.30**	0.17	0.10	0.27	0.20	0.25	0.50	0.21	0.21	0.22	0.25
t_0	**-0.96**	**-1.18**	**-0.83**	**-0.77**	**-0.78**	**-0.87**	**-0.63**	-2.03	-3.68	-1.10	-1.09	-1.34		-1.45	-1.40		-1.51
ϕ'	**2.78**	**2.76**	**2.79**	**2.86**	**2.86**	**2.77**	**2.86**	2.70	2.55	2.70	2.82	2.80	2.86	2.73	2.71	2.73	2.76
n	**409**	**6867**	**7276**					533	883	121	349	2115		878	538		163
Length range (cm)	**16-48**	**14-50**		**14-46**	**18-49**	**14-46**	**18-49**		16-54	16-43	9-56	13-41	13-41	4-42		4-48	12-49

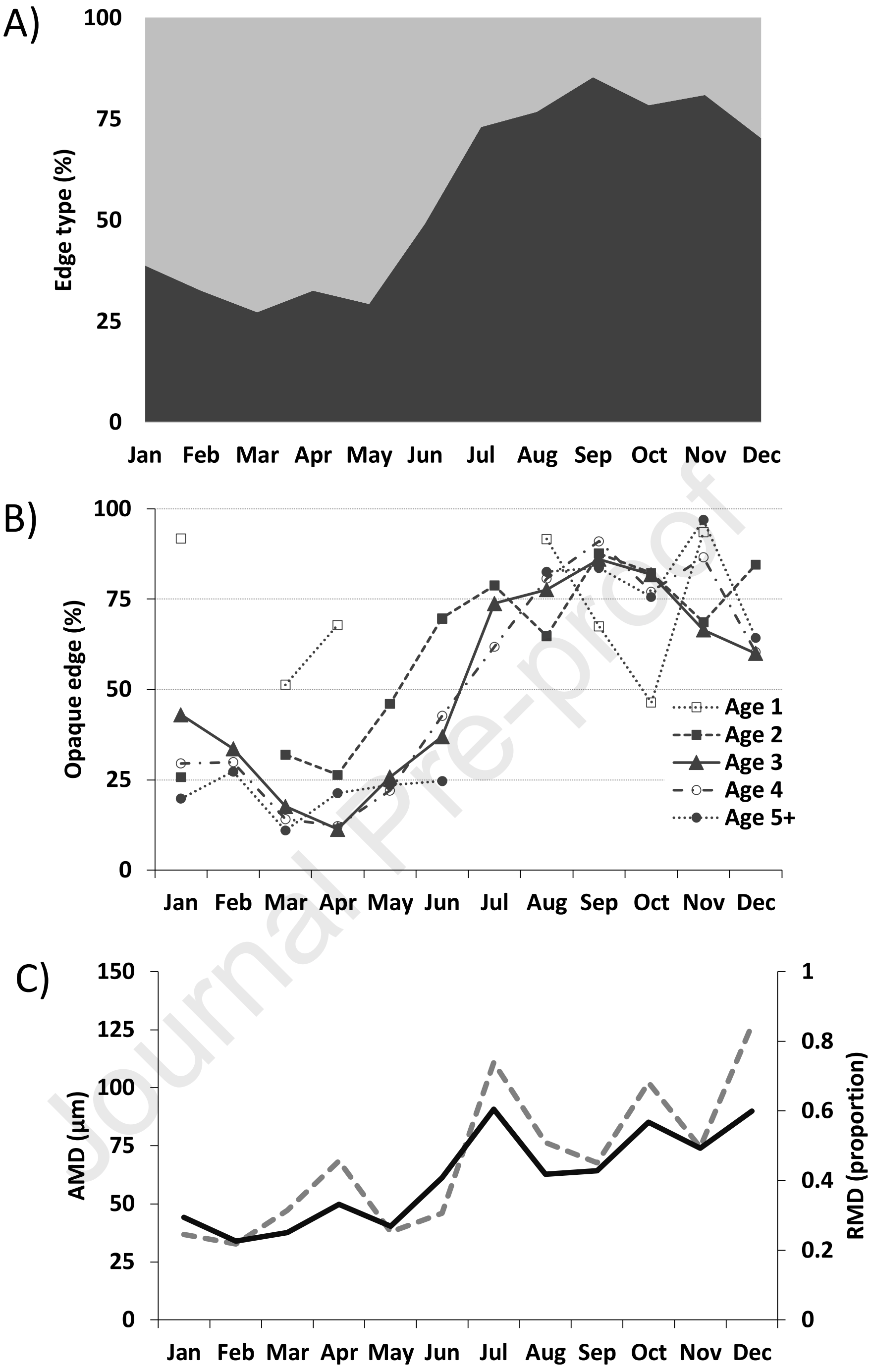

