

## Spatial variability of life-history parameters of the Atlantic chub mackerel (*Scomber colias*), an expanding species in the northeast Atlantic

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**Summary:** Atlantic chub mackerel is a pelagic species present in the Atlantic Ocean that in recent decades has expanded northwards in the eastern Atlantic. Fish samples were collected in scientific surveys and commercial catches between 2011 and 2019. We analysed the geographical variation of the biological parameters (age, length, weight and condition), as well as the length-weight relationship, maturity-at-length and spawning season onset and duration in five geographical areas (from south to north): the Canary Islands, Gulf of Cadiz, western Portuguese coast, northwestern Spanish coast and Cantabrian Sea. The influence of sea surface temperature (SST) on fish length was modelled as a potential driver of geographical variability. All biological parameters increased progressively northwards, while the spawning season was delayed and prolonged with increasing latitude, from January in the Canary Islands to May-August in the Cantabrian Sea, when SST was between 15°C and 19°C. SST had a positive effect on length in three study areas and a negative one in two of them, suggesting that each group is at a different position within their thermal tolerance range. Deviance from the geographical pattern of some biological parameters in the Gulf of Cadiz suggests that it could be a hinge or mixing zone between Atlantic African, Mediterranean and Atlantic Iberian population components.

**Keywords:** growth; maturity; condition; reproductive phenology; climate change.

**Variabilidad espacial de los parámetros de historia vital del estornino (*Scomber colias*), una especie en expansión en el Atlántico noreste**

**Resumen:** El estornino es una especie pelágica presente en el océano Atlántico que en las últimas décadas se ha expandido hacia el norte en el Atlántico Oriental. Se recogieron muestras de peces procedentes de campañas científicas y capturas comerciales entre 2011 y 2019. Se analizó la variación geográfica de los parámetros biológicos (edad, longitud, peso y condición), así como la relación longitud-peso, la talla de madurez y el inicio y la duración de la temporada de desove en cinco áreas geográficas (de sur a norte): las islas Canarias, el Golfo de Cádiz, la costa occidental portuguesa, la costa noroccidental española y el mar Cantábrico. Se modeló la influencia de la SST en la talla de los peces como posible causa de la variabilidad geográfica. Todos los parámetros biológicos aumentaron progresivamente hacia el norte, mientras que la temporada de desove se retrasó y prolongó con el aumento de la latitud, desde enero en las islas Canarias hasta mayo-agosto en el mar Cantábrico, cuando la SST estaba entre 15°C y 19°C. La SST tuvo un efecto positivo sobre la talla en tres áreas de estudio y negativo en dos de ellas, lo que sugiere que cada grupo se encuentra en una posición diferente dentro de su rango de tolerancia térmica. La desviación del patrón geográfico de algunos parámetros biológicos en el Golfo de Cádiz, sugiere que podría ser una zona bisagra o de mezcla entre componentes poblacionales atlánticos africanos, mediterráneos e ibéricos.

**Palabras clave:** crecimiento; madurez; condición; fenología reproductiva; cambio climático.

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## INTRODUCTION

Distribution shifts of marine fishes towards polar areas due to global warming have been reported or predicted in the northeast (Perry et al. 2005, Rjinsdorp et al. 2009) and northwest Atlantic (Murawski 1993), in Australian waters (Cheung et al. 2012 and references therein) and in the Pacific Ocean (Alabia et al. 2018, Cheung et al. 2015). Moreover, changes in marine biodiversity have been foreseen as a result of climate change (Cheung et al. 2009). Variations in temperature, pH and oxygen dissolved in the ocean affect the physiology and dynamics of all marine organisms (Pörtner et al. 2005, Rjinsdorp et al. 2009, Ottersen et al. 2010) and, together with distributional shifts, alter trophic structures, the composition of marine communities and thus ecosystem balances (Vergés et al. 2014). While any alteration in marine ecosystems will have a major impact on the services they provide, it is especially evident that changes affecting species exploited by fisheries will have a direct impact on the economy and human health because of the importance of fisheries in the economic development of coastal communities and in the provision of healthy food (Hollowed et al. 2013).

Atlantic chub mackerel (*Scomber colias*, Gmelin, 1789) is a medium-sized migratory coastal pelagic fish distributed in warm and temperate waters on both sides of the Atlantic Ocean (Castro and Santana 2000), including the Macaronesian archipelagos and reaching the Mediterranean and southern Black seas (Collette and Nauen 1983, Whitehead et al. 1984, Collette et al. 2011). Although for many years the Atlantic chub mackerel was considered the same species as the Indo-Pacific chub mackerel (*Scomber japonicus*, Houttuyn 1789), morphologic and genetic studies carried out in the first decade of the 20<sup>th</sup> century demonstrated that they are two different species (Infante et al. 2007, Catanese et al. 2010, Cheng et al. 2011).

In the Canary Islands (FAO area 34.1.2), small pelagic fish are targeted by the artisanal purse-seine fleet, and the Atlantic chub mackerel is the species most commonly caught all year around (FAO 2020a). In the Gulf of Cadiz (FAO area 27.9.a.s), Atlantic chub mackerel is jointly with anchovy and sardine one of three target species fished by the purse seine fleet operating in this area. Additionally, a specifically dedicated seasonal purse-seine fishery targets the species during the second and third quarters of the year, supplying the regional canning industry and providing food for caged bluefin tuna. On the western Portuguese coast (FAO area 27.9.a.c), the northwestern Spanish coast (FAO area 27.9.a.n) and the Cantabrian Sea (FAO area

27.8.c), Atlantic chub mackerel has gained economic importance in recent decades, becoming an important resource for the fishing fleet, especially purse seiners, which are responsible for the bulk of the total landings of this species (ICES 2020, 2021a). In these last three areas, increasing landings of Atlantic chub mackerel have coincided with the decrease in European sardine (*Sardina pilchardus*) landings and restrictions on Atlantic mackerel (*Scomber scombrus*) catches.

Despite its wide distribution, 90% of the Atlantic chub mackerel catches in the northeast Atlantic proceed from northwest African waters (FAO 2020b). More northerly, in the Atlantic Iberian waters, landings have increased significantly in the most recent years (ICES 2020). This increase has been associated with a higher availability of the fish, as it has expanded its distribution northwards (Martins et al. 2013, Punzón et al. 2016, ICES 2020). This phenomenon has been suggested to be probably driven by the increase in the sea temperature (Costoya et al. 2015, Jurado-Ruzafa et al. 2019) as a result of climate change (Tasker 2008, Reid and Valdés 2011). This distribution expansion makes Atlantic chub mackerel an interesting case study for the analysis of the impact of climate change on exploited species. In fact, Atlantic chub mackerel could compete in the new habitats with other important commercial pelagic species such as the congener Atlantic mackerel (*S. scombrus*), horse mackerel (*Trachurus trachurus*), sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) (Bachiller and Irigoien 2015, Garrido et al. 2015a, b, Veiga-Malta et al. 2019), especially in areas where its presence has increased recently. This competition could affect the fishing yields as well as the pelagic ecosystem balance.

Genetic, morphologic and parasite studies have shown significant differences between Atlantic chub mackerel from the western Atlantic and the eastern Atlantic (Scoles et al. 1998, Roldán et al. 2000, Costa et al. 2011), supporting the existence of two different populations at either side of the Atlantic Ocean. However, whether this species constitute a single stock or not in the eastern Atlantic is still unknown, as the studies performed in this area provide conflicting results (Scoles et al. 1998, Mele et al. 2014, Muniz et al. 2020). The information available on the northeast Atlantic suggests that in both African and European waters the species migrates from the wintering areas (mainly located in Mauritanian waters, southern Portugal and the inner part of the Bay of Biscay) towards northern waters in summertime and, in the case of the Bay of Biscay, towards the western Iberian Peninsula (ICES 2021a). However, knowledge regarding population dynamics,

life-history traits, migration patterns and connectivity of Atlantic chub mackerel in the northeast Atlantic and environmental drivers of their variation is scarce and fragmented. Therefore, large-scale studies such as the present one are essential to understand not only the population structure of Atlantic chub mackerel in the eastern Atlantic but also the influence of climate change on the dynamics of this expanding commercial species and, subsequently, on the ecosystems it colonizes and the fisheries targeting it.

The aim of this study was to analyse the spatial variation of the biological parameters of Atlantic chub mackerel between the traditional areas of distribution (Canary Islands and Gulf of Cadiz) and those of recent expansion further north on the Atlantic coast of the Iberian Peninsula (W Portuguese Coast, NW Spanish waters and Cantabrian Sea), as well as the role of sea surface temperature (SST) as a climate change-linked driver of life-history traits. The results of the present work will be useful for the future assessment of the species in European Atlantic waters, which has been promoted by ICES (2020).

## MATERIAL AND METHODS

The study area covered most of the distributional range of Atlantic chub mackerel in the northeast Atlantic (Fig.1), from the Canary Islands (FAO area 34.1.2) to the Cantabrian Sea (FAO area 27.8.c). Table 1 contains information about the characteristics of the sampling procedures in each study area.

The Spanish Institute of Oceanography (IEO, CSIC, Spain) and the Instituto Português do Mar e da Atmosfera (IPMA, Portugal) collect biological data of Atlantic chub mackerel (length, weight and maturity) in the Atlantic Iberian waters from regular (monthly or quarterly) sampling of the commercial fleet (including landings, observers on board and biological sampling in the laboratory), as well as from the acoustic and demersal research surveys carried out within the EU Data Collection Framework. In the Canary Islands, the IEO monitors fleet activity and collects biological information on Atlantic chub mackerel monthly from

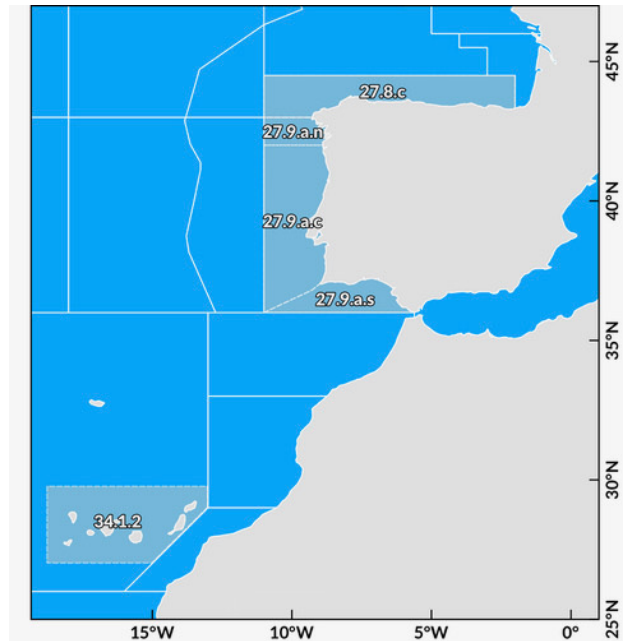


Fig. 1. – Map of the study area including the FAO subdivisions considered in the present analyses. 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea

commercial landings exclusively. For the present study, biological information on Atlantic chub mackerel collected between 2011 and 2019 from the monitoring programmes mentioned above was analysed.

For all collected specimens, total length (TL), total weight (TW) and sex were recorded. TL was recorded to the nearest 0.1 cm and TW to the nearest 0.1 g in the Canary Islands, 0.01 g for laboratory sampling and 0.5 g for scientific surveys in the remaining areas. Maturity stages were determined through macroscopic examination of the gonads in all areas. In the Canary Islands, maturity classification was based on the Holden and Raitt (1974) maturity key (I, immature; II, maturing virgin or resting; III, maturing; IV, spawning; V, spent), while in the remaining ar-

Table 1. – Description of the dataset used in the present study, including study area. Subdivision, FAO code of the study areas; Period, range of sampled years; N, number of sampled specimens (number of sampled females); Length range, total length range of sampled specimens (cm); Age range, age range of sampled specimens (years); Origin, C-commercial landings; S-scientific surveys; n.a., not available.

Study area	Subdivision	Period	N	Length range	Age range	Origin
Cantabrian Sea	27.8.c.	2011-2019	10173 (4888)	11-51	0-14	C-S
NW Spanish Coast	27.9.a.n	2011-2019	3979 (2018)	12-42	0-6	C-S
W Portuguese waters	27.9.a.c	2011-2019	15075 (7458)	13-54	0-10	C-S
Gulf of Cadiz	27.9.a.s	2011-2019	12318 (5263)	11-40	0-7	C-S
Canary Islands	34.1.2	2013-2019	6778 (3426)	13-43	n.a.	C

as it was determined according to the Walsh et al. (1990) maturity key (I, immature; II, maturing; III, mature; IV, spawning; V, partial post-spawning; VI, final post-spawning).

