



Spatial and temporal analysis (2009–2020) of the biological parameters, abundance and distribution of *Trachurus mediterraneus* (Steindachner, 1868) in the Western Mediterranean

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ABSTRACT

Trachurus mediterraneus is captured as by catch by the fishing fleet in the Spanish Mediterranean and usually landed as the global category of *Trachurus* spp., consequently there is a prominent lack of biological data on this species. The knowledge of the spatial and temporal evolution of its distribution, abundance and main biological parameters is essential to achieve a proper management and sustainable exploitation. Data collected in the MEDiterranean International Acoustic Survey (MEDIAS) 2009–2020 time series, carried out in July, has been analyzed to determine the evolution of the main ecological aspects of *T. mediterraneus* in two GFCM management units: Northern Spain (GSA06) and Northern Alboran Sea (GSA01). The results suggest a possible neritic distribution of *T. mediterraneus*, mainly concentrated at depths less than 60 m in GSA01 and up to 105 m in GSA06, as well as the existence of significant differences in abundance and length frequency distributions among GSAs. Furthermore, preliminary results regarding *T. mediterraneus* age and growth seemed to indicate a faster growth during the first two years in GSA01 than in GSA06. In both areas, potential changes in the life history traits of this species were evidenced, with a decreasing trend in the size at first maturity and condition factor over the years. Finally, five persistent distribution areas were located along the study area, highlighting Málaga Bay as a possible recruitment ground. The relevance of this study lies in the growing need for robust and current biological data of intermediate species in the marine food web and it contributes to the global purpose of achieving an integrated management of fishery resources.

1. Introduction

Mediterranean horse mackerel, *Trachurus mediterraneus* (Steindachner, 1868), (Perciformes; Carangidae), is an important fishery resource in the Mediterranean Sea (Turan, 2014), mainly exploited in the coasts of Turkey and Greece (FAO, 2022). This species is a semi-pelagic and oceanodromous carnivorous fish, which forms large banks between 40 and 200 m depth, usually near muddy and sandy bottoms (Ragonese et al., 2002). It is distributed through the Mediterranean, Marmara and Black Sea, and along the northeast Atlantic coast from Morocco to the English Channel (Fischer et al., 1987). Furthermore, its geographical distribution overlaps with that of two very similar species of the same genus: *T. trachurus* and *T. picturatus* (Viette et al., 1997).

T. mediterraneus exhibits gonochoric reproduction and lacks sexual

dimorphism, spawning in the Mediterranean during spring and early summer (Meléndez-Vallejo et al., 2017). Thus, juveniles can be found in the pelagic environment in summer and early autumn (Mir-Arguimbau et al., 2019). In general, it feeds on other fish, in larval or adult stage (especially sardines and anchovies), and small crustaceans (Šantić et al., 2004).

In the Spanish Atlantic area, *T. mediterraneus* is captured by purse seine vessels directed to small and middle-sized pelagic fish, such as sardine (*Sardina pilchardus*), Atlantic mackerel (*Scomber scombrus*), Atlantic horse mackerel (*T. trachurus*), among others (Velasco et al., 2013). However, this species becomes accessory on the Spanish Mediterranean Sea, hence, there is no efficient monitoring of its exploitation. Nonetheless, it plays a relevant role in the trophic web by conditioning the presence, distribution and abundance of other small, medium and

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large pelagic fish, through the transference of energy to higher trophic levels, which are benefitted by feeding on these smaller fish during their migratory routes, and overall contributing to their reproductive success (Vollenweider et al., 2011). Consequently, the fluctuations in the populations of small and medium pelagic fish could modify the population structure of their predators (Cardona et al., 2015).

In the Mediterranean Sea, the first studies related to the biological characteristics, morphology and geographical distribution of *T. mediterraneus* were reported by Stastenenko (1956) in the Black Sea basin. Subsequently, investigations have been conducted on various biological aspects of this species, such as Karlou-Riga (2000), who examined the morphology of the otolith, along with the age and growth parameters in the Saronic Gulf, Greece (eastern Mediterranean), while Viette et al. (1997) and Demirel and Yuksek (2013) studied the reproductive biology of *T. mediterraneus* in the Adriatic and Marmara Sea, respectively, through histological analysis of the gonads. Additionally, Şahin et al. (2009) determined the stock structure and growth parameters of Mediterranean horse mackerel in the eastern Black Sea, and Šantić et al. (2011) evaluated the length-weight relationship and variation of the condition factor in the eastern Adriatic Sea.

However, biological data on *T. mediterraneus* are very limited for the Spanish Mediterranean region (Western Mediterranean). The study of Casaponsa (1993) analyzed the growth and reproduction of *T. mediterraneus* in the Catalan Sea, by direct reading of otoliths and counting of mature oocytes. Later on, Lloris and Moreno (1995) proposed a model of the bathymetric distribution pattern of Mediterranean horse mackerel in the Balearic and Alboran Sea, using data partially collected in commercial fishing boats. The research of Abad et al. (2001) evaluated, through acoustic methods, the biomass of small pelagic fish on the Alboran island shelf, including *T. mediterraneus*.

In particular, length-weight relationships have important applications in fisheries science and population dynamics, such as the conversion between length and weight for biomass estimation, the construction of stock assessment models, and the estimation of fish condition status (Froese, 2006). Furthermore, they allow monitoring seasonal variations in fish growth and comparing morphological and life history traits between species or populations from different habitats and regions (Richter et al., 2000). The indexes or condition factors are widely employed to study the biology of fish, as they provide relevant information related to their physiological state, based on the principle that individuals of a certain length that exhibit a greater weight are in better condition (Craig et al., 2005).

On the other hand, the size at first maturity (L_{50}) describes the average length at which 50 % of the individuals in a population reach the sexual maturity, and is considered one of the most important parameters for fisheries management (Fontoura et al., 2009; Hashiguti et al., 2018). This measure represents an index for assessing the maturity and reproductive cycle of a population as a compensation for variable life growth patterns (Lorenzen, 2016), allowing to establish maximum lengths and minimum catch sizes and, consequently, fishing gears restrictions in terms of the mesh or hook size (Stark, 2012).

Studies related to the age and growth pattern are very useful for determining geographic variations in a population dispersed within a given area, as well as understanding fish biology and ecology, which provides a basis for assessments of population dynamics (King, 2007). These parameters have multiple applications in fisheries management (Sponaugle, 2010), and their estimation through the analysis of otoliths can provide in particular species reliable results (Green et al., 2009). For several marine fish, the otoliths are structures used to differentiate the geographic growth pattern of a species (Campana and Casselman, 1993), because they can be affected by environmental factors such as temperature, salinity, and depth (Gauldie and Crampton, 2005).

Length frequency distributions (LFDs) provide valuable information on population dynamics, allowing to identify problems such as inconsistency in age class strength, slow growth, or excessive mortality (Neumann and Allen, 2007). Additionally, many regulations aimed at

the protection of populations are based on the length, hence their proper application requires an understanding of the size structure (Neumann et al., 2012).