Figure 2. Results of otolith marginal analyses of *S. colias:* (A) monthly proportion of opaque (dark) and hyaline (light) edge; (B) monthly proportion of opaque edge by age and (C) monthly mean values of relative marginal distance, RMD (continuous line) and absolute marginal distance, AMD (discontinuous line) in otoliths from N and NW Iberian waters.

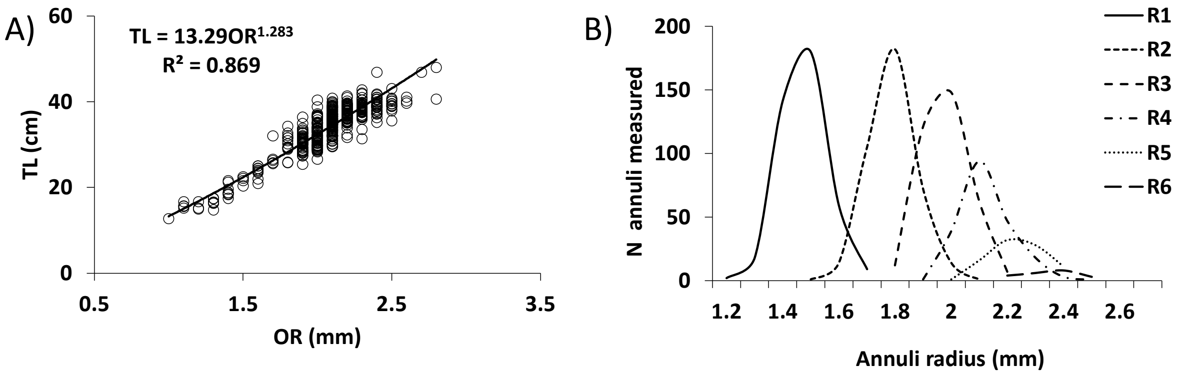

Figure 3. A) Relationship between fish (total) length (TL) and otolith radius (OR); and B) Frequency distribution of annuli radius (R_i) of otoliths of *S. colias* in N and NW Iberian waters.