More detailed information about the sampling schedules is provided in the supplementary material, including quarterly length distribution of sampled individuals in each study area (Table S1, Fig. S1).

In all study areas otoliths were collected from both males and females. Whole otoliths were mounted on black plastic slides, concave side up, covered with transparent resin and observed with a binocular microscope under reflected light for age estimation. Age readings from otoliths sampled from fish caught in the Canary Islands did not provide consistent results, so Canary data were not considered in the analyses involving age.

Since no sexual dimorphism has been found in this species (Tchetchach et al. 2019), all analyses were performed for both sexes combined, except for the study of the onset and duration of the spawning season (see details below).

### Length-weight relationship

The length-weight (TL-TW) model used was

$$TW_i = aTL_i^b, i = 1, \dots, N,$$

where  $TW_i$  and  $TL_i$  are the total weight and length of the individual  $i$ , respectively,  $N$  the total number of individuals, and  $a$  and  $b$  the parameters to be estimated. The model was linearized taking logarithms (with base 10) on both sides,  $\log_{10}(TW_i) = \log_{10}(a) + b\log_{10}(TL_i)$ , for fitting in R software (R Core Team 2021) using the common function *lm* for linear models.

In addition to TL, other covariables can be included in the model predictor. In particular, the TL-TW parameters  $a$  and  $b$  can be specific for each of the  $K$  categories of a factor (Note this  $K$  has not any relationship with Fulton's condition factor). Then the model including the interaction between length and the factor is formulated as follows.

$$\begin{aligned} \log_{10}(TW_i) = & \log_{10}(a_1)I_1 + \log_{10}(a_2)I_2 + \dots \\ & + \log_{10}(a_K)I_K + b_1\log_{10}(TL_i)I_1 \\ & + b_2\log_{10}(TL_i)I_2 + \dots + b_K\log_{10}(TL_i)I_K \end{aligned}$$

where  $a_j$  and  $b_j$  are the  $a$  and  $b$  estimates, respectively, for category  $j$  ( $j=1, \dots, K$ ) of the factor covariable, and the variables  $I_j, j=1, \dots, K$  are binary dummy variables which take the value of 1 if individual  $i$  corresponds to category  $j$ . Then, the model leads to  $a$  and  $b$  specific estimates for each category of the factor covariable. In the current analysis, the model has been implemented for estimating a specific TL-TW relationship in each study area.

### Condition

Condition was approached using Fulton's  $K$  condition index (Fulton 1902) to facilitate comparison with previous studies that used this proxy of condition.

### Spawning season

The spawning period was determined for each area based on maturity stage data of females, as males sampled for the present study were in the spawning capable stage almost all year around. Furthermore, the existence of spawning capable females is the limiting factor for effective breeding. For the analysis, the proportion of spawning capable over the total number of mature females was the selected index. In the case of the Canary Islands, only females in stage IV (Holden and Raitt's scale) were considered as spawning capable females, whereas in the rest of areas, they corresponded to females in stages IV and V (Walsh's maturity scale). Spawning season was defined as the period of consecutive months when the proportion of spawning capable females was higher than 25%.

### Length at maturity

The percentage of mature females at length class was fitted to the logistic equation:

$$\hat{P} = \frac{1}{1 + e^{-(a+bTL)}}$$

where  $\hat{P}$  is the predicted mature proportion,  $a$  and  $b$  the estimated coefficients of the logistic equation and TL the total length.

The length at which 50% of specimens are mature (length at first maturity,  $L_{50}$ ) was estimated as the minus ratio of the coefficients ( $-a/b$ ). All maturity ogive parameters were estimated using the *sizeMat* (Torrejon-Magallanes 2020) package of the R software (R Core Team, 2021), applying a frequentist generalized linear model with 500 iterations in the bootstrap resampling.

### Modelling

#### Geographical variability

Comparisons of length, age, weight and condition between study areas were delivered by the Kruskal-Wallis rank sum test (Kruskal and Wallis 1952; *kruskal.test* function of the R software), because variances were not homogeneous between areas.

For post hoc comparisons between group levels, the Wilcoxon pairwise Rank sum Test was used (*pairwise.wilcox.test* function of the R software) with the Benjamini and Hochberg (1995) method for multiple testing corrections. These functions are from the *stats* R package (R Core Team, 2021).

#### Temperature effects

To explain the potential geographical differences in biological parameters between study areas, SST was chosen as an explanatory environmental variable because it is directly linked to global warming. SST data for the study areas were downloaded from the *SST Aqua MODIS, NPP, 4km, Daytime (11 microns)*,

2003-2019 (Monthly Composite) dataset at NOAA West Coast Regional Node ERDDAP data server (<https://coastwatch.pfeg.noaa.gov/erddap>). After data download, a 0.25x0.25-degree grid was used to average the SST, and subsequently the monthly averaged SST was assigned to the centroid of each grid cell. The R script for data download and averaging replication is available at <https://git.csic.es/jtornero/erddap-sst-download>.

A correlation analysis showed that TL and TW were highly correlated and that the condition factor, K, was also correlated with both length and weight (Fig. S2). We used generalized linear models (GLMs; Wood 2017) to model the effect of SST and geographical distribution (study area) on TL exclusively, assuming that their variability would be reflected directly in TW and partially in K, because these variables were correlated.

GLMs are an extension of linear models for which the distribution of the response variable can be other than Gaussian. For this reason, a link function,  $g$ , is required between the linear predictor and the conditional expectation of the response variable  $Y$ ,  $\mu(X)=E(Y|X)$ , and the GLM is formulated as

$$g(\mu(X)) = \beta_0 + \beta_1 X_1 + \dots + \beta_p X_p$$

where  $X=(X_1, \dots, X_p)$  are the covariables,  $\mu(X)=E(Y|X)$  is the conditional expectation of the response variable  $Y$ ,  $g$  is a link function between  $\mu(X)$  and the linear predictor, and  $(\beta_0, \beta_1, \dots, \beta_p)$  are the unknown model parameters.

A GLM assumes that the response variable follows a distribution belonging to the exponential distribution

family; in our analysis, it is assumed that our response variable (i.e. TL) follows a Gamma distribution with a natural logarithm link because it is a strictly positive continuous variable.

In GLM, the effects of categorical variables are considered fork-1 of the  $J$  factor levels, with the remaining one being considered the base level. Hence the estimated coefficient of each factor level will indicate the deviation from the value of the base level.

The presence of influence points, outliers that greatly affect the regression estimates, was checked using the *influence* function of the *mgcv* package (Wood 2011), which was also used to perform the GLMs.

All statistical analyses were performed with R v.4.0.5 (R Core Team 2021) and RStudio v.1.4.1717 (RStudio Team 2021). In all analyses, results were considered statistically significant when the p-value was  $<0.01$ . All figures were plotted using the *ggplot2* R package (v.3.3.5. Wickham 2016).

## RESULTS

The TL of specimens collected for this study ranged between 11 and 54 cm (between 6 and 1498 g TW), corresponding to estimated ages between 0 and 14 years (Table 1). The largest and oldest specimens were collected on the western Portuguese coast and the Cantabrian Sea.

Results of the Kruskal-Wallis test demonstrated that the medians of all biological parameters (age, TL, TW and Fulton's K) were significantly different between the study areas ( $p<0.01$ , Fig. 2). In fact, the Wilcoxon test revealed that all variables differed significantly be-

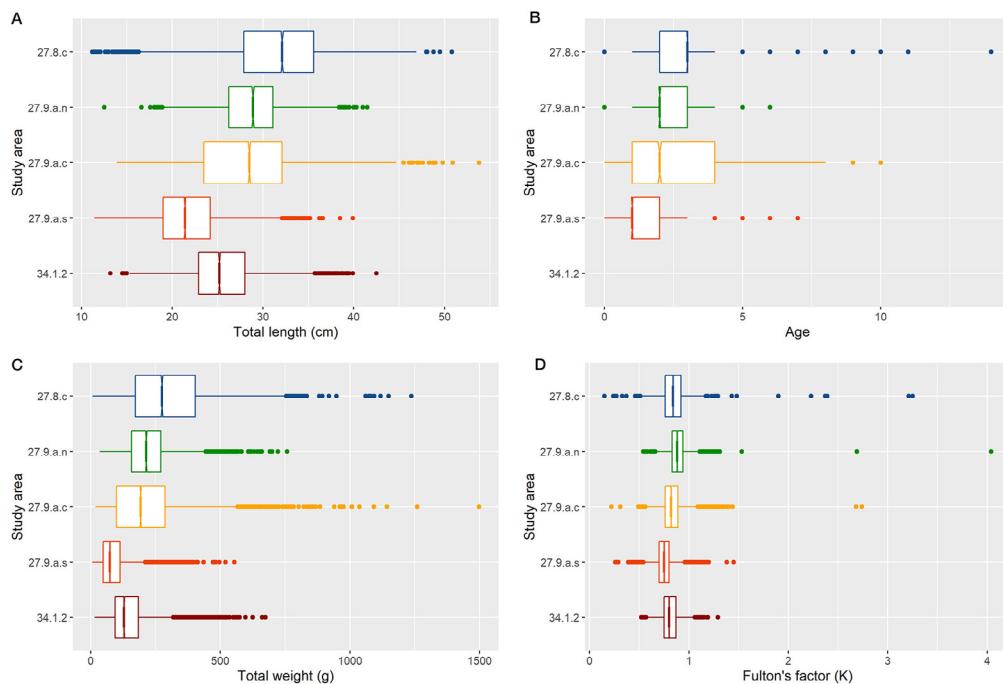


Fig. 2. – Boxplot of biological parameters by study area. A, total length; B, age (years); C, total weight and D, Fulton's condition factor (K). Geographical study areas from south to north are 34.1.2, Canary Islands (red); 27.9.a.s, Gulf of Cadiz (orange); 27.9.a.c, W Portuguese coast (yellow); 27.9.a.n, NW Spanish coast (green); and 27.8.c, Cantabrian Sea (blue). Vertical line within the boxes represents the median, boxes represent the inter-quartile range (IQR) or distance between the first (25%) and third (75%) quartiles, the notch represents the 95% confidence interval of the median, the whiskers represent  $\pm 1.5 * IQR$  and dots represent the outliers.



Table 2. – Descriptive statistics of variables analysed in each study area. N, number of specimens; sd, standard deviation; min, minimum; max, maximum; se, standard error. Study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, Portuguese W coast; 27.9.a.n, NW Spanish coast; 27.8.c, Cantabrian Sea. SST, sea surface temperature; totL, total length (cm); totW, total weight (g); K, Fulton's condition factor; gonW, gonad weight (g). N in SST refers to the number of values extracted from the NOAA database according to the procedure explained in the Material and methods section (one value per day and cell of the 0.25x0.25-degree grid).