Therefore, the condition of the fish, their length-weight relationship, size at first maturity, age and growth patterns, as well as their length frequency distribution are parameters that contribute to understanding the general state, growth, survival, maturity and reproduction of a species (Richter et al., 2000). To achieve adequate management of economically important populations and to guarantee a sustainable exploitation, monitoring and determining their bio-ecological characteristics is essential (Şahin et al., 2009).

The study of small pelagic fishes through hydroacoustic methods in the Mediterranean Sea began in the Adriatic in the 1950 s. Since 2009, within the frame of the MEDiterranean International Acoustic Survey (MEDIAS), great efforts have been made to refine the methodology and sampling protocols, making it possible to obtain robust spatial and biological data (Leonori et al., 2021). However, there may be uncertainties in the estimates obtained from acoustic data, due to variations in the sampling effort, distribution and distance of the transects, as well as the spatial structure of the fish concentrations (Barra et al., 2021; Tugores et al., 2010).

This scientific research analyzes a time series (2009–2020) of data from the MEDIAS survey carried out in the Spanish Mediterranean Sea during July, with the aim of (i) determining the distribution pattern of *T. mediterraneus*, emphasizing the recruitment areas location and (ii) analyzing the interannual fluctuations of the main biological parameters (LFD, length-weight relationship, condition factor and size at first maturity), testing for differences in the two main geographical subareas established by the GFCM (GSA) that make up the study area: Northern Spain (GSA06) and Northern Alboran Sea (GSA01). Moreover, the growth pattern of *T. mediterraneus* in 2019 was determined based on otolith reading, presenting at this preliminary stage possible differences between GSAs. In addition to contributing to fill in the gaps of knowledge, this study attempts to solve three main questions: Is there a preferential distribution of *T. mediterraneus* according to its size or age? Do their biological parameters present any interannual trend? Are there differences in their growth, maturity, or condition throughout the study area?

2. Material and methods

2.1. Study area and sampling

The MEDIAS survey annually prospects the continental shelf of the Spanish Mediterranean Sea (Fig. 1) from 30 to 200 m depth, between the French border and the Strait of Gibraltar, during June-July. Two Geographical Sub-Areas (GSA) established by the General Fisheries Commission for the Mediterranean (GFCM) in 2009 (GFCM, 2009) are covered, namely Northern Spain (GSA06) and Northern Alboran Sea (GSA01). The survey design was based on parallel transects running perpendicular to the coastline/bathymetry with a separation of 8 nautical miles (NM) in GSA06 (from the French border to Palos Cape) and 4 NM in GSA01 (from Palos Cape to Strait of Gibraltar) (Fig. 1). During each survey, the GSAs were covered one after the other, always starting from GSA06, using the same research vessel and methodology (Rodríguez Castañeda, 2021).

The total abundance and biomass per length class were estimated from the acoustic data recording at 38 kHz frequency. The echograms examination was done based on the identification/verification of hauls. These pelagic hauls were used to (i) identify the fish echotraces, (ii) determine the species composition and proportion and (iii) perform biological measurements (MEDIAS, 2021). The fishing hauls were carried out during the day and their position was identified by geographical coordinates (i.e., latitude and longitude).

The total catch was sorted by species, determining the total weight and number of individuals. A random selection of *Trachurus*

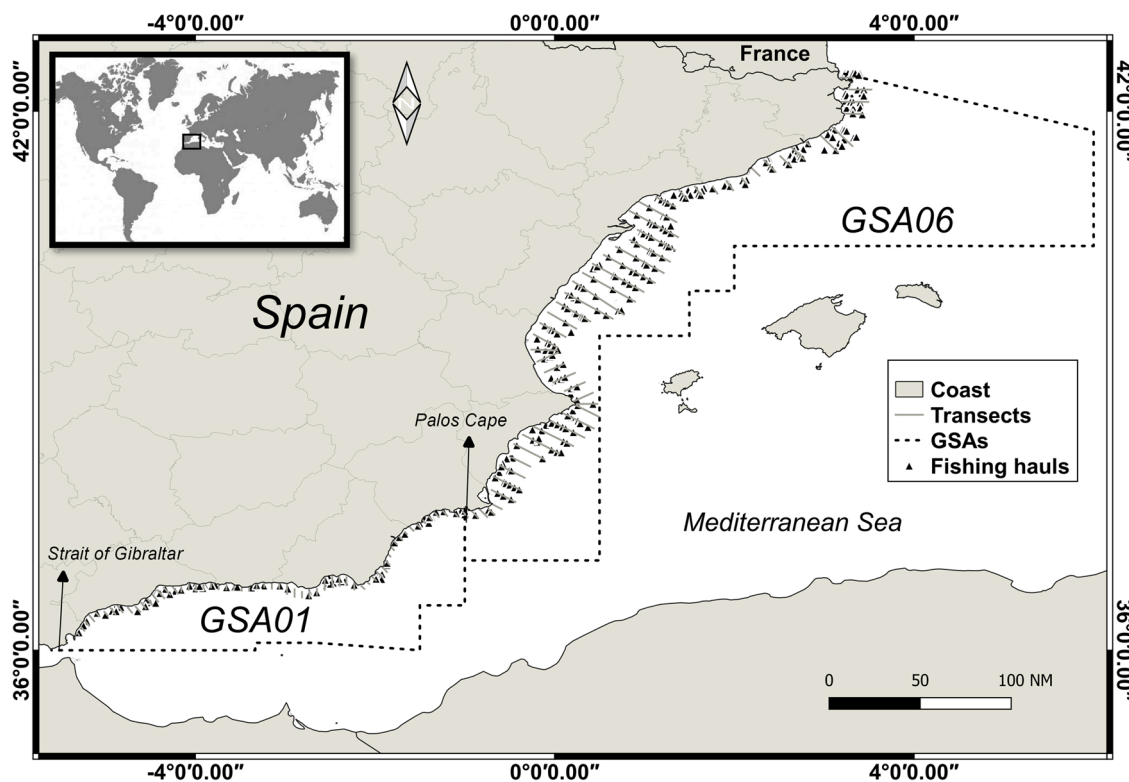


Fig. 1. Map of the study area: Spanish Mediterranean Sea, showing the GFCM subareas GSA06 (Northern Spain) and GSA01 (Northern Alboran Sea), the systematic sampling survey design in the MEDiterranean International Acoustic Survey based on parallel transects and fishing haul locations for the analyzed time series (2009–2020).

mediterraneus individuals was measured to the nearest 0.5 cm (random sampling) to determine the length frequency distribution (LFD) of each haul. Afterwards, subsamples of five individuals were selected for each 0.5 cm group (stratified sampling by sizes) for the biological analysis, estimating the total length in mm, total individual wet weight in grams, sex, and maturity stage following the recommendations of Carrillo (1978) and ICES (2008). In addition, otoliths were extracted in 2019 for the age determination of the individuals.