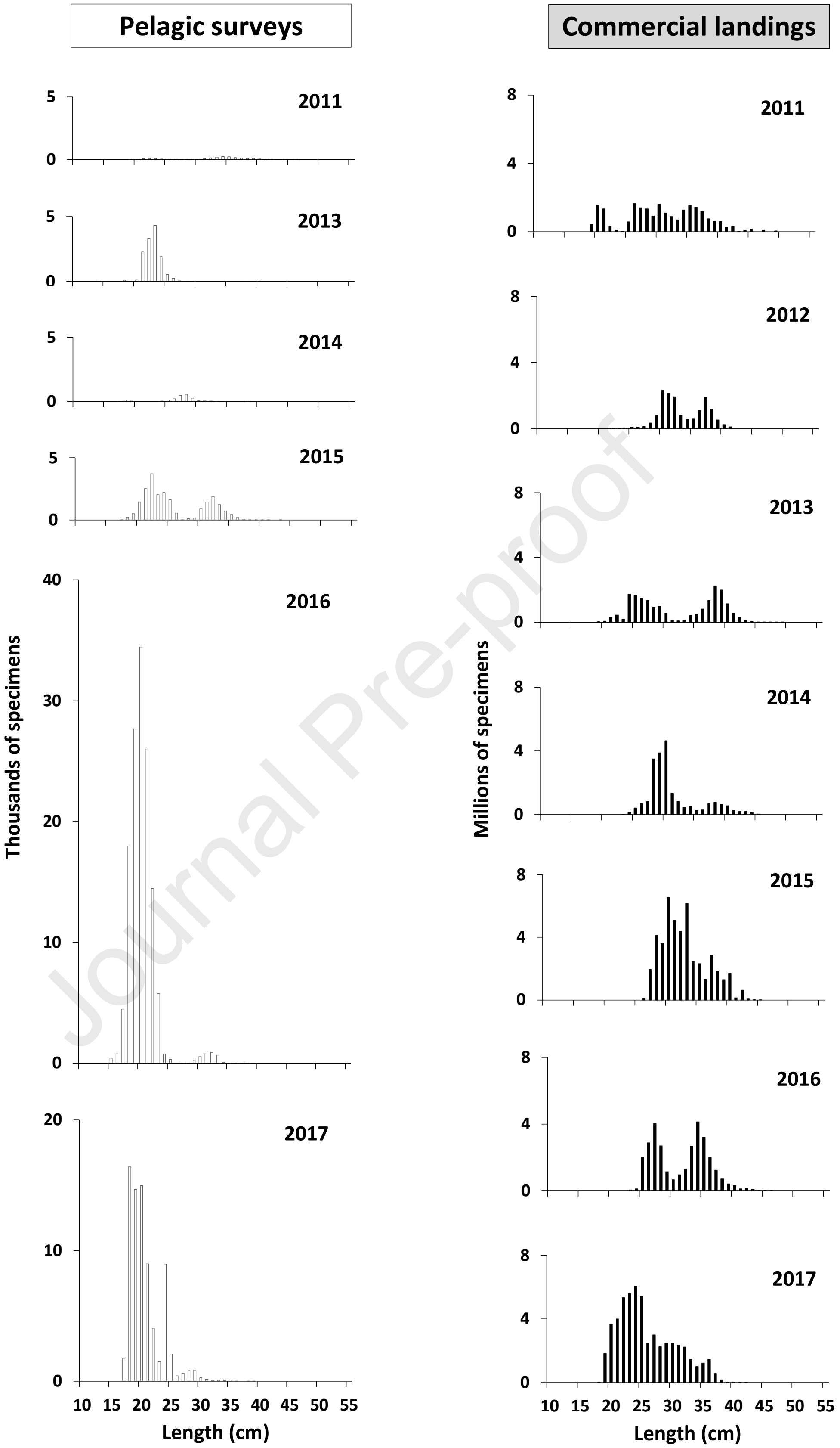

Figure 4. Length composition of *S. colias* catches by year of surveys (left), in thousands of specimens, and commercial landings (right), in millions of specimens, in N and NW Iberian waters.