Area:	27.8.c						
	N	mean	sd	median	min	max	se
SST	10055	15.85	3.02	14.4	10.88	21.95	0.03
totL	10173	31.31	5.99	32.1	11.2	50.8	0.06
totW	10163	295.46	166.07	275	8	1237	1.65
K	10163	0.84	0.12	0.84	0.15	3.25	0
gonW	2828	4.46	9.92	1.51	0.01	128.2	0.19
Age	8084	2.75	1.37	3	0	14	0.02
Area:	27.9.a.n						
	N	mean	sd	median	min	max	se
SST	3979	16.38	2.15	16.05	12.84	20.7	0.03
totL	3979	28.4	4	28.9	12.5	41.5	0.06
totW	3977	218.45	95.89	214.34	35.6	757.71	1.52
K	3977	0.89	0.11	0.88	0.54	4.04	0
gonW	1454	1.39	2.76	0.78	0.01	66.48	0.07
Age	2356	2.28	1.02	2	0	6	0.02
Area:	27.9.a.c						
	N	mean	sd	median	min	max	se
SST	14899	18.04	2.32	18.36	13.65	22.36	0.02
totL	15074	27.94	5.46	28.5	13.9	53.8	0.04
totW	15072	207.56	127.54	192.55	18.14	1497.92	1.04
K	15072	0.82	0.11	0.82	0.22	2.74	0
gonW	10662	2.49	5.01	1.02	0.01	124.45	0.05
Age	6072	2.71	1.76	2	0	10	0.02
Area:	27.9.a.s						
	N	mean	sd	median	min	max	se
SST	12318	21.05	1.7	21.74	16.08	22.84	0.02
totL	12318	21.75	3.87	21.4	11.4	39.9	0.03
totW	12318	88.22	57.12	74	6.5	554	0.51
K	12318	0.75	0.09	0.75	0.26	1.45	0
gonW	1418	1.46	2.77	1	0.04	32.9	0.07
Age	3008	1.51	0.96	1	0	7	0.02
Area:	34.1.2						
	N	mean	sd	median	min	max	se
SST	6721	22.1	1.81	22.1	18.73	25.66	0.02
totL	6778	25.65	3.81	25.2	13.2	42.5	0.05
totW	6778	150.06	80.44	128.9	15.4	674.1	0.98
K	6778	0.82	0.09	0.8	0.52	1.29	0
gonW	6778	1.7	4.2	0.5	0.1	89.5	0.05
Age	0	NA	NA	NA	NA	NA	NA

tween all areas ( $p < 0.01$ ; Fig. S3). In general, age, TL and TW progressively increased northwards from the Canary Islands to the Cantabrian Sea, with the exception of the Gulf of Cadiz, where the values were lower than expected according to the geographical pattern mentioned above. Mean age increased by 86.6% from the Gulf of Cadiz (1.5 years) to the Cantabrian Sea (2.8 years); mean TL decreased by 21.8% from the Canary Islands (25.7 cm) to the Gulf of Cadiz (21.8 cm) and then increased by 43.6% from Cadiz to the Cantabrian Sea (31.3 cm; by 21.8% compared with the Canary Islands); finally, mean TW decreased by 70.2% from Canary Islands (150.1 g) to the Gulf of Cadiz (88.2 g) and increased by 335% from here to the Cantabrian Sea (2955 g; by 96.9% compared with the Canary Islands). Table 2 shows the basic descriptive statistics of the biological variables analysed in this study.

The condition factor  $K$  ranged between 0.15 and 4.04. Individuals in the best condition were observed in the northern areas (NW Spanish waters and the Cantabrian Sea), but the geographical trend in  $K$  was not as clear as that observed in age, TL and TW. Similar mean  $K$  values were obtained in Atlantic chub mackerel from the Cantabrian Sea (27.8.c), the western Portuguese coast (27.9.a.c) and the Canary Islands (34.1.2) ( $\bar{K}$  between 0.82 and 0.84). The highest ( $\bar{K}=0.89$ ) and lowest ( $\bar{K}=0.75$ ) mean values were found on the northwestern Spanish coast (27.9.a.n) and the Gulf of Cadiz (27.9.a.s), respectively (Table 2). As expected, TW increased with TL and the values fitted to a power relationship, but this relationship differed significantly between study areas ( $p < 0.01$ , Fig. 3), even when only the overlapping size range was considered. Though the intercept and slope was significantly different between all study areas ( $p < 0.01$ ; Fig. S4), the length-weight relationship was more similar among the groups from the Cantabrian Sea, the western Portuguese coast and the Canary Islands than for the groups from the northwestern Iberian Peninsula and the Gulf of Cadiz, which were more similar to each other, as observed in the condition factor. The final model predicts that the largest specimens from the northwestern Spanish waters and the Gulf of Cadiz are heavier than those from the other three areas.

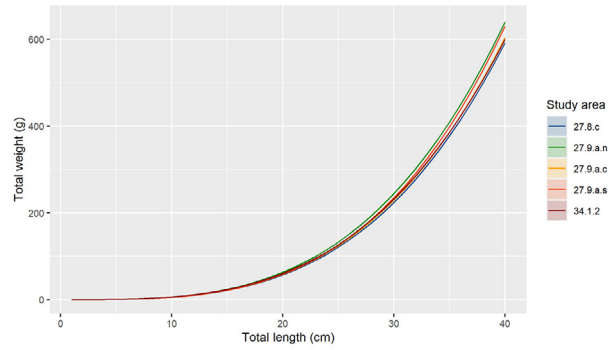


Fig. 3. – Plot of the modelled relationship between the total length (cm) and the total weight (g) by study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Shadow area, 95% confidence intervals.

Spawning activity was detected in all study areas based on monthly variability in the proportion of actively spawning females, although on the northwestern Spanish coast it was negligible (<25%) compared with the remaining areas. In the Canary Islands the peak of spawning activity was recorded in January, when 58% of females were active. In the Gulf of Cadiz a peak of 70% was recorded in February, on the western Portuguese coast a peak of 61% was recorded in March, on the northwestern Spanish coast a peak of 20% was recorded in April-May, and in the Cantabrian Sea a peak of 27% was recorded in May. Assuming that spawning period corresponds to the consecutive months when the proportion of actively spawning females is greater than 25%, a certain prolongation of the spawning season is also observed towards the north. While in the Canary Islands spawning is concentrated in a single month (January), in the Gulf of Cadiz it lasts three months (February-April) and on the western Portuguese coast it lasts six months (January-June). Spawning activity on the northwestern Spanish coast did not reach the threshold established in this study and in the Cantabrian Sea. Though spawning females were detected from January to September, their proportion was less than 25% only in May and July (Fig. 4). In summary, the peak of spawning was delayed and the spawning season extended northwards.

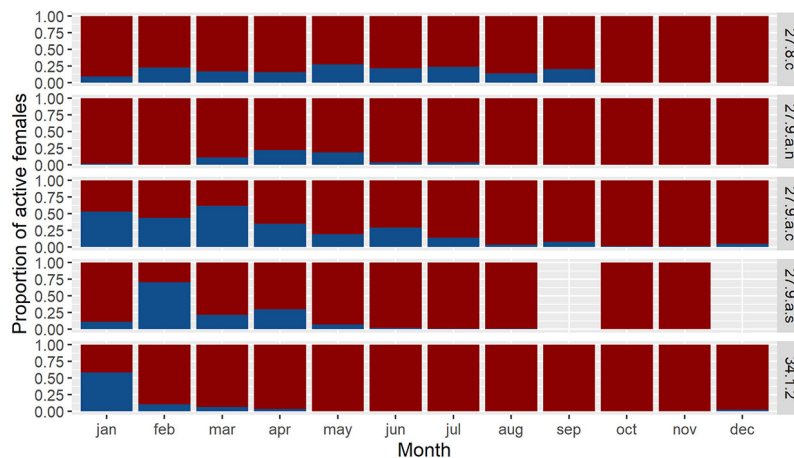


Fig. 4. – Monthly proportion of sexually active (blue) and inactive (red) females in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

Regarding size at first maturity, significant differences in the maturity ogive were detected between areas in both the intercept and the slope ( $p < 0.01$ , Fig. 5). Maturity ogives were estimated based on macroscopic maturity classification of ovaries, so a certain degree of inaccuracy is expected owing to the difficulty in distinguishing macroscopically between immature and recovering ovaries. The best fit of maturity ogives was obtained in the Cantabrian Sea ( $R^2 = 0.73$ ), while in the remaining areas the goodness of fit was lower ( $R^2 < 0.42$ ), especially in the Gulf of Cadiz (Table 3). However, the proportion of mature specimens was significantly related to length in all areas and fitted to the logistic model ( $p < 0.01$ ), although the adjustment can only be considered really good in the Cantabrian Sea.

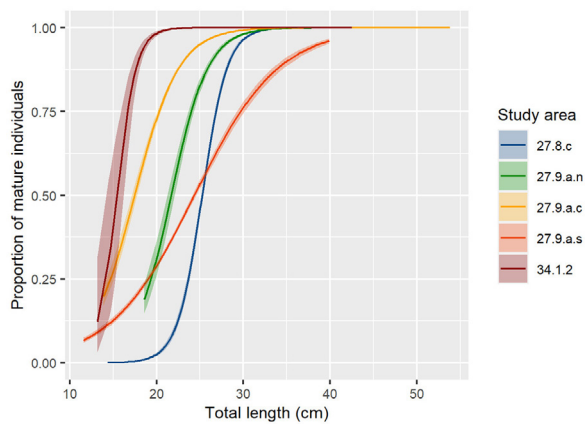


Fig. 5. – Estimated proportion of mature females at length in each study area based on macroscopic maturity classification of ovaries. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Shaded area, 95% confidence intervals.

Table 3. – Parameters of maturity ogives obtained in each study area. 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

Study area	a	b	$L_{50}$	$R^2$
27.8.c	-17.84	0.71	25.23	0.73
27.9.a.n	-10.21	0.47	21.70	0.41
27.9.a.c	-6.91	0.40	17.49	0.36
27.9.a.s	-5.71	0.24	23.98	0.19
34.1.2	-13.98	0.90	15.49	0.38

All these limitations imply that the results should be interpreted with caution. However, according to our analysis, a progressive increase in the  $L_{50}$  towards the north was observed, from 15.5 cm in the Canary Islands to 25.2 cm in the Cantabrian Sea, with the exception, once again, of the Gulf of Cadiz ( $L_{50} = 24$  cm).

The SST in the study areas fluctuated between 10.9°C and 25.7°C (Table 2), with a significant and progressive decrease in mean SST from the Canary Islands (22.1°C) to the Cantabrian Sea (15.9°C) ( $p < 0.01$ ,

Fig. S5). Spawning season was detected to take place between 14°C and 21°C in all study areas. More specifically, mean SST during the spawning season decreased progressively from the Canary Islands (20.5°C) to northwestern Spanish waters (14.6°C), increasing again in the Cantabrian Sea (18.1°C). Our results demonstrated that SST influences total fish length. In fact, our model, which includes the study area, mean annual SST and interaction between them as covariates, explains 33.3% of TL deviance (Table 4). In the Atlantic Iberian waters, the SST-TL relationship showed a positive slope in the Cantabrian Sea (mean SST = 15.8°C), which decreased and became negative southwards, coinciding with the increase in SST: 16.4°C on the northwestern Spanish coast, 18°C on the western Portuguese coast and 21°C in the Gulf of Cadiz. Whereas in the Cantabrian Sea and on the northwestern Spanish coast the slope was positive, on the western Portuguese coast and in the Gulf of Cadiz it was negative. On the other hand, in the Canary Islands, with the highest mean annual SST (22.1°C), the SST-TL relationship showed the steepest slope (Fig. 6).

Table 4. – Parameters and coefficients of the total length model. 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

	Estimate	Std. Error	t value	p-value
Intercept	3.34	0.009	348.8	< 0.01
27.9.a.n	-0.07	0.024	-2.93	< 0.01
27.9.a.c	0.01	0.015	0.721	0.47
27.9.a.s	-0.03	0.022	-1.174	0.24
34.1.2	-0.42	0.029	-14.834	< 0.01
SST	0.01	0.001	10.655	< 0.01
27.9.a.n:SST	-0.001	0.001	-1.264	0.21
27.9.a.c:SST	-0.01	0.001	-8.795	< 0.01
27.9.a.s:SST	-0.02	0.001	-15.648	< 0.01
34.1.2:SST	0.01	0.001	6.184	< 0.01
$R^2$	0.329		Dev.Expl.	33.3%

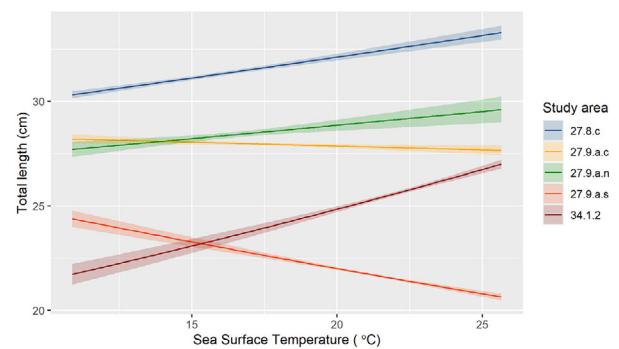


Fig. 6. – Predicted effect of sea surface temperature on total length in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Shaded area, 95% confidence intervals.



## DISCUSSION

Our results show a clear latitudinal gradient of biological parameters of Atlantic chub mackerel from the Canary Islands (division 34.1.2) to the Cantabrian Sea (27.8.c), with the exception of the Gulf of Cadiz (27.9.a.S), where the estimated values in general break this trend. Both the age range and mean age increase northwards, leading to an increase not only in length and weight, but also in length at first maturity and condition factor, though in the latter case the progression is not as evident as for the other parameters. The smallest, lightest and youngest specimens were collected in the Gulf of Cadiz. Growth was not estimated in this work because age data were not available for all study areas. However, the differences in length suggest that the age structure in Canary waters is likely to be biased towards younger ages than in the Iberian Peninsula groups (with the exception of the Gulf of Cadiz). Although the sampling in the Gulf of Cadiz was biased towards the second half of the year (Fig. S1), the lengths of the specimens caught in this area were smaller than in the other areas in all quarters of the year, so these differences were not due to sampling bias but rather to the biological attributes of this component of the north-east Atlantic population of Atlantic chub mackerel, as we discuss below.

The increase in size with latitude coincides with Bergman's rule (Bergmann 1847). Several works have attempted to verify Bergman's rule on ectothermic species, with contradictory results for fishes (Belk and Houston 2002 and references therein). Rypel (2014) suggested that the expression of Bergman's rule in fishes is linked to the species' thermal niches and is only applicable to coldwater species. However, Atlantic chub mackerel is a temperate species (Castro and Santana 2000), so our results suggest that Rypel's hypothesis could also be extended to this type of species or, at least, to those with a wide distribution range, such as Atlantic chub mackerel (Whitehead et al. 1984). Recent studies show that pelagic fish, including Atlantic mackerel, also belonging to the genus *Scomber*, follow Bergmann's rule, confirming that temperature is one of the most important determinants of body size (Hattab et al. 2021). Similarly, latitudinal differences in length at maturity have been observed in the horse mackerel (*Trachurus trachurus*) in the Mediterranean Sea (Ferrerri et al. 2019), which some authors have associated with primary production and temperature (Bonanno et al. 2016; Basilone et al. 2017). Pörtner et al. (2005) concluded that eurytherms are able to dynamically adjust the range of their tolerance windows according to temperature fluctuations, so adapted eurytherms show better fitness than native stenotherm species. These authors further suggested that natural selection should favour the adapted eurytherm species, which are energy-efficient, grow fast and reproduce successfully. These results are especially relevant when one considers global warming and its combined impact with fisheries exploitation, as the most commonly exploited pelagic species have shown a drastic decline in growth, condition and size (Van Beveren et al. 2014; Brosset et

al. 2017). Given the wide distribution of Atlantic chub mackerel, it can be considered a highly adaptive eurytherm, so its ability to colonize new habitats is likely to be high, and it may continue to expand northwards as long as water becomes warmer within its temperature tolerance or preference, so it is able to adapt to global warming even better than native species.

This type of geographical gradients of life-history traits has been reported in other species from both freshwater and marine habitats (Vila-Gispert et al. 2002, Blanck and Lamouroux 2006), as well as different life stages, from early ones (Castro et al. 2002, Takahashi et al. 2012) to adults (Huret et al. 2019). Hughes et al. (2017) relate the latitudinal gradient of life-history traits to temperature, while other authors relate it to other environmental processes such as upwelling events (Gertseva et al. 2017), meso- and large-scale oceanographic processes (Castro et al. 2009, Stocks et al. 2014), fishing pressure (Gertseva et al. 2010), food quality and availability (Perrotta et al. 2005) or a combination of several of them (Huret et al. 2019). The reality is that energy trade-offs in fish are complex and depend on the balance between energy inputs and the metabolic costs of maintenance, growth or maturity. Additionally, all these metabolic processes are strongly influenced by the physical and biological environment in which individuals develop their life stages (Kooijman 2009) and by their life strategies. Because of this, linking geographical clines of biological parameters to specific environmental drivers is difficult, especially in widely distributed species such as the Atlantic chub mackerel.

In the case of pelagic fish, latitudinal changes of biological parameters have been documented in several life-history traits. For example, in *Arripis trutta* from Australia the number of large and old fish was reported to increase northwards, from the cold waters of Tasmania to the warm waters of southern Queensland, although the initial growth rate was higher in the southern areas (Hughes et al. 2017). Furthermore, Huret et al. (2019) observed an increase in growth rate, body size and length at maturity with latitude in European anchovy, and suggested a combination of factors (food availability, maintenance costs, environmental seasonality and temperature) as drivers of these latitudinal gradients.

The present study demonstrates that geographical differences in age and length structure, condition, spawning and maturity of NE Atlantic chub mackerel are significant, showing a clear latitudinal gradient with small and early maturing individuals in the south (the Canary Islands). As the maturity classification was based on macroscopic staging, the results for this parameter must be interpreted with caution; however, considering that we found significant differences between areas in the other biological parameters, the differences in length at first maturity detected in this study can be expected to be real. Latitudinal gradient is also detected in reproductive phenology, with earlier, shorter and more intense spawning activity in the southern study areas than in the northern ones. Latitudinal variability of reproductive season onset and duration has been re-

ported in other fish species too. Huret et al. (2019) reported a delay and shortening of the reproductive season of European anchovy in more northern latitudes, linked to seasonal variability of temperature and food availability and the ability of individuals to accumulate energy reserves. Barbee et al. (2011) found that, in the diadromous fish *Galaxias maculatus*, spawning season onset occurred earlier at high latitude (New Zealand), where spawning fish were older and larger than on the south coast of Australia. These authors linked this geographical variability of life-history traits to key environmental parameters that vary seasonally, such as temperature, day-light duration and productivity. In our case, latitudinal differences in reproductive phenology could be related not only to temperature and food availability, but also to population structure. However, more analyses are required to corroborate this hypothesis.

The maximum length observed in the present study was between 40 and 54 cm (mean between 21.8 and 31.3 cm), while the maximum age recorded was between 6 and 14 years (mean between 1.5 and 2.8 years). These results are in accordance with the observations of previous studies (Velasco et al. 2011, Jurado-Ruzafa et al. 2021, Navarro et al. 2021b).

Mean Fulton's K ranged between 0.82 and 0.89 considering all study areas, except in the Gulf of Cadiz, where K was slightly lower (mean = 0.75). In Atlantic chub mackerel, condition factor is significantly related to TL (Fig. S6). Therefore, the low values observed in the Gulf of Cadiz may be due to the small size of specimens from this area. Fulton's K values between 0.7 and 1.1 have been reported for the Atlantic chub mackerel from the Atlantic Portuguese coast (Alves 2016, Santos et al. 2017, Barboza et al. 2020), suggesting that the mean condition indices obtained in the study period and areas are in the lower part of this range. Fish body condition is closely related to feeding, metabolic rates and the capacity to store energy reserves, i.e. to energetic trade-offs (Sabrido-Rey and Kjesbu 2005), all of which are modulated by environmental factors such as temperature or prey availability and diversity, i.e. marine community biodiversity. Changes in the pelagic ecosystem induced by global warming, fishing pressure or any other environmental driver may lead to a decrease in the health status of native pelagic fishes (Shephard et al. 2014, Muhling et al. 2017).

The biological characteristics of Atlantic chub mackerel from the Gulf of Cadiz (young, small and low-condition specimens) should be also addressed from the environmental-induced point of view. In this area, there has been an increase in landings of Atlantic chub mackerel since 2007. While this increase coincides with the recent expansion of the species throughout Ibero-Atlantic waters, it also coincides with the decline of the Ibero-Atlantic sardine stock, which led to severe restrictions on fishing opportunities for this species. These limitations may have led to a change in the behaviour of the fleet, which may have redirected its effort towards Atlantic chub mackerel to compensate for the decline in sardine catches (ICES 2021a). This increase in fishing effort could be behind the juvenescence of Atlantic chub mackerel in this area. However,

as explained below, the Gulf of Cadiz could also be either a mixing area between the Atlantic and Mediterranean populations or a hinge area in the latitudinal and longitudinal biological gradient observed for Atlantic chub mackerel in the NE Atlantic and Mediterranean.

Regarding the onset and duration of the spawning season, most of the existing studies of Atlantic chub mackerel are based on the analyses of the monthly prevalence of active females and the gonado-somatic index, showing some variability among regions. The spawning season in North African waters has been reported from December to March in Morocco (Tchetchach et al. 2010, Wahbi et al. 2011) and from January to March in Mauritania and Senegal (ICES 2020). In the Atlantic islands the spawning season of Atlantic chub mackerel has been reported from November/December to March in the Canary Islands (Lorenzo and Pajuelo 1996, Jurado-Ruzafa et al. 2021), from January to April in Madeira (Vasconcelos et al. 2012) and from March to July/August in the Azores (Carvalho et al. 2002). Finally, in the Atlantic Iberian waters spawning season has been reported from December to March in waters of southern Portugal waters (ICES 2020), from December to May in western Portuguese waters (Nunes et al. 2019) and, lastly, from March to July on the northwestern Spanish coast and the Cantabrian Sea (Villamor et al. 2017, Navarro et al. 2021a). The spawning period of Atlantic chub mackerel in the Mediterranean Sea has been reported from April to August (Rizkalla 1998, Cengiz 2012, Allaya et al. 2013). Our results show a clear latitudinal gradient of spawning season onset and duration that matches with previous studies. Reviewing all this information together, there seems to be a latitudinal trend from the Strait of Gibraltar towards the poles, but also a longitudinal one from the Strait of Gibraltar towards the Mediterranean Sea and the central Atlantic. Changes in reproductive phenology are usually associated with environmental drivers (Rogers and Dougherty 2019, Slesinger et al. 2021), although they could be related to the age structure of populations, as spawning season onset and duration may change depending on the age of reproductive specimens (Lambert 1987, Wright and Trippel 2009). However, with the available data we cannot distinguish whether the phenological differences observed in this study are due to environmental drivers or to the differences in the population structure of each study area. This is especially important in the context of global warming, which is leading to distribution shifts of fish species because reproductive phenology affects population resilience (Lowerre-Barbieri et al. 2017), and more attention should be paid to this issue in the near future.

Regarding the size at first maturity ( $L_{50}$ ) of Atlantic chub mackerel, our results based on macroscopic observations showed a latitudinal trend, with the lowest value in the Canary Islands (15.5 cm) and increasing progressively towards the north (17.5 cm on the western Portuguese coast and 25.2 cm in the Cantabrian Sea). Once again, the  $L_{50}$  values for the Gulf of Cadiz (24 cm) break with this trend, despite the fact that in general the individuals in this area are the smallest. Previous studies reported higher values in the Bay of

Biscay ( $L_{50}=29$  cm; Lucio 1997) and in Portuguese waters ( $L_{50}=27$  cm; Martins 1996), although more recent investigations showed  $L_{50}$  values in the Bay of Biscay similar to those reported here (25 cm; Villamor et al. 2017, Navarro et al. 2021a). In western Portuguese waters, Nunes et al. (2019) reported an  $L_{50}$  equal to 22.6 cm and 19.2 cm for females and males, respectively; while Gonçalves et al. (2016) in southern Portugal reported an  $L_{50}$  for both sexes combined of 18.6 cm. These Portuguese values are slightly higher than our estimations (17.5 cm). In the case of the Canary Islands, our estimate of  $L_{50}$  is the smallest one and lower than previous estimations reported in the same area (18–19 cm; Lorenzo and Pajuelo 1996, Jurado-Ruzafa et al. 2021). This difference is likely due to differences in the data used to calculate the  $L_{50}$ , which in previous studies included post-spawning and spawning specimens collected exclusively during the spawning period. In Atlantic Moroccan waters,  $L_{50}$  values increased from 23 cm in the north (Techetach et al. 2010) to 25 to 27.5 cm in the south (Wahbi et al. 2017). High values of  $L_{50}$  were reported in the Azores (27.8 cm; Carvalho et al. 2002), followed by Madeira (22 cm; Vasconcelos et al. 2012) and the Mediterranean Sea (16.8 and 19 cm; Cengiz 2012, Cikeš and Zorica 2012, Techetach et al. 2019). Spatial patterns of size at first maturity do not seem to be as clear as spawning onset and duration, although the  $L_{50}$  values presented here should be interpreted with caution, as stated above. Nevertheless, certain latitudinal and longitudinal trends of maturity patterns can be glimpsed and should be corroborated by histological studies. In any case, the spatial differences observed in size and age structure and condition suggest the existence of different life-history patterns, so spatial differences in maturation can also be expected. This aspect would be especially relevant for stock assessment purposes.

The spatial population structure of the Atlantic chub mackerel in the eastern Atlantic, the migration processes through the distribution range and the connectivity, including the Mediterranean Sea, remain unknown (ICES 2021a). The geographical differences in life-history traits estimated in this and previous studies suggest that there may be at least two population components: one in the Canary Islands and one in the Iberian Peninsula. Furthermore, the Iberian unit could include two subcomponents in the Cantabrian Sea (Bay of Biscay) and the Portuguese coast, whose degree of connection could vary depending on the abundance and migration intensity of Atlantic chub mackerel in each area (ICES 2020 and references therein). Additionally, the Gulf of Cadiz could be considered a hinge area, or even a mixing area between the northeast and central east Atlantic populations of Atlantic chub mackerel as well as between the northeast Atlantic and Mediterranean stocks, as suggested by ICES (2021a). The results of the growth analysis carried out by Velasco et al. (2011) support the hypothesis of a mixing area, as they found no differences in growth between the Gulf of Cadiz and the Alboran Sea, suggesting that the Strait of Gibraltar is not a geographical barrier for this species. However, in general, results of studies targeting

the stock structure of Atlantic chub mackerel in the northeast Atlantic and the Mediterranean Sea show differences depending on the methodological approach. Some genetic studies showed no significant differences between the Atlantic chub mackerel from the Mediterranean and eastern Atlantic areas (Scoles et al. 1998, Zardoya et al. 2004). However, significant regional differences have been found between smaller areas in the east Atlantic Ocean, including the Mediterranean Sea and Macaronesian islands, based on the analysis of morphology, meristic characteristics (Allaya et al. 2016, Bouzzammit and El Ouizgami 2019, Muniz et al. 2020) and associated parasites (Mele et al. 2014). Muniz et al. (2020), based on otolith morphology analysis, suggested the existence of one group in the northeast Atlantic islands (Azores, Madeira and the Canary Islands) and another one on the Iberian Portuguese coast. Correia et al. (2021), according to microchemical analysis of the same otoliths, suggested the existence of at least four stock components in the northeast Atlantic (Azores, Madeira, Canary Islands and Iberian Portuguese coast). There is no information on the migratory behaviour of this species in the study area, although by analogy with the previous study on the species in northwest African waters (García 1982), we assume that the Atlantic chub mackerel performs annual reproductive migrations all along its distributional range. If so, connectivity between the different population components may exist, but the extent of this migration and therefore the degree of potential connectivity remain unknown. Many of these studies have been approached on a local or regional scale, and thus lack the global vision required to investigate the population structure of a species as widely distributed as the Atlantic chub mackerel. Jansen et al. (2013) proposed for the northeast Atlantic mackerel (*S. scombrus*) that the population structure is more a dynamic cline rather than connected contingents, and this could also be the case of the Atlantic chub mackerel. However, more studies targeting migration behaviour, genetics, morphometry and meristic characterization from a global perspective should be carried out to confirm meaningful biological management units for assessment purposes.

Considering that the increase in abundance of Atlantic chub mackerel in the Atlantic Iberian waters is assumed to be a relatively recent event (Villamor et al. 2017), it is striking that individuals in the northernmost (i.e. most recently occupied) study areas show the greatest diversity of age and size and the best condition. There are two possible explanations for this: a) the presence of older and larger individuals of Atlantic chub mackerel could be due to the fact that they have a greater capacity for movement and therefore a greater capacity for expansion to new suitable habitats in a global warming scenario; and/or b) fishing pressure or predation could be less intense in the north than in northwest African waters, reducing the presence of larger and older individuals in this area. With the information available, we cannot determine the causes of the age and size structure observed in each study area. According to Saunders and Tarling (2018), greater body size in mesopelagic fishes is a necessary attri-

bute to reach colder regions, which supports our first hypothesis that the largest individuals are those with the greatest migratory capacity.

In most studied fish species, great size, age and condition are associated with high reproductive potential owing to the existence of maternal effects (Green 2008). In addition, a prolonged reproductive season increases the probability of offspring finding optimal environmental windows for their development, thus increasing their survival (Mertz and Myers 1994). Given the biological characteristics of the groups analysed in this study and the duration of the reproductive season in each area, the geographical variability of the reproductive potential of this species and its impact on stock resilience should be analysed in the future. This variability may be a mechanism of adaptation to the environmental conditions (temperature, productivity and turbulence) that could favour or jeopardize offspring survival and hence recruitment.

Our model indicates that SST does indeed play a relevant role in the size of Atlantic chub mackerel and, presumably, on its growth. While on the western Portuguese coast and the Gulf of Cadiz this effect is negative, in the remaining areas it is positive. The rates of physiological processes usually increase with temperature up to a certain limit, above which the temperature effect becomes negative. This temperature effect is also observed in the growth of fish, so at low temperatures growth increases as temperature increases until a tipping point (optimum temperature) when growth decreases with increasing temperature (Jobling 1995). The temperature range at which fish populations exhibit this behaviour changes geographically owing to acclimation mechanisms (Sunday et al. 2011). Therefore, growth is expected to increase with temperature in areas that are below their optimum temperature and to decrease in areas that have exceeded this threshold. Assuming the total length as a proxy of the growth rate of Atlantic chub mackerel for each study area, and based on the slope of the SST-TL relationship, we could conclude that *S. colias* in the Cantabrian Sea and on the northwestern Spanish coast is farther from its optimum temperature than it is on the western Portuguese coast, where it is slightly above it, and in the Gulf of Cadiz, where it is clearly above it. In the Canary Islands, where mean annual SST is considerably higher than in the rest of the study areas, the effect of SST on the TL of Atlantic chub mackerel was the most markedly positive. We do not know the reasons behind this relationship but it could be related to the comparatively small specimens of Atlantic chub mackerel inhabiting the Canary waters. Further knowledge of this relationship between SST and growth would help to better understand the dynamics and population structure of Atlantic chub mackerel in the northeast Atlantic in order to properly calibrate the assessment and manage this resource adequately under future global warming scenarios.

Many fish species have been reported to be moving to higher latitudes as a consequence of climate change (Perry et al. 2005, Rijnsdorp et al. 2009). One of the most emblematic cases in recent decades is that of the Atlantic mackerel (*S. scombrus*), whose distribution

has expanded northwards and westwards in the NE Atlantic Ocean, reaching the waters of Svalbard and Iceland (Berge et al. 2015) driven by stock size and temperature (Astthorsson et al. 2012, Olafsdottir et al. 2019). Similarly, landings of Atlantic chub mackerel in the Atlantic Iberian waters have increased during the last few decades (Martins et al. 2013, Villamor et al. 2017, ICES 2020), likely associated with an increase in stock size and its northward expansion linked to global warming. The arrival of new species in ecosystems can have a major impact on trophic balances and the dynamics of other species (Cheung et al. 2009, Hollowed et al. 2013, Muhling et al. 2017). The Atlantic chub mackerel is an opportunistic pelagic species that feeds mainly on euphausiids and decapod crustaceans, but also significantly on eggs, larvae and juveniles of other pelagic and demersal fish species (Torres et al. 2013). In fact, Garrido et al. (2015a) identified sardine eggs as an important component of the diet of Atlantic chub mackerel and reported a considerable overlap in the prey spectrum between European sardine and juvenile chub mackerel. Taking this into account, it is probable that the expansion of Atlantic chub mackerel in Atlantic Iberian waters played an important role in the decline of Iberian sardine populations observed in the same period. To corroborate this hypothesis, the trends of both species in the Atlantic Iberian waters in the coming years should be monitored, especially when the sardine population has started to recover (ICES 2021b). Another question that would be worth investigating further is whether the change in the distribution of *S. scombrus* could have reduced the occupation of certain pelagic niches in Atlantic Iberian waters, which could be being occupied by warmer-water species such as the Atlantic chub mackerel. Furthermore, its expansion in Atlantic Iberian waters may also impact on predators, as it has been reported as an important prey for other commercial species such as European hake, sharks, bluefin tuna and marine mammals (Torres et al. 2013, Varela et al. 2013, Giménez et al. 2017).

This paper outlines the population structure of the Atlantic chub mackerel in the northeast Atlantic from a broad geographical perspective and provides information on the regional variability of key biological parameters commonly required for assessment, such as length-weight relationships, the maturity ogive and size composition. However, there are still many gaps to be filled. In relation to population structure, it would be desirable to extend the study to North African and western Mediterranean waters in order to carry out not only analyses of life-history parameters such as growth and maturation, but also other stock identification studies such as genetic, morphometric and parasite analyses with a wider perspective. Similarly, it would be necessary to analyse how the biological differences detected between the study areas affect the productivity and resilience of the species. This would require time series of fecundity, egg and larval quality and recruitment. Additionally, analysing biodiversity changes in the pelagic ecosystem of the study areas would allow us to understand the impact of new species arrivals on fisheries yields. Ulti-

mately, from an ecological point of view, this species is a promising case study for monitoring the impact of climate change on pelagic ecosystems.

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## SUPPLEMENTARY MATERIAL

Table S1. – Detailed description of all samples considered in the present study, including study area (subdivision), sampling source (S, research cruise; C, commercial vessels), scientific survey name, survey methodology, sampling dates, number of samples (samples), number of individuals in each sample (n), size range of sampled specimens (cm), and maturity key used for macroscopic maturity staging (Mat. Scale). Attached as a separate PDF file.

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
Cantabrian Sea (27.8.c)	S	PELACUS0411	Acoustic-trawl	mar/11	11	364	192-469	Walsh et al. (1990)
	S	DEMERSALES2011	Bottom-trawl	oct/11	1	9	127-175	Walsh et al. (1990)
	S	PELACUS0412	Acoustic-trawl	mar/12	16	186	166-425	Walsh et al. (1990)
	S	DEMERSALES2012	Bottom-trawl	oct/12	9	20	147-177	Walsh et al. (1990)
	S	PELACUS0313	Acoustic-trawl	mar-apr/13	13	202	144-437	Walsh et al. (1990)
	S	PELACUS0314	Acoustic-trawl	mar-apr/14	17	255	176-444	Walsh et al. (1990)
	S	DEMERSALES2014	Bottom-trawl	oct/14	8	37	145-195	Walsh et al. (1990)
	S	PELACUS0315	Acoustic-trawl	mar-apr/15	22	461	185-431	Walsh et al. (1990)
	S	DEMERSALES2015	Bottom-trawl	oct/15	13	140	112-261	Walsh et al. (1990)
	S	PELACUS0316	Acoustic-trawl	mar/16	11	287	174-381	Walsh et al. (1990)
	S	DEMERSALES2016	Bottom-trawl	sep-oct/16	15	68	146-400	Walsh et al. (1990)
	S	PELACUS0317	Acoustic-trawl	mar-apr/17	9	216	181-391	Walsh et al. (1990)
	S	DEMERSALES2017	Bottom-trawl	sep-oct/17	32	335	142-488	Walsh et al. (1990)
	S	PELACUS0318	Acoustic-trawl	mar-apr/18	10	288	171-406	Walsh et al. (1990)
	S	DEMERSALES2018	Bottom-trawl	sep-oct/18	16	124	167-320	Walsh et al. (1990)
	S	PELACUS0319	Acoustic-trawl	mar-apr/19	13	348	180-368	Walsh et al. (1990)
	S	DEMERSALES2019	Bottom-trawl	oct/19	6	10	169-362	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/11	1	97	241-344	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/11	1	92	250-381	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/11	1	100	299-384	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/11	1	85	316-420	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/11	2	95	293-395	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/11	1	71	330-480	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/11	1	93	330-410	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/11	1	52	365-402	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/11	1	65	316-410	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/11	3	123	286-418	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/11	1	69	325-405	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/12	1	99	262-430	Walsh et al. (1990)
	C	Commercial	Gillnet	feb/12	1	67	336-411	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/12	2	152	254-411	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/12	1	71	359-422	Walsh et al. (1990)
	C	Commercial	Gillnet	may/12	2	105	307-385	Walsh et al. (1990)
C	Commercial	Gillnet	jun/12	2	94	287-469	Walsh et al. (1990)	
C	Commercial	Purse-seine	jun/12	1	35	297-392	Walsh et al. (1990)	
C	Commercial	Gillnet	jul/12	1	18	321-353	Walsh et al. (1990)	
C	Commercial	Purse-seine	ago/12	1	64	330-452	Walsh et al. (1990)	
C	Commercial	Gillnet	sep/12	2	61	343-428	Walsh et al. (1990)	
C	Commercial	Purse-seine	oct/12	2	101	341-465	Walsh et al. (1990)	
C	Commercial	Purse-seine	nov/12	1	82	373-453	Walsh et al. (1990)	
C	Commercial	Purse-seine	dic/12	1	100	277-435	Walsh et al. (1990)	
C	Commercial	Purse-seine	ene/13	1	94	337-435	Walsh et al. (1990)	

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Gillnet	feb/13	1	39	320-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/13	1	92	357-441	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/13	1	68	349-411	Walsh et al. (1990)
	C	Commercial	Gillnet	may/13	2	105	292-430	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/13	1	76	342-508	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/13	1	39	237-286	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/13	1	100	270-329	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/13	1	100	355-429	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/13	1	127	312-438	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/13	1	50	317-422	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/13	1	39	276-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/13	2	117	272-495	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/13	1	12	244-300	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/14	1	99	273-357	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/14	1	100	264-351	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/14	1	80	304-495	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/14	1	54	275-340	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/14	1	84	325-430	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/14	1	20	327-409	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/15	1	95	302-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	abr/15	1	2	335-342	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/15	2	100	266-400	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/15	1	67	295-367	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/15	1	31	265-339	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/15	1	70	314-420	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/16	1	85	317-428	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/16	2	102	183-412	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/16	1	100	282-387	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/16	2	138	278-382	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/16	1	86	287-369	Walsh et al. (1990)
	C	Commercial	Gillnet	ago/16	1	101	311-379	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/16	2	183	270-377	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/17	1	105	303-401	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/17	1	100	222-340	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/17	1	112	261-382	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/17	1	100	215-295	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/17	1	64	268-402	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/18	1	6	258-278	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/18	1	100	276-393	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/18	1	100	227-310	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/18	2	189	242-391	Walsh et al. (1990)
	C	Commercial	Gillnet	ago/18	1	100	293-388	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/18	1	100	280-356	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/18	1	100	264-346	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/19	1	120	260-405	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/19	1	98	256-328	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/19	1	99	254-341	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/19	1	90	296-356	Walsh et al. (1990)



Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Purse-seine	jul/19	1	94	269-320	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/19	1	104	280-366	Walsh et al. (1990)
	C	Commercial	Gillnet	ago/19	1	83	302-418	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/19	1	100	258-314	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/19	2	95	292-373	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/19	1	118	281-442	Walsh et al. (1990)
	Total			317	10173	112-495		
NW Spanish Coast (27.9.a.n)	S	PELACUS0315	Acoustic-trawl	mar/15	4	31	238-350	Walsh et al. (1990)
	S	PELACUS0317	Acoustic-trawl	mar/17	5	129	125-276	Walsh et al. (1990)
	S	DEMERSALES2017	Bottom-trawl	sep/17	1	10	232-263	Walsh et al. (1990)
	S	PELACUS0318	Acoustic-trawl	apr/18	6	70	190-292	Walsh et al. (1990)
	S	PELACUS0319	Acoustic-trawl	apr/19	4	17	249-285	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/11	1	20	207-279	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/11	1	100	241-373	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/11	1	90	262-380	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/11	1	100	257-336	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/11	1	100	282-376	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/11	2	125	218-326	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/11	1	100	275-353	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/11	2	92	279-415	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/12	1	96	284-335	Walsh et al. (1990)
	C	Commercial	Gillnet	feb/12	1	95	269-372	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/12	1	89	288-328	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/12	2	176	193-384	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/12	1	92	289-356	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/12	2	101	166-355	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/12	2	113	205-344	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/12	1	110	190-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/12	1	140	186-255	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/12	1	100	310-403	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/13	1	100	191-245	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/13	1	91	210-351	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/13	1	61	252-335	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/13	1	113	245-320	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/13	1	100	248-325	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/13	2	183	220-375	Walsh et al. (1990)
	C	Commercial	Gillnet	dic/13	1	111	261-378	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/14	2	150	250-326	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/14	1	75	254-324	Walsh et al. (1990)
	C	Commercial	Purse-seine	dic/14	1	120	254-343	Walsh et al. (1990)
	C	Commercial	Purse-seine	ene/15	1	97	261-356	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/15	2	105	268-387	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/18	1	99	214-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	ago/18	1	89	276-356	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dic/18	1	90	259-360	Walsh et al. (1990)
	C	Commercial	Purse-seine	abr/19	2	200	248-320	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Purse-seine	jul/19	1	99	240-331	Walsh et al. (1990)
	Total			64	3979	125-415		
W Portuguese Coast (27.9.a.c)	S	IBTS11	Bottom-trawl	oct/11	3	195	176-312	Walsh et al. (1990)
	S	PELAGO13	Acoustic-trawl	apr-may/13	6	308	176-278	Walsh et al. (1990)
	S	JUVESAR13	Acoustic-trawl	nov/13	4	46	186-314	Walsh et al. (1990)
	S	IBTS13	Bottom-trawl	oct/13	5	210	182-318	Walsh et al. (1990)
	S	PELAGO14	Acoustic-trawl	apr-may/14	5	166	187-281	Walsh et al. (1990)
	S	IBTS14	Bottom-trawl	oct/14	2	135	205-322	Walsh et al. (1990)
	S	PELAGO15	Acoustic-trawl	apr-may/15	3	89	217-326	Walsh et al. (1990)
	S	IBTS15	Bottom-trawl	oct/15	1	46	192-259	Walsh et al. (1990)
	S	PELAGO16	Acoustic-trawl	apr/16	1	6	294-328	Walsh et al. (1990)
	S	JUVESAR16	Acoustic-trawl	dec/16	2	109	153-267	Walsh et al. (1990)
	S	IBTS16	Bottom-trawl	nov-oct/16	9	172	143-325	Walsh et al. (1990)
	S	PELAGO17	Acoustic-trawl	apr/17	1	39	162-215	Walsh et al. (1990)
	S	PELAGO_N17	Acoustic-trawl	aug/17	5	363	170-269	Walsh et al. (1990)
	S	JUVESAR17	Acoustic-trawl	dec/17	2	97	188-258	Walsh et al. (1990)
	S	PELAGO17	Acoustic-trawl	may/17	6	266	150-311	Walsh et al. (1990)
	S	IBTS17	Bottom-trawl	nov-oct/17	11	357	167-287	Walsh et al. (1990)
	S	IBTS18	Bottom-trawl	dec/18	3	52	183-307	Walsh et al. (1990)
	S	PELAGO18	Acoustic-trawl	may/18	8	538	172-309	Walsh et al. (1990)
	S	IBERAS18	Acoustic-trawl	nov/18	4	293	176-310	Walsh et al. (1990)
	S	IBTS18	Bottom-trawl	nov-oct/18	5	119	171-265	Walsh et al. (1990)
	S	PELAGO19	Acoustic-trawl	apr/19	1	61	203-294	Walsh et al. (1990)
	S	MPDO19	Bottom-trawl	feb/19	3	110	178-273	Walsh et al. (1990)
	S	PELAGO19	Acoustic-trawl	may/19	2	98	174-340	Walsh et al. (1990)
	S	IBERAS19	Acoustic-trawl	sep/19	6	228	181-300	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/11	1	62	256-399	Walsh et al. (1990)
	C	Commercial	Purse-seine	jan/11	2	218	286-395	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/11	1	68	255-402	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/11	1	84	276-348	Walsh et al. (1990)
	C	Commercial	Trammelnet	mar/11	1	26	264-336	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/11	1	82	198-397	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/11	1	45	233-298	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/11	1	69	253-381	Walsh et al. (1990)
	C	Commercial	Purse-seine	apr/11	2	98	286-429	Walsh et al. (1990)
C	Commercial	Gillnet	may/11	2	91	277-414	Walsh et al. (1990)	
C	Commercial	Bottom trawl	may/11	1	59	283-338	Walsh et al. (1990)	
C	Commercial	Gillnet	jun/11	1	99	216-416	Walsh et al. (1990)	
C	Commercial	Bottom trawl	jun/11	1	57	264-337	Walsh et al. (1990)	
C	Commercial	Purse-seine	jun/11	1	59	254-385	Walsh et al. (1990)	
C	Commercial	Gillnet	jul/11	1	49	275-348	Walsh et al. (1990)	
C	Commercial	Bottom trawl	jul/11	2	117	273-372	Walsh et al. (1990)	
C	Commercial	Purse-seine	jul/11	1	76	283-378	Walsh et al. (1990)	
C	Commercial	Bottom trawl	aug/11	2	127	271-357	Walsh et al. (1990)	
C	Commercial	Gillnet	sep/11	2	94	270-362	Walsh et al. (1990)	

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Bottom trawl	sep/11	2	127	283-365	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/11	1	41	302-362	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/11	2	121	277-352	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/11	1	48	258-401	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/11	2	124	283-364	Walsh et al. (1990)
	C	Commercial	Purse-seine	nov/11	1	67	312-355	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/11	2	63	305-391	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/11	1	63	286-413	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/12	2	122	264-406	Walsh et al. (1990)
	C	Commercial	Trammelnet	feb/12	1	36	314-429	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/12	1	37	254-356	Walsh et al. (1990)
	C	Commercial	Trammelnet	mar/12	2	109	263-382	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/12	1	57	325-396	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/12	1	58	245-330	Walsh et al. (1990)
	C	Commercial	Gillnet	may/12	2	80	255-398	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/12	1	40	293-342	Walsh et al. (1990)
	C	Commercial	Hook and Line	jun/12	2	51	331-418	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/12	1	70	288-365	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/12	1	120	221-349	Walsh et al. (1990)
	C	Commercial	Gillnet	aug/12	1	34	307-393	Walsh et al. (1990)
	C	Commercial	Hook and Line	sep/12	1	24	345-406	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/12	2	102	171-267	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/12	1	59	279-353	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/12	1	61	292-376	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/12	2	109	250-384	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/12	1	35	290-405	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/13	2	120	282-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/13	2	127	237-421	Walsh et al. (1990)
	C	Commercial	Purse-seine	apr/13	1	45	329-411	Walsh et al. (1990)
	C	Commercial	Drift longline	may/13	1	32	313-388	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/13	1	69	260-347	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/13	2	125	240-345	Walsh et al. (1990)
	C	Commercial	Trammelnet	jul/13	1	21	310-396	Walsh et al. (1990)
	C	Commercial	Drift longline	jul/13	1	12	422-538	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/13	1	52	247-323	Walsh et al. (1990)
	C	Commercial	Gillnet	aug/13	1	16	414-490	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/13	1	55	243-375	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/13	1	77	218-283	Walsh et al. (1990)
	C	Commercial	Bottom trawl	sep/13	2	101	253-363	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/13	1	48	220-290	Walsh et al. (1990)
	C	Commercial	Longline	oct/13	1	16	372-462	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/13	1	81	273-354	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/13	1	38	267-365	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/13	1	74	251-316	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/13	1	21	292-387	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/14	1	49	257-335	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/14	1	50	233-292	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/14	1	49	252-355	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Bottom trawl	apr/14	1	99	240-337	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/14	1	50	254-351	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/14	1	30	302-416	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/14	1	31	268-351	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/14	1	66	264-367	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/14	1	51	312-412	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/14	1	45	224-300	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/14	1	59	284-372	Walsh et al. (1990)
	C	Commercial	Bottom trawl	sep/14	1	52	307-376	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/14	1	57	208-280	Walsh et al. (1990)
	C	Commercial	Drift longline	oct/14	1	41	253-365	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/14	1	38	312-355	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/14	2	117	203-435	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/14	1	52	244-309	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/14	1	62	257-346	Walsh et al. (1990)
	C	Commercial	Trammelnet	jan/15	1	31	302-392	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/15	2	67	233-368	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/15	2	110	274-386	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/15	1	53	210-296	Walsh et al. (1990)
	C	Commercial	Purse-seine	mar/15	1	38	225-270	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/15	1	47	237-299	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/15	2	150	257-433	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/15	1	30	321-375	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/15	1	49	268-354	Walsh et al. (1990)
	C	Commercial	Trammelnet	jul/15	1	24	311-349	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/15	2	95	239-347	Walsh et al. (1990)
	C	Commercial	Trammelnet	aug/15	1	25	335-418	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/15	1	42	266-326	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/15	1	41	276-359	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/15	1	52	272-364	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/15	2	86	270-344	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/15	1	63	241-320	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/15	1	26	264-329	Walsh et al. (1990)
	C	Commercial	Trammelnet	dec/15	1	31	322-404	Walsh et al. (1990)
	C	Commercial	Purse-seine	dec/15	2	114	244-373	Walsh et al. (1990)
	C	Commercial	Gillnet	jan/16	1	58	307-399	Walsh et al. (1990)
	C	Commercial	Trammelnet	jan/16	1	32	313-379	Walsh et al. (1990)
	C	Commercial	Purse-seine	feb/16	2	77	248-384	Walsh et al. (1990)
	C	Commercial	Trammelnet	mar/16	2	120	239-440	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/16	1	50	239-303	Walsh et al. (1990)
	C	Commercial	Gillnet	may/16	2	55	267-393	Walsh et al. (1990)
	C	Commercial	Trammelnet	jun/16	1	28	320-382	Walsh et al. (1990)
	C	Commercial	Purse-seine	jun/16	1	76	266-353	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/16	1	32	312-385	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/16	2	123	219-342	Walsh et al. (1990)
	C	Commercial	Trammelnet	aug/16	1	52	230-318	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/16	2	109	238-367	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/16	2	72	260-365	Walsh et al. (1990)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Purse-seine	sep/16	1	34	139-229	Walsh et al. (1990)
	C	Commercial	Trammelnet	oct/16	2	81	150-323	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/16	1	52	286-393	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/16	2	60	242-345	Walsh et al. (1990)
	C	Commercial	Longline	nov/16	1	27	354-403	Walsh et al. (1990)
	C	Commercial	Gillnet	dec/16	1	52	237-373	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/16	1	56	166-224	Walsh et al. (1990)
	C	Commercial	Trammelnet	jan/17	1	17	297-404	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jan/17	1	48	287-348	Walsh et al. (1990)
	C	Commercial	Bottom trawl	feb/17	1	67	259-355	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/17	1	55	276-364	Walsh et al. (1990)
	C	Commercial	Gillnet	apr/17	1	49	218-392	Walsh et al. (1990)
	C	Commercial	Bottom trawl	apr/17	1	55	263-359	Walsh et al. (1990)
	C	Commercial	Gillnet	may/17	1	57	272-394	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/17	1	13	191-239	Walsh et al. (1990)
	C	Commercial	Purse-seine	may/17	1	26	332-377	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/17	1	24	306-377	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/17	1	70	257-335	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/17	1	46	281-359	Walsh et al. (1990)
	C	Commercial	Trammelnet	jul/17	1	28	284-369	Walsh et al. (1990)
	C	Commercial	Trammelnet	aug/17	1	10	405-483	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/17	1	57	266-360	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/17	1	50	208-286	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/17	2	77	185-363	Walsh et al. (1990)
	C	Commercial	Purse-seine	sep/17	4	118	180-405	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/17	1	28	290-336	Walsh et al. (1990)
	C	Commercial	Purse-seine	oct/17	1	48	192-273	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/17	1	87	256-365	Walsh et al. (1990)
	C	Commercial	Trammelnet	nov/17	1	77	181-303	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/17	2	49	237-360	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/17	1	48	253-337	Walsh et al. (1990)
	C	Commercial	Purse-seine	jan/18	1	57	228-361	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/18	2	104	227-345	Walsh et al. (1990)
	C	Commercial	Purse-seine	apr/18	1	27	291-386	Walsh et al. (1990)
	C	Commercial	Gillnet	may/18	1	31	317-394	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/18	1	55	247-335	Walsh et al. (1990)
	C	Commercial	Gillnet	jun/18	1	68	231-343	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/18	1	23	281-377	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jul/18	1	32	296-363	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/18	1	51	195-257	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/18	1	55	214-268	Walsh et al. (1990)
	C	Commercial	Purse-seine	aug/18	1	49	254-379	Walsh et al. (1990)
	C	Commercial	Bottom trawl	sep/18	1	51	246-315	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/18	1	45	258-312	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/18	1	17	291-355	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/18	1	57	228-325	Walsh et al. (1990)
	C	Commercial	Gillnet	dec/18	2	76	238-389	Walsh et al. (1990)
	C	Commercial	Gillnet	jan/19	1	28	271-380	Walsh et al. (1990)



Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Bottom trawl	jan/19	1	54	273-355	Walsh et al. (1990)
	C	Commercial	Gillnet	feb/19	1	39	256-343	Walsh et al. (1990)
	C	Commercial	Bottom trawl	mar/19	1	45	250-376	Walsh et al. (1990)
	C	Commercial	Gillnet	apr/19	1	54	189-302	Walsh et al. (1990)
	C	Commercial	Gillnet	may/19	1	29	334-395	Walsh et al. (1990)
	C	Commercial	Bottom trawl	may/19	1	52	252-332	Walsh et al. (1990)
	C	Commercial	Longline	jun/19	1	25	327-362	Walsh et al. (1990)
	C	Commercial	Bottom trawl	jun/19	1	41	218-258	Walsh et al. (1990)
	C	Commercial	Gillnet	jul/19	1	26	307-359	Walsh et al. (1990)
	C	Commercial	Purse-seine	jul/19	1	51	217-279	Walsh et al. (1990)
	C	Commercial	Gillnet	aug/19	1	62	274-396	Walsh et al. (1990)
	C	Commercial	Bottom trawl	aug/19	1	44	285-368	Walsh et al. (1990)
	C	Commercial	Pots and Traps	sep/19	1	14	309-381	Walsh et al. (1990)
	C	Commercial	Gillnet	sep/19	1	74	282-402	Walsh et al. (1990)
	C	Commercial	Gillnet	oct/19	3	114	221-417	Walsh et al. (1990)
	C	Commercial	Bottom trawl	oct/19	1	55	222-298	Walsh et al. (1990)
	C	Commercial	Gillnet	nov/19	2	65	227-321	Walsh et al. (1990)
	C	Commercial	Bottom trawl	nov/19	1	53	250-333	Walsh et al. (1990)
	C	Commercial	Gillnet	dec/19	1	5	260-300	Walsh et al. (1990)
	C	Commercial	Bottom trawl	dec/19	1	53	264-345	Walsh et al. (1990)
	Total			326	15074	139-538		
Gulf of Cadiz (27.9.a.s)	S	BOCADEVA 0711	GoC anchovy DEPM	22/07-02/08/2011	16	560	137-300	WKSPMAT 2008
	S	ECOCADIZ 0813	Acoustic-trawl	02 – 13/08/2013	11	4549	194-332	WKSPMAT 2008
	S	ECOCADIZ 2014-07	Acoustic-trawl	24/07 – 06/08/2014	15	525	167-300	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2014-10	Acoustic-trawl	13 – 31/10/2014	13	363	201-302	WKSPMAT 2008
	S	ECOCADIZ 2015-07	Acoustic-trawl	28/07 – 10/08/2015	13	346	178-315	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2015-10	Acoustic-trawl	10-29/10/2015	14	362	185-335	WKSPMAT 2008
	S	ECOCADIZ 2016-07	Acoustic-trawl	29/07 – 12/08/15	26	1212	114-364	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2016-10	Acoustic-trawl	16/10-03/11/2016	11	476	116-307	WKSPMAT 2008
	S	ECOCADIZ 2017-07	Acoustic-trawl	31/07-13/08/2017	21	832	159-349	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2017-10	Acoustic-trawl	12-24/10/2017	4	151	180-315	WKSPMAT 2008
	S	ECOCADIZ 2018-07	Acoustic-trawl	31/07-13/08/2018	24	970	157-283	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2018-10	Acoustic-trawl	10-29/10/2018	24	835	165-318	WKSPMAT 2008
	S	ECOCADIZ 2019-07	Acoustic-trawl	31/07-13/08/2019	24	739	132-343	WKSPMAT 2008
	S	ECOCADIZ-RE-CLUTAS 2019-10	Acoustic-trawl	09-30/10/2019	18	564	182-323	WKSPMAT 2008

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	S	ECOCADIZ 2020-08	Acoustic-trawl	01-14/08/2020	26	1198	163-388	Walsh et al. (1990)
	S	ECOCADIZ-RE-CLUTAS 2020-10	Acoustic-trawl	02-20/10/2020	18	688	177-396	Walsh et al. (1990)
	C	Commercial	Purse-seine	14/03/2019	1	100	222-309	WKSPMAT 2008
	C	Commercial	Purse-seine	15/05/2019	1	100	283-348	WKSPMAT 2008
	C	Commercial	Purse-seine	27/06/2019	1	100	268-315	WKSPMAT 2008
	C	Commercial	Purse-seine	25/07/2019	1	100	281-366	WKSPMAT 2008
	C	Commercial	Purse-seine	09/09/2020	1	100	257-323	Walsh et al. (1990)
	Total			283	14870	114-396		
Canary Islands (34.1.2)	C	Commercial	Purse-seine	ene-13	1	81	215-287	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-13	1	111	173-219	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-13	1	111	175-223	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-13	1	52	264-331	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-13	1	59	256-331	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-13	1	44	279-339	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-13	1	89	217-295	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-13	1	37	270-352	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-13	1	34	294-381	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-13	1	111	229-339	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-13	1	93	199-273	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-13	1	52	261-346	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-14	1	81	212-270	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-14	2	59	237-383	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-14	1	95	230-285	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-14	1	81	191-283	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-14	1	155	197-361	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-14	1	72	213-290	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-14	1	60	252-313	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-14	1	100	174-299	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-14	1	43	282-337	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-14	1	100	193-254	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-14	1	100	197-235	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-15	1	100	187-272	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-15	1	100	185-269	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-15	1	50	217-350	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-15	1	50	267-336	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-15	1	94	203-274	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-15	1	100	198-282	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-15	1	78	223-288	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-15	1	56	179-326	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-15	1	72	236-292	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-15	1	100	195-264	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-15	1	99	150-260	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-16	1	39	269-348	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-16	1	100	190-277	Holden and Rait (1974)

Study Area	Source	Name	Method	Dates	# samples	n	Size range	Mat. Scale
	C	Commercial	Purse-seine	mar-16	1	100	203-280	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-16	1	88	212-270	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-16	1	93	215-275	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-16	1	65	232-302	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-16	1	42	259-326	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-16	1	74	232-296	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-16	2	94	167-375	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-16	1	109	145-305	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-16	1	106	216-279	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-17	1	87	206-332	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-17	1	104	198-284	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-17	2	231	185-270	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-17	2	154	177-329	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-17	1	64	245-310	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-17	2	111	217-363	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-17	2	139	210-346	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-17	1	62	234-305	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-17	1	53	253-312	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-17	1	102	202-275	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-17	1	84	212-291	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-17	1	100	208-251	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-18	1	69	227-312	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-18	1	98	212-283	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-18	1	100	212-283	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-18	1	53	259-320	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-18	2	98	209-354	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-18	2	109	193-387	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-18	1	89	239-342	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-18	1	45	261-307	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-18	1	79	145-281	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-18	1	44	242-319	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-18	2	174	207-353	Holden and Rait (1974)
	C	Commercial	Purse-seine	dic-18	1	95	153-277	Holden and Rait (1974)
	C	Commercial	Purse-seine	ene-19	1	76	214-293	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-19	1	66	239-296	Holden and Rait (1974)
	C	Commercial	Purse-seine	mar-19	2	103	168-399	Holden and Rait (1974)
	C	Commercial	Purse-seine	abr-19	2	73	132-425	Holden and Rait (1974)
	C	Commercial	Purse-seine	may-19	2	105	226-344	Holden and Rait (1974)
	C	Commercial	Purse-seine	jun-19	1	48	231-337	Holden and Rait (1974)
	C	Commercial	Purse-seine	jul-19	1	67	270-388	Holden and Rait (1974)
	C	Commercial	Purse-seine	ago-19	2	78	258-365	Holden and Rait (1974)
	C	Commercial	Purse-seine	sep-19	2	96	147-342	Holden and Rait (1974)
	C	Commercial	Purse-seine	oct-19	1	36	280-370	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-19	1	57	233-320	Holden and Rait (1974)
	C	Commercial	Purse-seine	feb-20	1	47	164-343	Holden and Rait (1974)
	C	Commercial	Purse-seine	nov-20	2	106	224-386	Holden and Rait (1974)
	Total			97	6931	132-425		

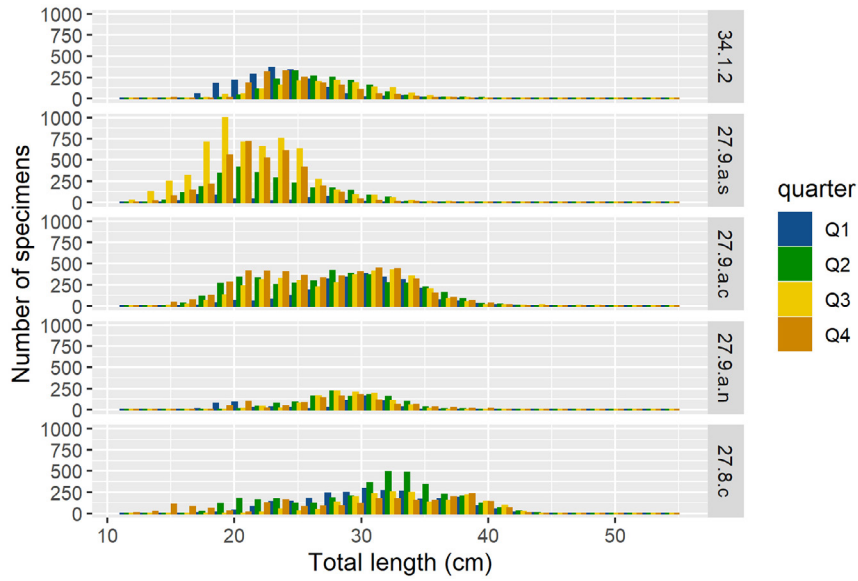


Fig. S1. – Total length distribution of sampled fish per quarter in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.

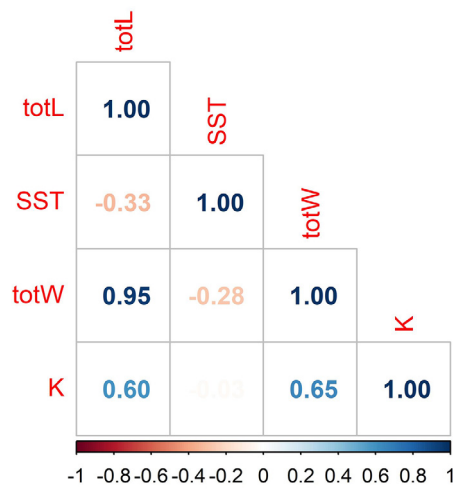


Fig. S2. – Correlation plot among variables. totL, total length (cm); totW, total weight (g); SST, sea surface temperature (°C); and K, Fulton's condition factor.

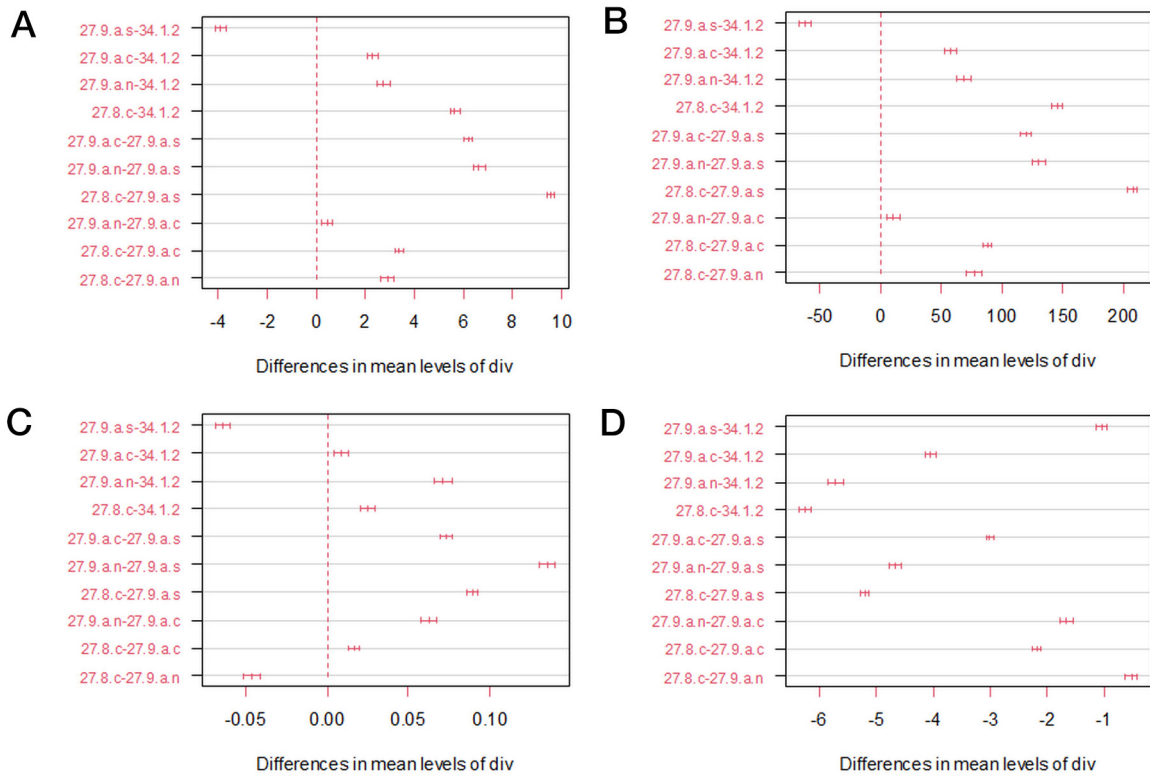


Fig. S3. – Plots of the estimated differences in mean levels of pairwise comparison between study areas. A) total length (cm); B) total weight (g); C) Fulton's condition factor (K); D) sea surface temperature (°C). Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Whiskers, 95% confidence interval. Results are highlighted in red when pairwise comparison is significant.

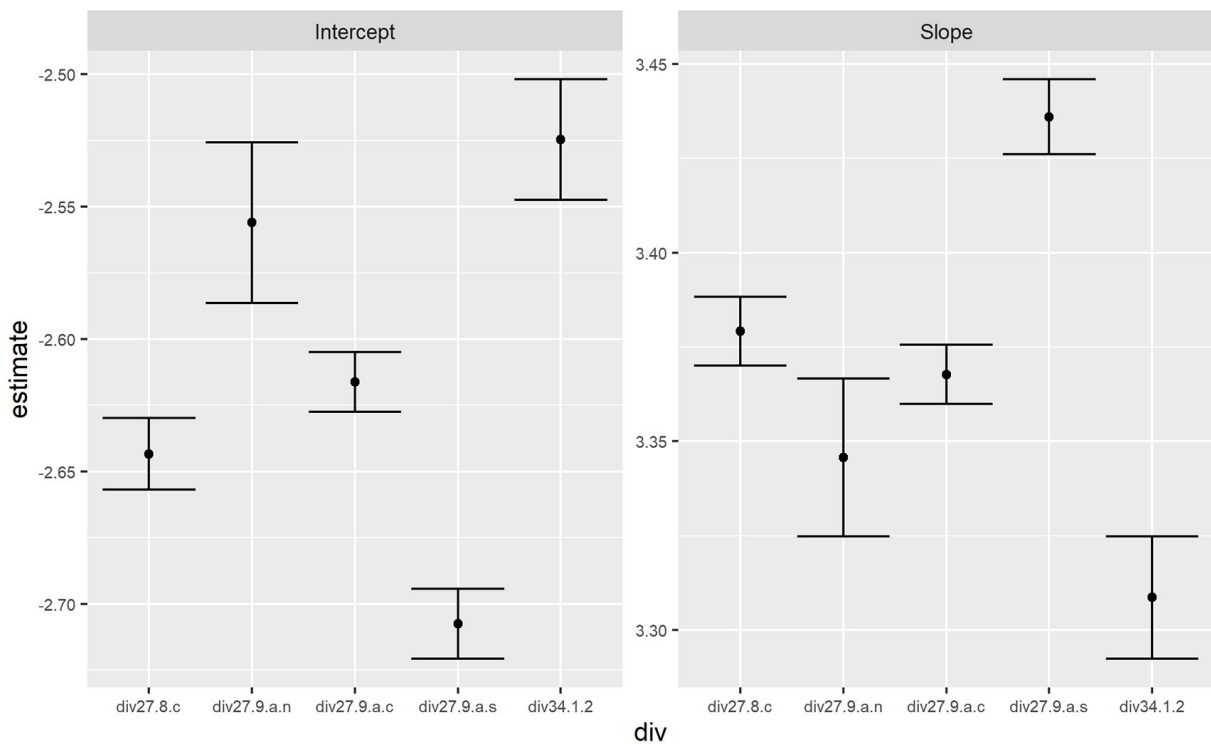


Fig. S4. – Estimations of the intercept and slope of the relationship between total length (cm) and total weight (g) in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Dots represented the mean value; whiskers represented the standard error.

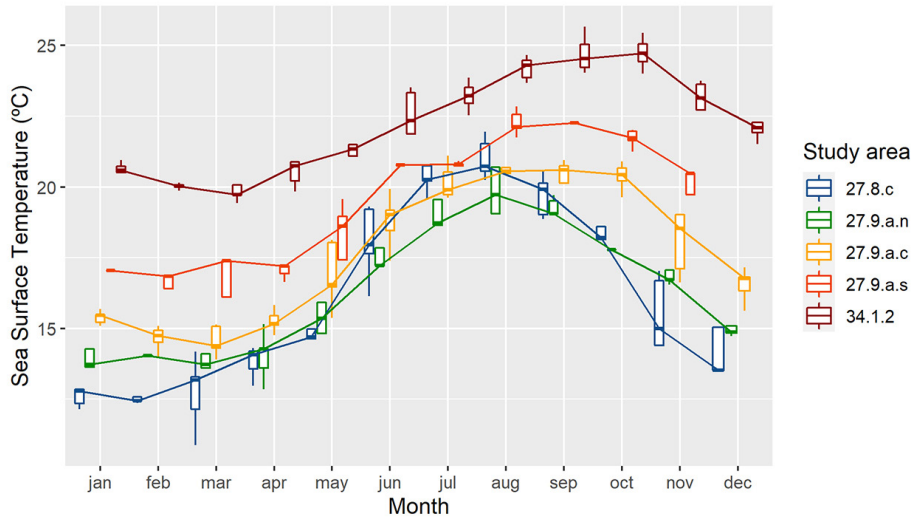


Fig. S5. – Monthly variability of sea surface temperature (SST) in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea. Horizontal line within the boxes represents the median, boxes represent the inter-quartile range (IQR) or distance between the first (25%) and third (75%) quartiles, whiskers represent  $\pm 1.5 * IQR$  and solid line connect the medians.

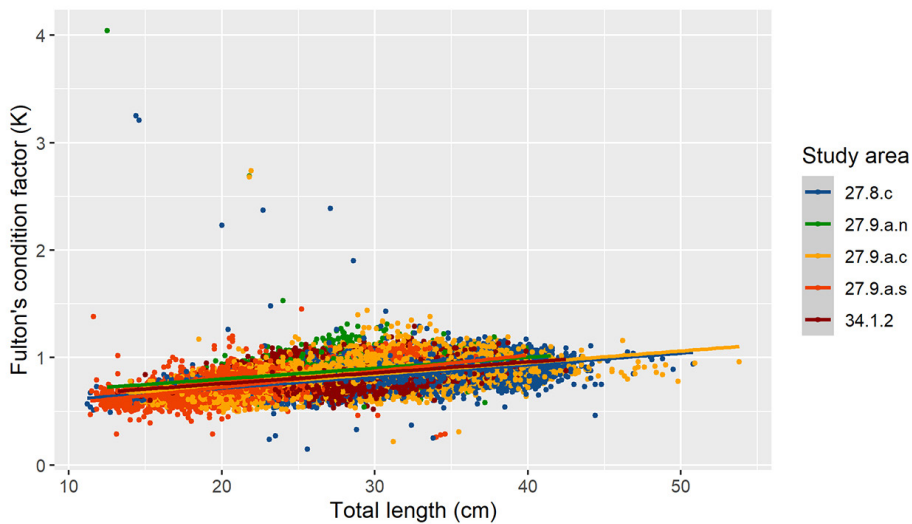


Fig. S6. – Relationship between Fulton's condition factor (K) and Atlantic chub mackerel total length (cm) in each study area. Geographical study areas from south to north are 34.1.2, Canary Islands; 27.9.a.s, Gulf of Cadiz; 27.9.a.c, W Portuguese coast; 27.9.a.n, NW Spanish coast; 27.8.c., Cantabrian Sea.