2.2. Acoustic data processing and abundance estimation

Echoview software Pty Ltd (formerly Myriax Pty Ltd) was used for acoustic data analysis. The result of the echo integration, the nautical-area scattering coefficient ($m^2 \text{ mile}^{-2}$; s_A ; MacLennan et al., 2002), was divided into species using the species composition in the pelagic trawl catches and applying the Nakken and Dommasnes (1975) method for multiple species, but using backscattering cross section by length class rather than mean backscattering cross section (see Tugores et al., 2010 for more details). Finally, the target strength equation and the length-weight relationship were applied to estimate the *T. mediterraneus* abundance and biomass, respectively. The estimation of indexes of abundance in number of individuals (millions) and biomass in metric tons (t) for *T. mediterraneus* in the pelagic community from 2009 to 2020 was calculated based on the acoustic records detected at 38 kHz frequency, by GSA and year.

Additionally, the annual spatial distribution of the *T. mediterraneus* biomass in kilogram (Kg) per EDSU was mapped using the QGIS 3.10 software. To detect the *T. mediterraneus* persistent areas, the average biomass map was calculated for the time series (2009–2020). An interpolation tool (Inverse Distance Weighting) was used to convert the point shapefile to raster, using a grid cell (2×2 EDSU). The mean biomass was estimated with the “cell statistics” tool (Rodríguez-Castañeda et al., 2021).

2.3. Estimation of biological parameters and data analysis

To detect possible differences in the *T. mediterraneus* LFD between the GSAs and years, a two-sample Kolmogorov-Smirnov test (K-S test) was performed (Neumann and Allen, 2007). Given that more than two years were considered in the analysis, the *p*-values of each comparison were adjusted for an increasing experimental error rate due to multiple comparisons (Ogle, 2016).

The length-weight relationship of *T. mediterraneus* in the Spanish Mediterranean was estimated for the 2009–2020 time series by GSA (except for 2009 and 2011 when GSA01 was not totally covered). This was achieved through the following power function:

$$W = \alpha L^\beta \tag{1}$$

Where: *W* represents the weight in grams, *L* the total length in cm, α and β are the constants of the power model.

Afterwards, the logarithm was applied to Eq. 1, to allow the errors to be additive and stabilize the variations in the model, which facilitated the execution of linear regression methods and the estimation of parameters.

$$\ln W = \ln \alpha + \beta \ln L \tag{2}$$

Where: β is the slope and $\ln \alpha$ the intercept.

To determine possible differences in the length-weight relationships between GSAs, a two-way analysis of variance (ANOVA II) was performed, for which the assumptions of normality and homogeneity of variances among groups were verified through the graphical representation of the model residuals.

The growth type of *T. mediterraneus* was established by applying a *t*-Student test, considering the allometry coefficient to verify if the estimated growth corresponded to the isometric type ($\beta = 3$). When $\beta > 3$, the individuals of larger size increase their weight in a greater

proportion compared to their length, presenting a positive allometric growth. On the contrary, when $\beta < 3$, individuals increase their relative length more than their weight (Froese, 2006).

To evaluate the state or condition of *T. mediterraneus* and assess the well-being of the population in relation to its nutritional state, the methodology proposed by Le Cren (1951) was applied. In this regard, the values of the condition factor (Kn) greater than 1 denote a better condition. The parameter K was calculated with data from 2009–2020, however, data was not available for 2009 and 2011 in the GSA01. The following equation was used:

$$Kn = \frac{W}{\alpha * L^\beta} * 100 \quad (3)$$

Where: *W* represents the weight in grams, *L* the length in cm, α and β are the constants of the power model (see Eqs. 1 and 2).

Additionally, the logarithm was applied to simplify the analysis and perform linear models. A generalized additive model (GAM) was fitted to detect possible differences in the condition factor between GSAs and years (Potts and Rose, 2018). A Spearman rank correlation analysis was also applied to examine the tendency in the wellbeing of the fish over the years.

The sex ratio of *T. mediterraneus* in the Spanish Mediterranean was calculated for the time series (2012–2020) and each year, considering the GSA of origin. Furthermore, a Chi-square test (X^2) was applied to establish if there were significant differences in the sex ratio (Zar, 1996), based on Fisher's hypothesis, which indicates that there is one female per male (1 F:1 M).

The maturity stage, macroscopically assigned to each specimen, was used to calculate the size at first maturity (L_{50}) of the two sexes combined for the time series (2012–2019) and each GSA. The period in which the individuals were collected coincided with the spawning season of the species, which occurs between April and September. The estimation of the L_{50} and the maturity range (length range between L_{75} and L_{25} ; $MR = L_{75} - L_{25}$, where L_{75} and L_{25} are the lengths at which 75% and 25% of the individuals are mature, respectively) (Follesa et al., 2019) was done obtaining the percentage of active or mature individuals (Carrillo, 1978) by size class every 1 cm, and subsequently these values were adjusted to the following logistic model:

$$p = \frac{100}{1 + e^{(\alpha + \beta)L}} \quad (4)$$

Where: *p* represents the percentage of mature specimens and *L* the total length in cm, while α and β are the constants.

Additionally, the sample size range (SR) was reported according to the minimum and maximum total lengths of the individuals analyzed to estimate the L_{50} .

To establish whether the adjusted logistic regressions of GSA01 and GSA06 differed significantly from each other, a generalized linear model with binomial distribution was executed. The differentiation in the slope of the models was determined by the Chi-square contrast test when the variable that represented the interaction between the GSA and total length factors was detected as a significant term in the model. Additionally, a Pearson's correlation analysis was performed to describe the association between the L_{50} estimates and the years of study.

Following the recommendations of ICES (2018), Carbonara and Follesa (2019), Vitale et al. (2019), and Villamor et al. (2020), the age was estimated from the analysis of otoliths extracted from the specimens captured during the 2019 survey. On the other hand, the growth was described according to the equation of Von Bertalanffy (1938):

$$l(t) = L_\infty [1 - e^{-k(t-t_0)}] \quad (5)$$

Where: $l(t)$ represents the average length at the age *t*, L_∞ is the asymptotic average maximum length, *k* is the growth coefficient or the exponential rate at which $l(t)$ reaches L_∞ , and t_0 is the theoretical age at which $l(t)$ would correspond to the age zero.

The modified method of Wetherall (1986) was applied for the calculation of L_∞ and *k*. Due to the lack of homoscedasticity in the length between age groups, a generalized least squares (GLS) analysis was performed to assess possible differences in the length of *T. mediterraneus* between GSAs by age. Afterwards, the differences were interpreted with a Tukey post-hoc analysis.

The global growth curve estimated in this research, without considering GSAs, was compared with those published by other authors (Carrillo, 1978). The criteria employed to compare the growth curves was the length-based index of growth performance (Eq. 6) (Munro and Pauly, 1983).

$$\phi' = \log(k) + 2\log(L_\infty) \quad (6)$$

Where: ϕ' , referred as phi-prime, corresponds to the average growth performance index, while *k* is the growth coefficient and L_∞ the asymptotic average maximum length calculated previously (see Eq. 5).

The coefficient of variation (CV%) was also estimated by analyzing the relationship between the standard deviation and ϕ' , considering not to exceed a value of 4 % in order to assume that the results were statistically similar.

All the statistical analyses were executed using the R package, version 4.0.3 (R Core Team, 2022). The *p*-values obtained from the statistical tests were calculated using a 95 % confidence interval, thus, the results were considered statistically significant only when $p < 0.05$.

3. Results

3.1. Abundance, biomass and density

The abundance of *Trachurus mediterraneus* in the Spanish Mediterranean exhibited oscillations during the study period (2009–2020), reaching the highest level in 2017 for GSA01 with 160 million individuals. The lowest value (9 million individuals) for this GSA was recorded in 2009 when the area was not entirely covered. For GSA06, the highest value (155 million individuals) was recorded in 2020 and the lowest (27 million individuals) in 2016 (Table 1).

Although the maximum values fluctuated between GSAs for the time series studied, the density (number of individuals or t/NM^2) was higher in GSA01 compared to GSA06, which would indicate a preferential distribution of the resource in GSA01. On the other hand, the influence of large-sized individuals on the biomass values was reflected in GSA06, especially in 2014 and 2015 when the estimated abundance was similar between the two GSAs, but the biomass estimated in GSA06 almost doubled that estimated in GSA01.

3.2. Spatial distribution

T. mediterraneus exhibited a patched distribution in the Spanish Mediterranean shelf during the MEDIAS survey, highlighting five hot-spots (Fig. 2), two located in GSA06 and three in GSA01. In GSA06, the areas of greatest abundance were located off the coast of Barcelona and Alicante. In contrast, GSA01 demonstrated the highest values of abundance in the coasts of Murcia, Almería and, to a lesser extent, Málaga. In areas where the continental shelf reaches its greatest extent (up to 33 nautical miles wide), from Tarragona to Valencia, *T. mediterraneus* distribution was restricted to shallow waters, suggesting a potential neritic behavior. In general, *T. mediterraneus* appeared more frequently between 30 and 60 m depth, given that 81 % of the catches for this species were concentrated in this bathymetric layer. At depths greater than 105 m, very few individuals were found.

3.3. Length frequency distribution (LFD)

For the studied time series (2009–2020), the length frequency distribution of *T. mediterraneus* obtained in the MEDIAS survey ranged from

Table 1

Interannual variation of the abundance (millions of individuals), biomass (metric tons), density of individuals (thousands of individuals per square nautical mile) and density of the biomass (tons per square nautical miles) of *Trachurus mediterraneus* in the GSA06 and GSA01 zones, during the 2009–2020 period. Data from the Mediterranean International Acoustic Survey.

Year	Abundance (millions)		Biomass (t)		Density (thousands/NM ²)		Density (t/NM ²)	
	GSA06	GSA01	GSA06	GSA01	GSA06	GSA01	GSA06	GSA01
2009	128	5 [‡]	11,909	308 [‡]	21	5	2	0
2010	58	31	7178	2339	9	35	1	3
2011	44	28 [‡]	5156	3910 [‡]	7	31	1	4
2012	28	76	3513	11,199	4	85	1	12
2013	70	94	6028	8072	11	105	1	9
2014	143	144	8530	6157	23	160	1	7
2015	31	32	1601	2309	5	35	0	3
2016	27	98	896	3823	4	109	0	4
2017	65	160	2143	3675	11	178	0	4
2018	98	30	9532	1190	16	33	2	1
2019	102	95	5455	3389	16	106	1	4
2020	155	109	3591	5411	25	121	1	6

[‡]Biomass estimate by applying the GSA06 L-W relationship.

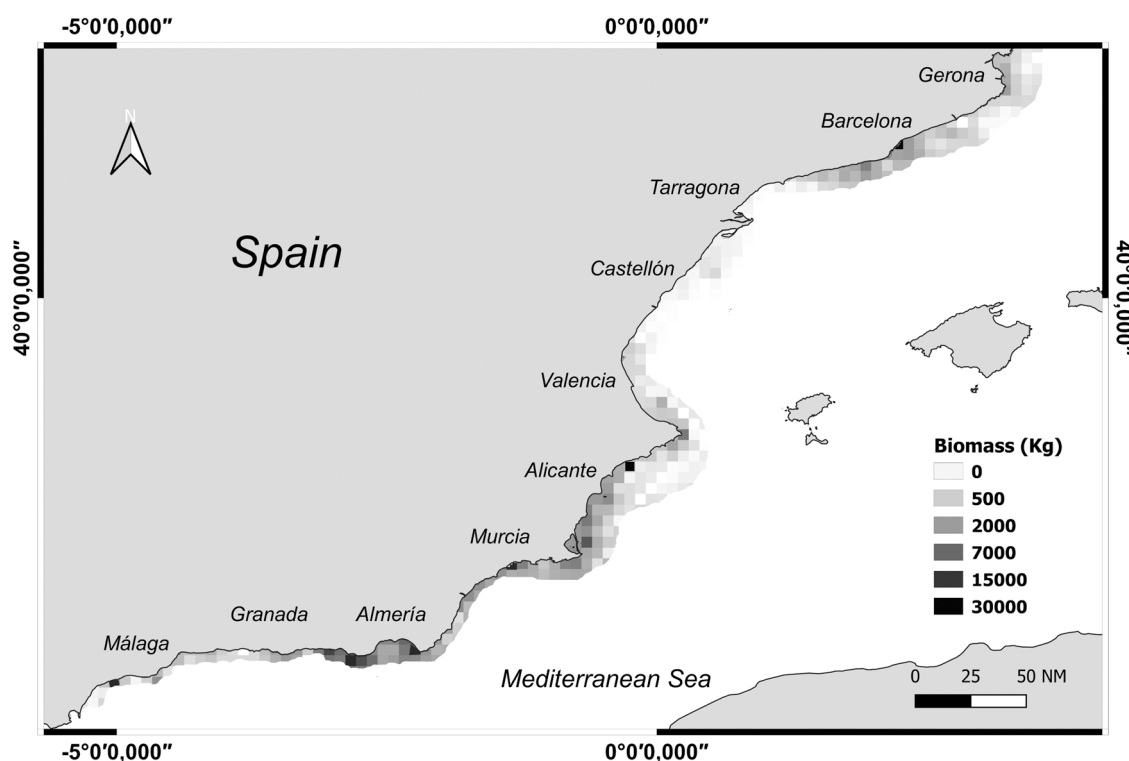


Fig. 2. Average time series (2009–2020) distribution map of the biomass in Kg of *Trachurus mediterraneus* on the Spanish Mediterranean Sea shelf during the Mediterranean International Acoustic Survey. The light coloration reflects the absence of fish and the black color the maximum biomass.

4 to 42.5 cm in total length. The K-S test for all the possible combinations of GSAs and years indicated that the LFDs differed significantly from each other ($p < 0.05$). The species was significantly larger in GSA01, and the contrasted modes of this area were between 1 and 1.5 cm above those of GSA06.

The differences in the length structure per year and GSAs can be observed in Fig. 3, evidencing a higher density of adult organisms in GSA06 and a greater presence of juveniles in GSA01. The early recruitment strength, understood as the abundance of the cohort before the first annual class, was pronounced for GSA01 during 2017 and, to a lesser extent in 2010, 2011 and 2012. These juveniles were found in the fishing hauls carried out in or near the Málaga Bay in GSA01. On the other hand, a slightly weaker recruitment was observed in GSA06 during 2011, 2012, 2013 and 2014, while for the remaining years it was not

evident.

3.4. Length-weight relationship

The length-weight relationship and condition factor of *T. mediterraneus* were estimated from the measurement of 7415 specimens. The data adjustment of the length-weight relationship to the power function for *T. mediterraneus* in the Spanish Mediterranean is represented in Table 2. *T. mediterraneus* in GSA06 presented a negative allometric growth in most of the years, except for 2013, 2017 and 2018. Similarly, its growth was negative allometric in GSA01, except for 2012, in which an isometric growth was observed. Nevertheless, no significant differences were detected between GSAs ($p < 0.05$).

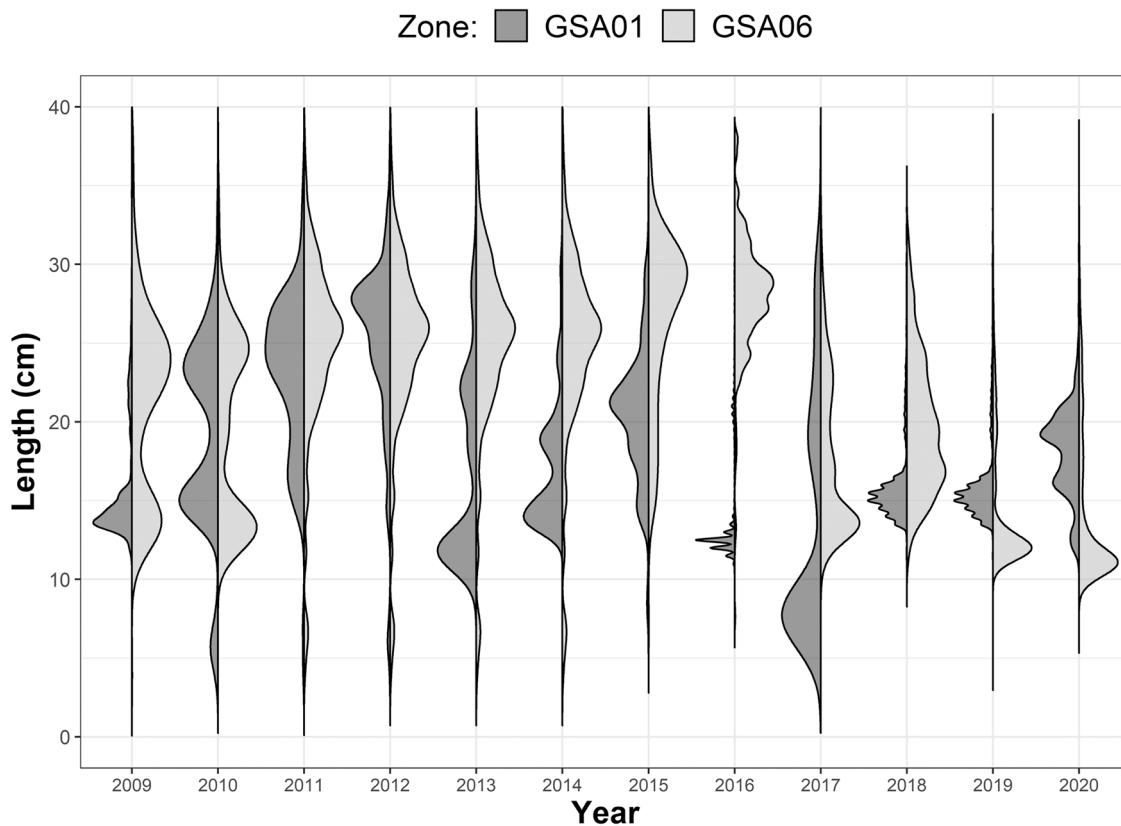


Fig. 3. Probability density function of *Trachurus mediterraneus* total length by GSA and year during the MEDiterranean International Acoustic Survey.

Table 2

Coefficients α and β , coefficient of determination (R^2), and associated P -values from the t -Student test for the length-weight relationship (length in cm and weight in g) of *Trachurus mediterraneus* by GSAs units during the 2009–2020 period. Data from the MEDiterranean International Acoustic Survey. n : sample size.

Year	GSA06					GSA01				
	α	β	n	R^2	P -value	α	β	n	R^2	P -value
2009	0.010	2.929	306	0.990	< 0.05*	–	–	–	–	–
2010	0.008	2.984	494	0.973	> 0.05	0.014	2.822	82	0.965	< 0.05*
2011	0.009	2.948	449	0.995	< 0.05*	–	–	–	–	–
2012	0.009	2.964	325	0.974	< 0.05*	0.007	3.030	143	0.982	> 0.05
2013	0.008	3.000	397	0.984	> 0.05	0.010	2.923	328	0.987	< 0.05*
2014	0.009	2.948	329	0.985	< 0.05*	0.012	2.862	472	0.952	< 0.05*
2015	0.011	2.887	166	0.975	< 0.05*	0.013	2.824	340	0.978	< 0.05*
2016	0.010	2.913	196	0.996	< 0.05*	0.010	2.904	536	0.994	< 0.05*
2017	0.007	3.019	483	0.994	> 0.05	0.009	2.933	185	0.997	< 0.05*
2018	0.007	3.040	480	0.980	> 0.05	0.012	2.876	349	0.989	< 0.05*
2019	0.009	2.937	613	0.993	< 0.05*	0.010	2.916	427	0.986	< 0.05*
2020	0.009	2.933	831	0.994	< 0.05*	0.012	2.841	239	0.984	< 0.05*

* Significant.

3.5. Condition factor

The average values of the condition factor (K_n) of *T. mediterraneus* ranged between 0.93 ± 0.06 (2020 in GSA06) and 1.09 ± 0.08 (2012 in GSA01), presenting significant differences ($p < 0.05$) in its annual condition state (Fig. 4) and a significant decline over the years ($\rho = -0.34$, $p < 0.05$). Although a slightly better condition was graphically evidenced in GSA01 (1.02 ± 0.08) compared to GSA06 (0.97 ± 0.03), the K_n did not differ between GSAs ($p > 0.05$).

3.6. Sex-ratio

To establish the sex ratio of the species, 5348 specimens were considered. Considering the total set of *T. mediterraneus* data, a higher

proportion of males were observed throughout the studied time series. Most of the sex ratios were similar during the study period and GSAs, however, a greater presence of females was recorded for GSA06 in 2013 (F:M = 1.26:1, $p < 0.05$) and 2016 (F:M = 1.88:1, $p < 0.05$), as well as a 1:1 ratio in 2012, 2015 and 2018. On the other hand, GSA01 only evidenced a greater presence of females in 2015 (F:M = 1.90:1, $p < 0.05$), while a 1:1 ratio was estimated in 2012, 2013, 2014 and 2017 (Table 3).

3.7. Size at first maturity (L_{50})

For the determination of the L_{50} of *T. mediterraneus*, 4426 specimens of combined sexes were examined. The values of the L_{50} for both sexes combined ranged between 14.7 cm (GSA06 in 2017) and 17.5 cm (GSA01 in 2014). The best model could explain 85.3 % of the deviance

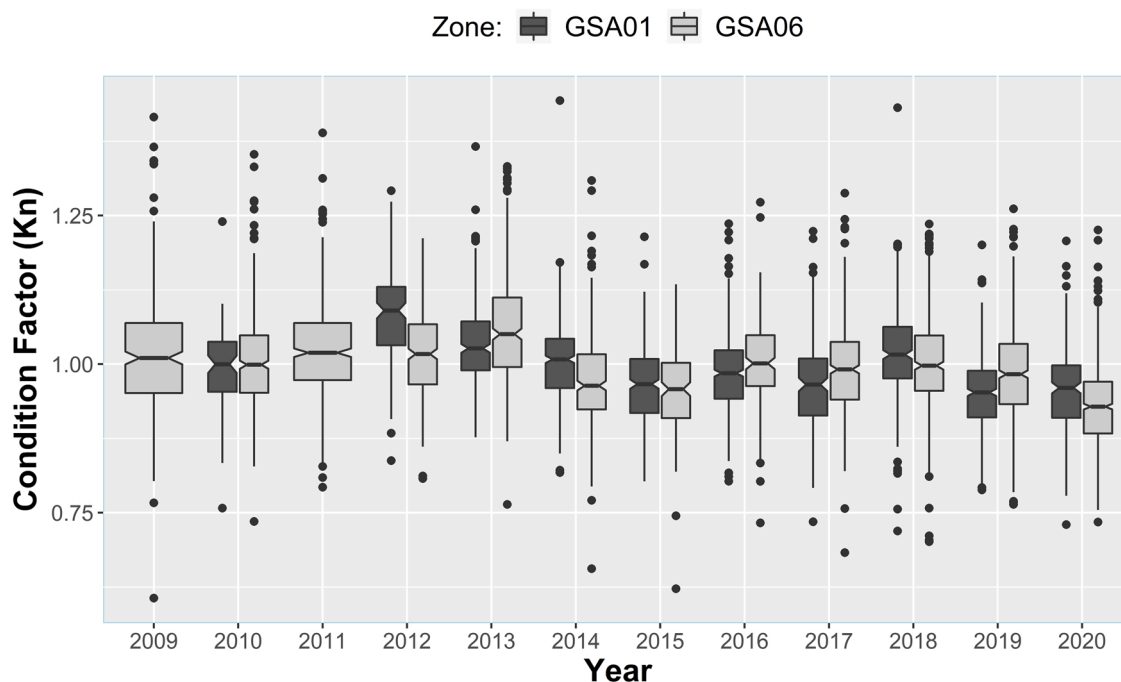


Fig. 4. Condition factor of *Trachurus mediterraneus* per year and GSA from data obtained in the MEDiterranean International Acoustic Survey.

Table 3

Variation in the sex ratio of *Trachurus mediterraneus* during the study period and GSAs from data obtained in the MEDiterranean International Acoustic Survey. M: Males; F: Females. X^2 : Chi-square statistic and associated p -value.

Year	GSA06			GSA01		
	F:M	X^2	P -value	F:M	X^2	P -value
2012	0.80:1	3.30	> 0.05	0.98:1	0.01	> 0.05
2013	1.26:1	4.10	< 0.05*	0.81:1	2.48	> 0.05
2014	0.57:1	16.21	< 0.05*	1.06:1	0.30	> 0.05
2015	0.87:1	0.38	> 0.05	1.90:1	28.29	< 0.05*
2016	1.88:1	16.24	< 0.05*	0.65:1	13.85	< 0.05*
2017	0.75:1	7.51	< 0.05*	0.82:1	1.09	> 0.05
2018	0.83:1	3.45	> 0.05	0.60:1	19.50	< 0.05*
2019	0.63:1	23.31	< 0.05*	0.67:1	31.00	< 0.05*
2020	0.64:1	32.00	< 0.05*	0.63:1	11.97	< 0.05*

* Significant

for 2017 in the GSA01 (Table 4), determining the highest L_{50} average with 16.4 cm. The highest deviance percentage for GSA06 was reported in 2017 (80.5 %), suggesting a L_{50} of 15.7 cm. The L_{50} measures per GSA for each year studied are represented in Fig. 5, in which significant differences ($p < 0.05$) were determined for 2016, 2017 and 2019, indicating that the specimens in GSA01 matured at a larger size compared with GSA06. Moreover, a significant negative relationship

($r = -0.74$; $p < 0.05$) was recorded between the years analyzed and the L_{50} estimates.

3.8. Age and growth

The age reading of 1022 pairs of otoliths collected in the MEDIAS 2019 survey showed that the population of *T. mediterraneus* is made up mainly of eight age classes, from age 0–7. The first annual classes (0, 1 and 2) presented a slightly overlapping LFD, while the overlapping of the LFD was more evident from age class 3 onwards, indicating a slowdown in growth. The largest specimen sampled came from the GSA06 with a total length of 42.5 cm that corresponded to an age of 9 years, while the largest specimen in GSA01 was only 34 cm in total length with 7 years. One-year old individuals presented total lengths between 11 and 18 cm, while those belonging to the age class 2 presented total lengths between 16 and 23 cm. Given the results of the L_{50} estimation in the present study, it can be inferred that *T. mediterraneus* reaches the sexual maturity by the second year of its life in the study area.

The global growth parameters, considering the data from both GSAs, were 44.45 cm for the L_{∞} , a growth coefficient (k) of 0.18 year^{-1} and a t_0 equal to -0.98 years. Significant differences in the length at age of *T. mediterraneus* were detected between GSAs in the age classes 1 and 2 ($p < 0.05$), evidencing larger specimens at ages 1 and 2 in GSA01 in

Table 4

Size at first maturity (L_{50}) of *Trachurus mediterraneus* in the Spanish Mediterranean by year and GSA zones, with data obtained in the MEDiterranean International Acoustic Survey. D^2 represents the percentage of deviance explained by the model, SE the relative standard error, MR the maturity range and SR the sample size range.

Year	GSA06							GSA01						
	Length (cm)	D^2 (%)	n	SE_{50}	MR	SE	SR	Length (cm)	D^2 (%)	n	SE_{50}	MR	SE	SR
2012	16.8	53.8	266	0.53	3.6	0.2	10–35	16.8	80.8	126	0.07	2.6	0.3	5–37
2013	17.1	63.7	316	0.23	1.9	0.2	10–37	17.1	72.6	238	0.17	1.6	0.3	10–35
2014	17.7	74.6	245	0.13	1.8	0.1	5–38	17.7	57.6	398	0.18	2.5	0.1	10.39
2015	16.3	77.1	159	0.14	1.1	0.6	10–37	16.3	63.1	293	0.19	2.3	0.3	11–33
2016	15.1	75.7	174	0.15	1.7	0.4	11–39	15.1	78.7	289	0.13	1.6	0.2	10–37
2017	15.8	80.5	468	0.09	1.2	0.1	8–34	15.8	85.3	158	0.06	1.4	0.2	7–35
2018	13.8	33.3	404	0.21	3.8	0.1	10–35	13.8	60.2	312	0.28	2.0	0.2	9–35
2019	14.7	62.9	493	0.39	3.4	0.1	7–42	14.7	84.5	359	0.06	1.5	0.3	5–34

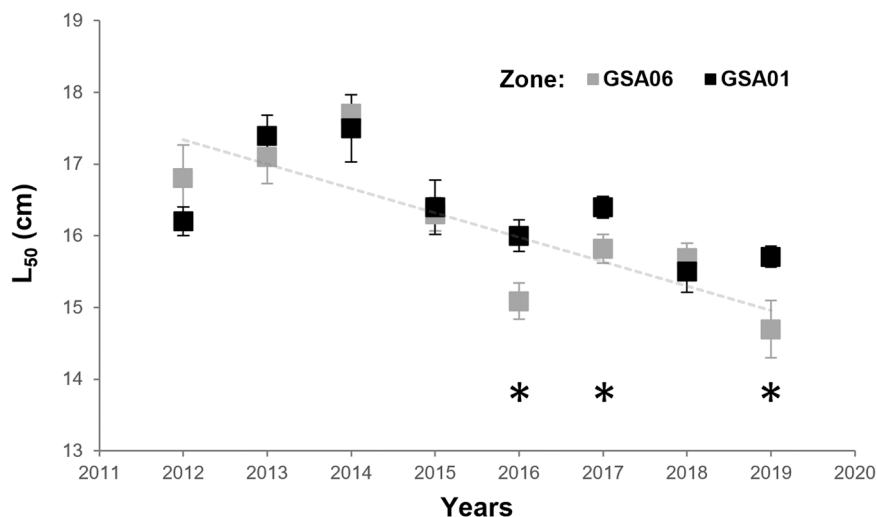


Fig. 5. Interannual evolution of the size at first maturity (L_{50}) of *Trachurus mediterraneus* in GSA01 and GSA06. The asterisks (*) denote significant differences ($p < 0.05$) in the L_{50} values between the GSAs. Data from the MEDiterranean International Acoustic Survey.

comparison to GSA06 (Fig. 6). On the other hand, the growth parameters showed small differences, with estimates for the GSA06 of 46.38 cm for the L_{∞} , a k of 0.17 year^{-1} and a t_0 of -1.02 years. For GSA01, a L_{∞} of 38.82 cm was determined, as well as a k of 0.23 year^{-1} and a t_0 of -0.90 years, which indicates a faster growth in GSA01 than in GSA06. The phi-prime (ϕ') was 2.56 in GSA06 and 2.54 in GSA01.

4. Discussion

This study identified the main distribution areas of *Trachurus mediterraneus* in the Spanish Mediterranean Sea during July, appearing to show the aggregation of juveniles mainly in GSA01 (Málaga). Furthermore, the results could suggest some changes in the life history traits of the species, as well as the possible existence of different stocks in the GSAs studied since the population dynamics, inter-annual trends in abundance and biomass, biological parameters and demographic structure seem to differ between them.

The interannual variations of the abundance and biomass of *T. mediterraneus* reported in this study may be associated with the characteristic oscillations of small and middle-sized pelagic species subjected to fishing pressure, describing interannual increases and decreases (Fréon et al., 2003). One of the characteristics of small and medium-sized pelagic fish is the high variability in the size of their

populations, which is mainly attributed to environmental fluctuations on different scales of space and time (Cury et al., 2000). Additionally, the current exploitation of stocks and climate change play important roles in these variations (Bowler et al., 2017). Our results indicate an inverse relationship between the abundance and biomass of *T. mediterraneus* influenced by the presence of small-sized specimens, which in certain years, such as 2017 in GSA01, contributed little to the total biomass, despite being very abundant.

The spatial analysis of the biomass showed a patchy distribution of the species, exhibiting preferential areas of distribution. In GSA01, these areas were located in the coasts of Málaga, Almería and Murcia (GSA01), which could be related to their high primary and secondary productivity caused by the influence of the water input from the Atlantic and the upwelling phenomenon in the area (Gómez, 2015). Moreover, Málaga Bay seemed to concentrate the highest abundance of juveniles recorded in the study area, which coincides with the study of Marina et al. (2015), who determined that the coasts of Málaga were spawning and nursery areas for several species, including *T. mediterraneus*. Similarly, some of the aspects that could promote the presence of this species in GSA06 are the presence of the Illes Columbretes Natural Reserve, the Ebro River discharges, and the presence of underwater canyons that offer shelter to fish larvae and juveniles and act as sources of nutrients through resuspension processes, contributing to the increase in the diversity and food

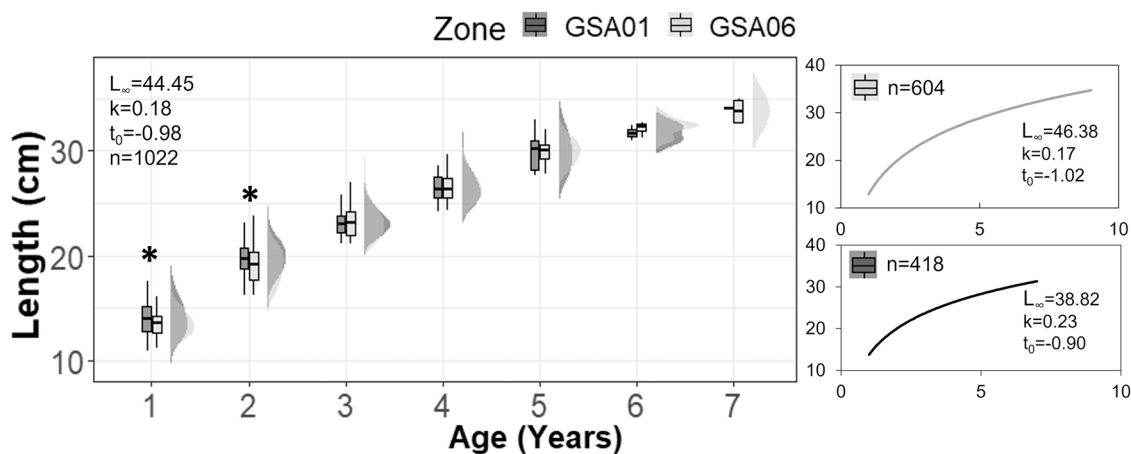


Fig. 6. In the left panel, probability density function of *Trachurus mediterraneus* total length per age class and GSA, and growth parameters for both areas combined. In the right panels, the von Bertalanffy adjusted growth equation for *Trachurus mediterraneus* in GSA06 and GSA01. The asterisks (*) denote significant differences ($p < 0.05$) in the length between the GSAs. Data from the MEDiterranean International Acoustic Survey.

availability (Carrió et al., 2014).

The neritic distribution of *T. mediterraneus* highlighted in the results, restricted mainly to the first 105 m depth, is in accordance with the work of Lloris and Moreno (1995), who described the distribution of *T. mediterraneus* by depth bands in the Spanish Mediterranean Sea, indicating that the species exhibited a neritic habitat prone to frequent environmental fluctuations and with less association with other individuals of the same genus. Moreover, these authors mention that the depth range of this species does not exceed 250 m. On the other hand, it has been reported that the thermocline can be located between 20 and 40 m depth during summer, favoring the presence of Mediterranean horse mackerel near its optimum temperature (17 ± 4 °C) below the layer of warm water. The superficial stratification and light availability in the water column also benefit the vertical migrations of plankton communities, which provide matter and energy to the higher trophic levels (Baro et al., 2012). In particular, at these depths, a large number of fish larvae has also been recorded off the coast of Málaga (Marina et al., 2015; Ventero et al., 2021), which are part of the diet of *T. mediterraneus* and, thus, can promote its occurrence.

The LFD results of the current study ranged from 4 to 42.5 cm and differ with those obtained by Tzikas et al. (2007), who indicated that 90 % of the fish were between 16.5 and 24 cm of total length in the northern Aegean Sea. This discrepancy might be due to the environmental differences between the Western and Eastern Mediterranean.

The sex ratio estimated in this study showed that the population of *T. mediterraneus* in the Spanish Mediterranean was dominated by males. These results are different from the reported by Meléndez-Vallejo et al. (2017), who determined that females dominated over males in the Alboran, and Carrillo (1978), who obtained a 1:1 ratio. In most fish, the sex ratio tends to be 1:1 between males and females, although it can vary from year to year within the same population, with the size groups and reproduction period (Franco, 1992).

The sampling month for this research corresponds to July, which falls in the spawning period of the species. Therefore, the variation in the proportion of females and males could be attributed to physiological factors or reproductive behavior during spawning (Jordán, 1976). Furthermore, in some cases males may be more vulnerable to the fishing gear than females (Cuscó, 2015). In species of the same genus, such as *T. trachurus*, a grouping occurs before spawning, that leads to an heterogeneous distribution of the sexual stages in the catches, which requires a greater number of samplings (Abaunza et al., 2003).

The L_{50} value estimated in this work for the Spanish Mediterranean is similar to the obtained by Samia et al. (2002) in northern Tunisia, Africa, with 15.7 cm. However, the results of this parameter differ from those reported by Karlou-Riga (1995), who recorded a superior mean of maturation length for *T. mediterraneus* in the Saronic Gulf, Greece, with 20.0 cm. In this case, the precision of the model is determined by the set of mature and immature individuals analyzed during the study, consequently, the lack of inactive specimens that are described as indeterminate increases the bias (Leal et al., 2013). Moreover, a large part of the scientific community does not cite the percentage of deviance obtained, which hinders making comparisons regarding the precision of the model.

The decrease in the L_{50} and condition factor of *T. mediterraneus* during the study period was similar to the results obtained by Albo-Puigserver et al. (2021), who reported a reduction in the L_{50} estimates of *Engraulis encrasicolus* and *Sardina pilchardus* in the GSA06 and GSA01. These findings suggest that species under exploitation, or affected by environmental variability, can demonstrate phenotypic adaptive responses with changes in the size at first maturity and age (Ernande et al., 2004). These adaptations may also be developed to buffer environmental events and improve the reproductive capacity (Barneche et al., 2018; Pennino et al., 2020).

Among the life history traits of *T. mediterraneus* analyzed during the study period, the condition factor and size at first maturity show a corresponding trend, with the decrease of both over the years. Based on

the life history theory, this pattern might reflect the strong influence that variability in the habitat quality can exert on the reproduction timing of this species (Roff, 1992). The reproduction process requires an energetic investment from both females (e.g., number and size of offspring) and males (e.g., territorial defense, mate protection, sperm size and quality; (Schwarzkopf and Shine, 1991), that may compromise their future growth, survival, or fecundity. Hence, to maximize the fitness of an organism, their life cycle must be optimal regarding the schedule of reproduction. Understanding the energetic trade-offs in the components of reproduction is the basis of life history theory, and differences in the reproductive strategy adopted by a species is informative when unraveling the mechanisms behind life history evolution (Glaudas et al., 2020). According to Roff (1992), mortality prior to maturity is more relevant when determining the optimal size of first reproduction than mortality after maturity, as it matters most that an individual gets the chance to reproduce at least once during its lifespan. Therefore, the deteriorating condition of *T. mediterraneus* in the Spanish Mediterranean, as a likely result of stressors such as over-fishing or decaying environmental conditions, could be contributing to the reduction of the size at first maturity of the population, to adapt and secure the most fitness under these constraints.

The preliminary results obtained on the demographic structure of *T. mediterraneus* could indicate differences in growth during the first two years of life between GSAs, as specimens of the same age (age class 1 and 2) exhibited larger sizes in GSA01 than in GSA06. These results are similar to those documented for *Engraulis encrasicolus* by Ventero et al. (2017) and *Sardina pilchardus*, by Alemany and Álvarez (1993). In both studies, the differences were attributed to the higher primary production and chlorophyll that is evidenced in GSA01 and, in general, the favorable environmental conditions, that could directly benefit *Trachurus mediterraneus* during the first two years, when the acquired energy is mainly used for growth, while in the remaining years part of it is destined for reproduction, making the readings of growth rings difficult (Carbonara and Follesa, 2019; Vitale et al., 2019; Villamor et al., 2020). Regarding the differences determined in the L_{∞} estimates, these could be mainly due to the differing maximum sizes sampled in each GSA during the survey, given that sizes up to 42.5 cm were reported in GSA06, while 35 cm was the highest size measured in GSA01. Nevertheless, the lower value of k in GSA06 indicated a slower growth, hence, a slightly longer life cycle would be expected in order to reach the asymptotic length (Ogle, 2016), which is also greatly influenced by the variations of environmental factors and the availability of food. The coefficient of variation (CV%) determined was 10.82% when comparing the results with other works. The values of the phi-prime growth index were similar in both GSAs, corresponding with the study of Carrillo (1978) ($\phi' = 2.39$) in the Catalan sea (GSA06).

The joint interpretation of the results obtained in this study revealed that *T. mediterraneus* exhibited a neritic behavior and distributed in preferential areas or hotspots along the Spanish Mediterranean Sea during the summer, highlighting Málaga as a potential nursery ground. Furthermore, it reached the sexual maturity at two years of age and presented a greater growth in GSA01 compared to GSA06, especially up to age class 2, probably due to the availability of nutrients.

Fishery-independent information obtained from research surveys, such as the MEDIAS survey, is of great value since the identification of the species is unbiased and its entire distribution area is covered, not having spatial or catch restrictions, although its time coverage is limited to one month per year (mainly July). For *T. mediterraneus*, whose spawning time falls in the sampling period, the data collected in the survey allow obtaining unique information on its spatial distribution over the entire continental shelf, the estimation of lengths at first maturity and growth parameters and offers the possibility of evaluating early recruitment processes. Therefore, our results, complemented with biological information collected throughout the year, could be used to establish different management measures for this species, considering the GSA, as previously proposed for the anchovy in the same areas

(Ventero et al., 2017).

CRedit authorship contribution statement

José Carlos Rodríguez-Castañeda: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review and Editing, Visualization. **Ana Ventero:** Conceptualization, Methodology, Resources, Writing - Original Draft, Writing - Review and Editing, Supervision, Project administration, Funding acquisition. **Manuela Gertrudis García-Márquez:** Methodology, Formal analysis, Investigation, Writing - Original Draft, Writing - Review and Editing. **Magdalena Iglesias:** Conceptualization, Methodology, Resources, Writing - Original Draft, Writing - Review and Editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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