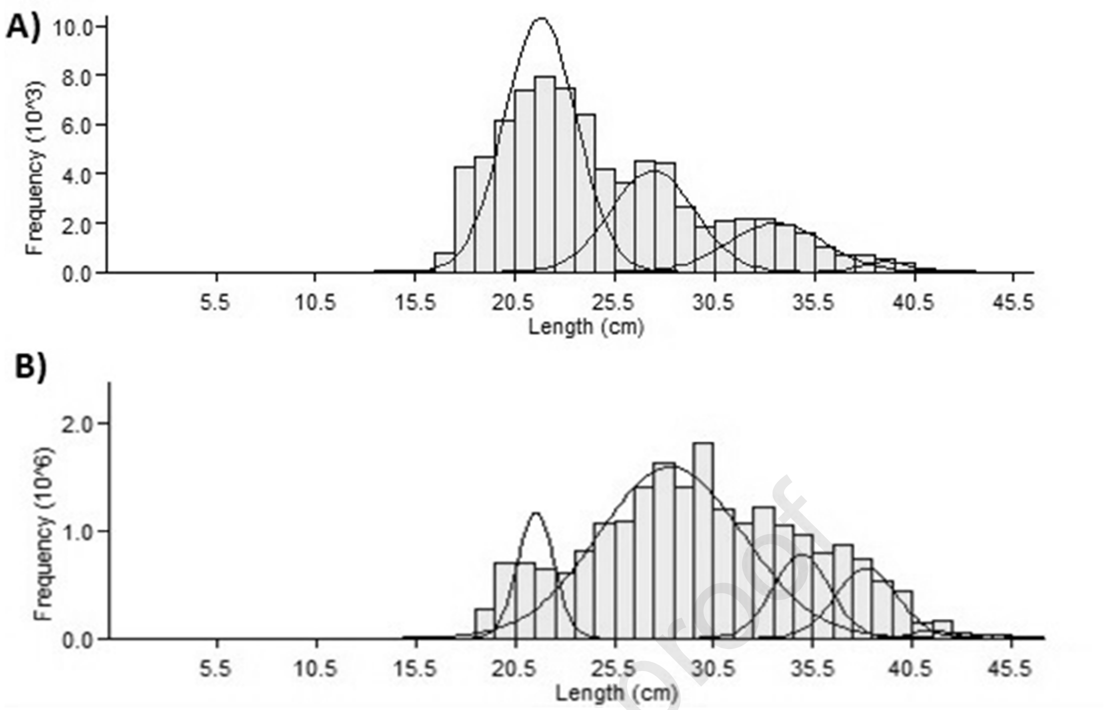

Figure 5. Histograms obtained by Bhattacharya method (FISAT II) from A) relative values of length distributions of *S. colias* from the six years analysed together (2011, 2013-2017) of scientific surveys PELACUS; and B) absolute values of length distributions of the first semester from the seven years analysed together (2011-2017) of commercial landings in N and NW Iberian waters. Rectangles: length classes frequencies; black lines: age groups identified.

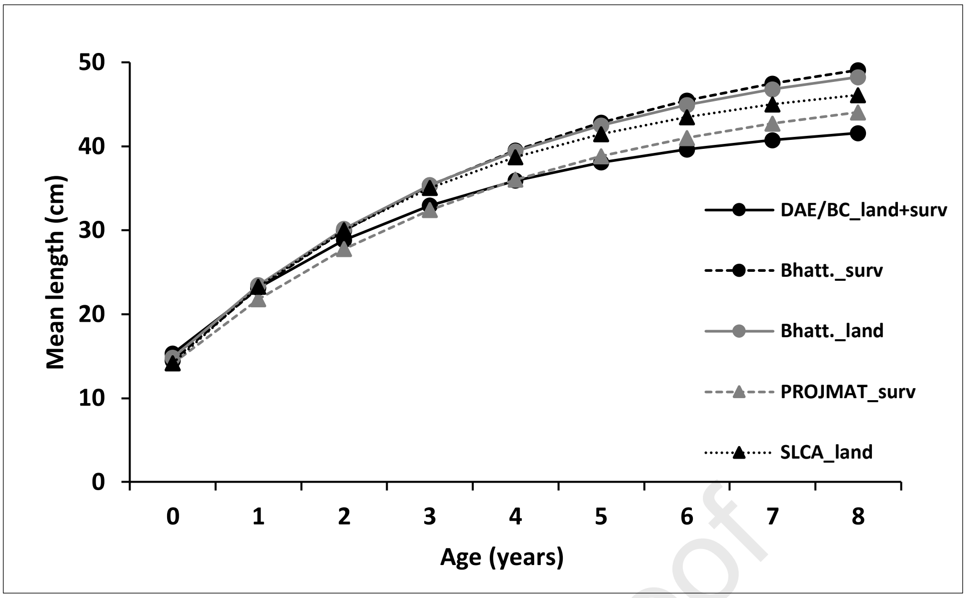

Figure 6. Von Bertalanffy growth curves of *S. colias* in N and NW Iberian waters obtained by different methods in this study: Direct Age Estimation/Back-calculation (DAE/BC), Bhattacharya (Bhatt.), PROJMAT and SLCA, from commercial landings (land) and surveys (surv).

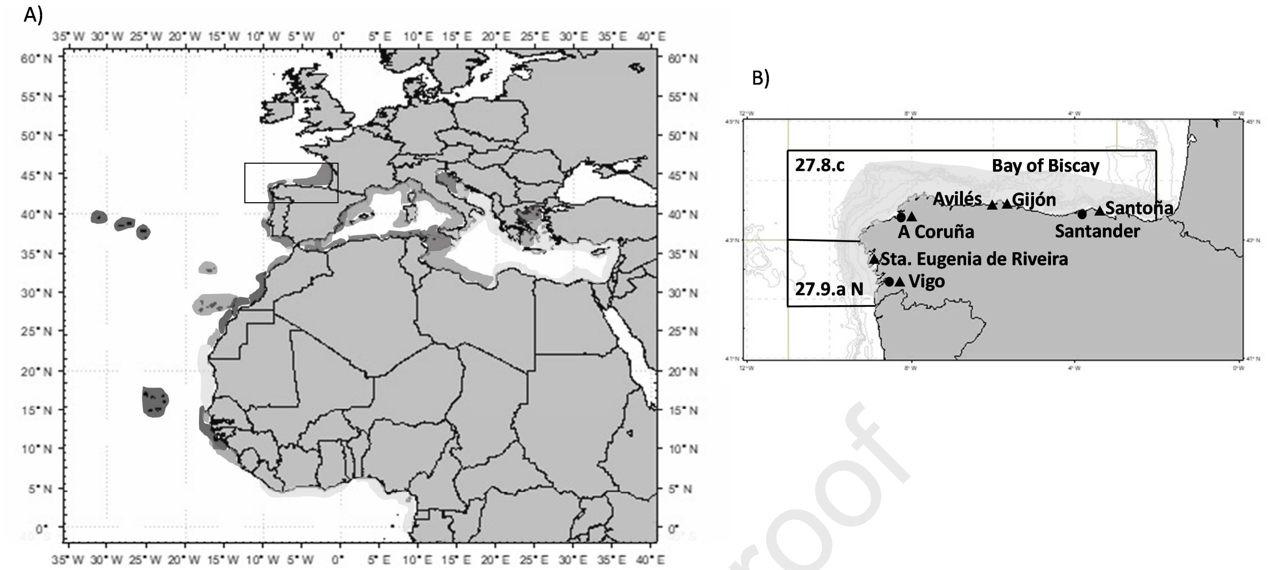

Figure 1. A) Distribution of *S. colias* in the East Atlantic and Mediterranean Sea, showing a gray gradient of abundance (more abundant in dark; less, in light) (source: www.fishbase.org); B) Area of study (gray shading) corresponding to the area covered by the pelagic surveys PELACUS and where the commercial fleet operates, with the ICES fisheries divisions (27.8.c and 27.9.a N), and highlighting the fishing harbours of origin of the specimens sampled (points) and length distributions of commercial landings (triangles).

Highlights

Growth study of Atlantic chub mackerel in north Iberian waters using different approaches.

Otolith marginal analysis showed annual periodicity in the annuli deposition.

Back-calculation and annuli radii distribution supported the age estimation criteria used.

Length frequency analyses resulted in higher growth rates than otolith age estimation.

Growth parameters estimations available for upcoming stock assessment.

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: