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Variability in size at maturity of the European anchovy (*Engraulis encrasicolus*) in the Mediterranean Sea

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Abstract

Size at first sexual maturity (L_{50}) represents an important life-history trait that needs to be considered in the development of management measures as it provides fundamental information for avoiding the exploitation of younger individuals. L_{50} is known to display variability due to fishing pressure, geographical gradients, and environmental features. In this study, to investigate L_{50} variability among areas in the Mediterranean and Black Seas, maturity ogives of anchovies (*Engraulis encrasicolus*) were estimated by considering samples collected during the anchovy spawning period in the framework of the MEDiterranean International Acoustic Survey (MEDIAS) program. Anchovy size and sexual maturity data from several geographical subareas (GSAs), i.e., northern Spain, Gulf of Lion, Tyrrhenian Sea, Strait of Sicily, Adriatic Sea and Black Sea, were gathered according to a standard methodological protocol. Maturity ogives were estimated by a logistic regression considering total length, condition factor, sex and GSA. The obtained results showed a significant effect of the condition factor, in that fish in better condition reached maturity earlier, and the results also indicated differences in L_{50} values among the areas and between the sexes, with males reaching maturity at lower lengths than females. Even though the obtained L_{50} estimates are relative to the spawning period only, the variability observed at the Mediterranean basin scale highlights the importance of explicitly considering specific habitat characteristics when providing management advice based on an ecosystem approach for fisheries.

Keywords: Macroscopic maturity stage; condition factor; geographical variability; Mediterranean Sea; Black Sea.

Introduction

According to recommendations by the Scientific, Technical and Economic Committee for Fisheries (STECF) of the European Union (STECF, 2016) and the General Fisheries Commission for the Mediterranean (GFCM), management plans should improve estimates of model parameters or biomass evaluations to provide sustainable stock exploitation (FAO, 2008; Fogarty, 2013). Knowledge of reproductive traits, among different life-history characteristics, represents one of the main tools for assessing population productivity and resilience, e.g., variations in size and age at maturity have a direct impact on productivity fluctuations in many populations, with implications for fisheries management (Morgan, 2018). Some recommendations even suggest that for sustainable exploitation, fish species should be caught only within a specific size range, with a lower size limit excluding immature individuals and an upper size limit excluding fishes with the greatest reproductive potential (Coleman *et al.*, 2000); however, this approach is quite debated (Conover & Munk 2002). Having accurate, up-to-date information on the maturity at a given fish size of commercially important species is essential for their sustainable exploitation since the age and length at first maturity may be modified by environmental changes or increased fishing pressure (Olsen *et al.*, 2004; McBride *et al.*, 2015).

In pelagic species with indeterminate fecundity, reproductive traits, including the size at maturity, often display plasticity, generally related to environmental conditions as well as geographical gradients (Somarakis *et al.*, 2004; Basilone *et al.*, 2006; Ganias *et al.*, 2015). For instance, fish have been observed to grow and mature at smaller sizes at low latitudes than other individuals of the same species at higher latitudes, suggesting fish have the ability to adapt to large-scale patterns in environmental conditions (Winton *et al.*, 2014; Ferreri *et al.*, 2019). Previous studies have observed an increase in body size with latitude (Ventero *et al.*, 2017; Huret *et al.*, 2019), mainly in response to differences in water temperature (Abaunza *et al.*, 1995). Therefore, the variability in L_{50} (i.e., the size at which half of a population reaches sexual maturity) could be crucial for developing specific management advice (Morgan, 2018), particularly when focusing on populations inhabiting different geographical areas.

Environmental factors such as photoperiod, temperature and food availability have been shown to influence internal fish characteristics and trigger maturation, mainly affecting growth. Poor somatic conditions (usually associated with poor feeding) may compromise reproductive potential. Some studies have examined this effect of condition on reproductive traits, generally highlighting an increased proportion of mature individuals at a given size or age for fish in better condition (Marteinsdottir & Begg, 2002; Morgan, 2004).

The European anchovy (*Engraulis encrasicolus*) is a pelagic fish widely distributed in the northeastern Atlantic Ocean, as well as in the Mediterranean and Black Seas, where it represents the most abundant resource for fisheries, with annual average landings reaching more than 300,000 t (FAO, 2020). In the past, three separate stocks were identified within the Mediterranean basin (FAO, 2006): the Adriatic Sea stock (involving Albania, Croatia, Italy, Slovenia and Serbia-Montenegro), the Aegean Sea stock (involving Greece and Turkey), and the northwestern Mediterranean stock (involving France and Spain). However, more recent studies widened this perspective, suggesting that the Aegean stock should also include anchovy populations inhabiting the Ionian Sea, south of Sicily and Malta, while the northwestern Mediterranean stock should also incorporate the Ligurian Sea population (Fiorentino *et al.*, 2014). Finally, separate stocks are detectable in the Alboran Sea (Ventero *et al.*, 2017), segregating the Adriatic Sea stock into two main populations, one in the northeastern region and one in the western region (Ruggeri *et al.*, 2016), as well as in the Black Sea. In the last case, the geographic configuration of this almost completely isolated basin strongly contributes to its isolation (Magoulas *et al.*, 2006).

Within the Mediterranean basin, riverine fallout (e.g., northwestern Mediterranean) and the presence of local upwellings (e.g., south of Sicily), as well as additional nutrient inputs from the marine aquaculture industry (Tičina *et al.*, 2020), cause significant variability in local productivity, thus leading to strong differences in the habitat conditions experienced by different stocks. Accordingly, even though the spawning period of anchovies in the Mediterranean and Black Seas starts in spring and occurs until early autumn with a peak in the warmer months (Basilone *et al.*, 2006; Tsikliras & Stergiou, 2013; Gücü *et al.*, 2017), the spawning peak may differ in timing and location associated with high productivity fluctuations, particularly food availability (e.g., zooplankton density, riverine outflows, and upwelling phenomena; Somarakis *et al.*, 2000; Basilone *et al.* 2013, 2020; Malavolti *et al.*, 2018). Moreover, L_{50} in income breeders such as anchovies may display variability at short time scales (McBride *et al.*, 2015). This scenario might explain the existence of several mature ogive estimates for both Atlantic and Mediterranean anchovy populations (e.g., Giraldez & Abad, 1995 and references therein; Basilone *et al.*, 2006; Sinovčić & Zorica, 2006).

The present study aims to evaluate how anchovy sexual maturity varies among eight areas in the Mediterranean and Black Seas by comparing the L_{50} estimated with a single coherent methodological framework. The obtained results should be useful for developing management measures taking into account ecosystem effects on anchovy reproductive traits.

Materials and Methods

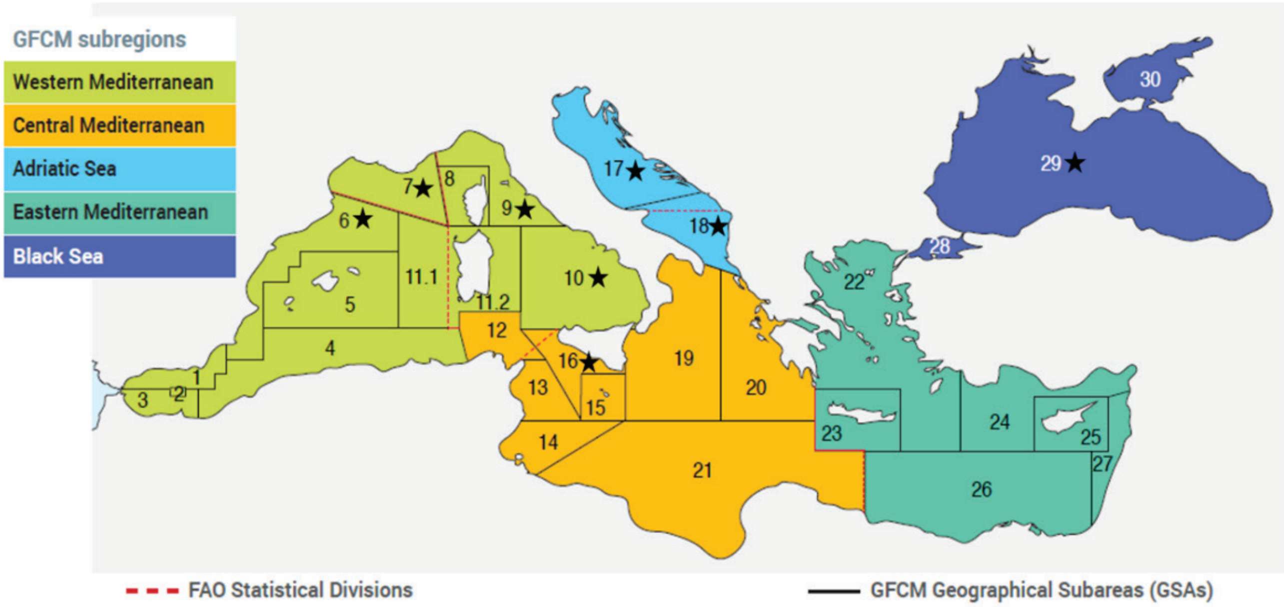
Study areas

Within the Mediterranean and Black Seas, several geographical subareas (GSAs; Fig. 1) have been identified for management purposes (GFCM, 2009).

Northern Spain (GSA 06), which includes the Balearic Sea and the Gulf of Valencia, is connected to the Gulf of Lions through the Northern Current flowing to the southwest (Ospina-Alvarez *et al.*, 2012). This area is characterized by a narrow continental shelf, which enlarges in front of the Ebro River delta. These latter conditions provide the nutrients needed for phytoplankton enrichment, particularly during summer (Palomera *et al.*, 2007).

The Gulf of Lion (GSA 07) is characterized by a wide continental margin and represents the most productive area in the northwestern Mediterranean Sea (Bănaru *et al.*, 2013). Productivity is strongly related to the mixing events induced by wind circulation and Rhone River inputs (Darnaude *et al.*, 2004; Feuilloley *et al.*, 2020), as well as by local upwelling phenomena (Millot, 1990).

The western Italian coast includes two geographical subareas, namely, GSA 09 (including the Ligurian Sea and the northern Tyrrhenian Sea) and GSA 10 (Central and Southern Tyrrhenian Sea). The surface circulation is



GFCM GSAs

01 - Northern Alboran Sea	07 - Gulf of Lion ★	13 - Gulf of Hammamet	19 - Western Ionian Sea	25 - Cyprus
02 - Alboran Island	08 - Corsica	14 - Gulf of Gabes	20 - Eastern Ionian Sea	26 - South Levant
03 - Southern Alboran Sea	09 - Ligurian Sea and Northern Tyrrhenian Sea ★	15 - Malta	21 - Southern Ionian Sea	27 - Eastern Levant Sea
04 - Algeria	10 - South and Central Tyrrhenian Sea ★	16 - South of Sicily ★	22 - Aegean Sea	28 - Marmara Sea
05 - Balearic Islands	11.1 - Sardinia (west) 11.2 - Sardinia (east)	17 - Northern Adriatic Sea ★	23 - Crete	29 - Black Sea ★
06 - Northern Spain ★	12 - Northern Tunisia	18 - Southern Adriatic Sea ★	24 - North Levant Sea	30 - Azov Sea

Fig. 1: The geographical subareas (GSAs) identified by the General Fisheries Commission for the Mediterranean (GFCM) (source: http://www.fao.org/gfcm/about/area-of-application/ru/), including the study areas (from west to east): northern Spain (GSA 06); Gulf of Lion (GSA 07); northern Tyrrhenian Sea (GSA 09); southern Tyrrhenian Sea (GSA10); south of Sicily (GSA 16); Adriatic Sea (GSA 17); southern Adriatic Sea (GSA 18); Black Sea (GSA 29). Black stars identified the study area.

characterized by fresh water of Atlantic origin (Atlantic Water) flowing in the Tyrrhenian Sea along the northern Sicily and Italian Peninsula coasts (Millot & Taupier-Letage, 2005). Moreover, the central areas are strongly influenced by the outflow of numerous medium and large rivers (Rinaldi, 2012).

In the south of Sicily (GSA 16), the Atlantic Ionian Stream mainly controls the upper layer circulation (Robinson *et al.*, 1999), inducing permanent coastal upwelling along the southern coast of Sicily despite being characterized by interannual variability in terms of shape, position, and strength (Bonanno *et al.*, 2014).

The Adriatic Sea is split into two GSAs with different oceanographic features: the northern Adriatic Sea (GSA 17) and the southern Adriatic Sea (GSA 18). The northern part of the Adriatic Sea mainly shows shallow depths and high river discharge amounts, particularly due to the Po River, which provides high nutrient inputs influencing phytoplankton biomass (Artioli *et al.*, 2008). A decreasing trend in nutrient concentration and production within the Adriatic basin is observed moving from north to south and from west to east. However, the eastern part of the Adriatic Sea is characterized by rocky coasts and very few small rivers (Tičina *et al.*, 2020), while the southern Adriatic Sea is mostly influenced by eastern Mediterranean waters and exhibits an oligotrophic character with local gyres, varying in intensity according to season (Zavatarelli *et al.*, 1998). In GSA 17, two acoustic surveys were carried out separately, one in the western part of the northern Adriatic (GSA 17 W) along the Italian coast and the other in the eastern part of the northern Adriatic (GSA 17E) along the Croatian coast (Tičina *et al.*, 2006; Leonori *et al.*, 2012).

The Black Sea (GSA 29) is an almost completely isolated area connected to the Mediterranean basin only by the Bosporus Strait, but the shallow sills in the Strait strongly reduce exchange between the basin and the Mediterranean. The northwestern part is mostly characterized by freshwater inputs from rivers, a large continental shelf, and high productivity due to run-off (Özsoy & Ünlüata, 1997).

Field sampling

Individuals of European anchovy sampled from 2013 to 2018 were considered. To avoid possible biases in the analysis, maturity data for each area and year were carefully inspected. In particular, only years characterized by a coherent proportion of mature and immature fish were selected in each area, as explained later in the text. Fish samples were collected during scientific acoustic surveys carried out on an annual basis in the framework of the MEDiterranean International Acoustic Surveys (MEDIAS), a specific action in the European Data Collection Framework (DCF). During the surveys, to evaluate the abundance and distribution of small pelagic fish stocks, acoustic data were collected along parallel transects, mostly perpendicular to the coast. To identify the fish echotraces, determine the species composition and proportion and perform biological measurements, fish samples were collected by pelagic trawl sampling mainly during the daytime (MEDIAS, 2019). The position of each trawl was identified by the geographical coordinates (i.e., latitude and longitude) of its starting point.

The surveys were mainly carried out following a common protocol during the anchovy spawning season (MEDIAS, 2019), with the exception of the Black Sea, where fall surveys were also performed according to the framework of the Pelagic Trawl Survey Black Sea under the DCF in Bulgarian Black Sea waters (Table 1).

From the trawl catches, a random selection of anchovy individuals was sampled, measured for total length (TL) and total weight (TW), and sexed. The reproductive maturity phase was assigned to each gonad, male and female, according to a six-phase scale proposed by the International Council for the Exploration of the Sea (ICES, 2008) for small pelagic fish, following the MEDIAS common protocol (MEDIAS, 2019).

Body condition and maturity estimate

The relative somatic condition factor (CF) was also estimated to evaluate possible effects on maturity ogives. For the CF calculation, the weight-length regression power model coefficients were estimated for each GSA and gender separately. The estimates were carried out according to the following equation (Le Cren, 1951):

$$CF = \frac{TW}{aTL^b}$$

where TW is the total body weight (g), TL is the total fish length (mm), and a and b are the parameters of the weight-length regression (i.e., TW vs. TL).

An evaluation of both ovaries and testes was carried out by identifying macroscopic features described in the classification schemes, specifically developed for anchovy (ICES, 2008). The six reproductive phases are the same for both sexes (ICES, 2008): I) immature or resting; II) developing; III) imminent spawning; IV) spawning; V) partial postspawning; and VI) spent. Phase I was considered immature (spawning not imminent this season), and phases II to VI were considered mature (they contribute to reproduction during the sampling season). Based on evidence in the literature (Silva *et al.*, 2013; Basilone *et al.*, 2021), maturity ogive fitting is negatively affected by a low proportion of immature fishes in the lower size classes, as well as an unbalanced proportion of mature and immature individuals among years. Consequently, to avoid possible bias in the maturity ogive estimation, for each considered area, only the years showing a similar proportion of immature fish were retained (i.e., years where the number of immatures was very low or absent were excluded). Moreover, generally, a macroscopic evaluation does not permit an accurate distinction between immature and spent individuals, as oocytes are not visible at either stage (Costa, 2009; Ferreri *et al.*, 2009). Since this misclassification has an impact on estimating the mature proportion of a stock and fish in stage VI, which should not be considered actively spawning individuals (ICES, 2008), the spent anchovies were not included in further estimates.

Data from selected years for each GSA were combined to obtain a single dataset, which was used for any further calculations for the GSAs. To evaluate the influence of different factors on sexual maturity, generalized linear models (GLMs) using a logit link function with a binomial error structure were used. In particular, maturity data were coded as 0 for immature fish and as 1 for mature fish. Explanatory variables were total length (TL), trawl latitude and CF as continuous covariates and sex and GSA as factors. The best model was selected by considering all the above-mentioned explanatory variables and two-way interactions. Model performances were evaluated based on residual and null deviance, and the presence of multi-

Table 1. Area (geographical sub-area, GSA) and sampling period. Sampling months were abbreviated as follow: Jun: June; Jul: July; Aug: August; Sep: September; Oct: October; Nov: November; Dec: December. NA: no data available.

	GSA 06	GSA 07	GSA 09	GSA 10	GSA 16	GSA 17 W	GSA 18	GSA 17 E	GSA 29
2013	Jul	Jul	Jun	Jun	Jun	Sep	Jul	Sep	NA
2014	Jun-Jul	Jul	Jun	Jun	Jul	Aug-Sep	Jul	Sep	NA
2015	Jun-Jul	Jul	Aug	Aug	Jul	Jun	Jun	Sep - Oct	Nov
2016	Jun-Jul	Jul	Jul-Aug	Jul-Aug	Jul	Jun	Jun	Sep	Jun
2017	Jun-Jul	Jul	Aug	Aug	Jul-Aug	Jun	Jun-Jul	Sep	Jun
2018	Jun-Jul	Jul	Aug	Aug	Aug	Jun-Jul	Jul	Sep	Nov-Dec

collinearity was evaluated by calculating the generalized variance inflation factor (GVIF; Fox and Monette, 1992). The presence of severe multicollinearity problems was evaluated using 10 as the threshold value for the GVIF (Borcard *et al.*, 2012). The importance of each term retained in the final model was assessed by calculating the average contribution of each predictor based on the general dominance calculation and using the McFadden fit index (Azen & Traxel, 2009). All statistical analyses were performed in the R statistical environment (R Core Team, 2020) using the "dominanceanalysis" package (Navarrete and Soares, 2020) to assess the relative importance of the explanatory variables.

Results

In most areas, sampling was performed during the summer (Table 1), which coincided with the main spawning period, as displayed by the presence and abundance of stages representing the active spawning phases (i.e., III - imminent spawning, IV – spawning, and V - partially postspawning) in almost all the GSAs (Table 2). In the northeastern Adriatic (GSA 17E), sampling was mainly performed in September, past the spawning peak, as revealed by the absence of developing (Stage II) and imminent spawning (Stage III) fish together with the high percentage of spent individuals (stage VI) (Table 2). The size distribution of immature females ranged from 6 cm to 14 cm in total length, with mean values of approximately 10 cm in all the study areas except for GSA 17E (11 cm), while the TL of mature females ranged between 8 cm and 17 cm (Fig. 2). Both anchovy males and females displayed larger sizes in the eastern part of the Adriatic Sea (GSA 17E) than in the other areas, although in the Strait of Sicily (GSA 16), mature males displayed a similar distribution and median TL pattern to those in GSA 17E, despite a slightly wider size range (Fig. 2). Even if sampling in the Black Sea (GSA 29) took place in different seasons (summer and fall) among the years, the size distribution of the mature females was in the same range as those in the other GSAs (Fig. 2), while males displayed a narrower TL distribution, resulting in a lower median TL than those in the other GSAs. Moreover, this result shows that it is difficult to obtain exhaustive information on size distribution within the Black Sea due to the very low number of caught fish, particularly immature fish (Table 2).

Therefore, due to the different sampling periods that particularly affected the distribution patterns of the maturity stages, the logistic regression model was applied to remove the northeastern Adriatic (GSA17E) and Black Sea (GSA 29) from the dataset. In the first step, the full model (i.e., the one considering all the fixed effects and two-way interactions) was evaluated. Some interactions among the considered predictors were found to be significant, but they only marginally reduced the residual deviance (~4%) and were thus excluded. All fixed terms were found to be significant, and by considering a threshold value of 10 for the GVIF, no severe multicollinearity problems occurred (Table 3). According to the McFadden index, the most important variable in the model was TL (McFadden index: 0.318), followed by GSA (McFadden

Table 2. Relative percentages of maturity stages (I to VI) by sex (female: F, male: M) for each geographical sub-area (GSA). The number of individuals is provided in parenthesis.

GSA	I		II		III		IV		V		VI	
	F	M	F	M	F	M	F	M	F	M	F	M
GSA06	1.65 (40)	0.80 (20)	4.29 (104)	7.53 (189)	48.33 (1173)	49.62 (1246)	0.33 (8)	1.47 (37)	44.00 (1068)	40.18 (1009)	1.40 (34)	0.40 (10)
GSA07	7.21 (64)	4.08 (29)	0.90 (8)	0.42 (3)	0.56 (5)	0.98 (7)	10.25 (91)	9.99 (71)	27.59 (245)	26.58 (189)	53.49 (475)	57.95 (412)
GSA09	12.64 (189)	14.24 (215)	13.04 (195)	22.12 (334)	47.02 (703)	40.26 (608)	0.33 (5)	0.00	25.75 (385)	23.31 (352)	1.20 (18)	0.07 (1)
GSA10	6.66 (160)	5.53 (147)	9.95 (239)	12.01 (319)	51.15 (1228)	46.27 (1229)	0.00	0.04 (1)	30.95 (743)	35.39 (940)	1.29 (31)	0.75 (20)
GSA16	3.97 (69)	2.03 (36)	8.52 (148)	6.67 (118)	47.55 (826)	57.57 (1019)	3.40 (59)	0.45 (8)	35.64 (619)	33.05 (585)	0.92 (16)	0.23 (4)
GSA17E	16.35 (449)	12.62 (259)	0.00	0.00	0.00	0.00	0.73 (20)	0.15 (3)	24.94 (685)	19.40 (398)	57.99 (1593)	67.84 (1392)
GSA17W	16.50 (424)	5.98 (124)	2.41 (62)	1.69 (35)	11.05 (284)	6.71 (139)	1.28 (33)	0.48 (10)	48.44 (1245)	63.92 (1325)	20.31 (522)	21.23 (440)
GSA18	7.00 (55)	3.44 (25)	8.27 (65)	6.34 (46)	19.59 (154)	18.32 (133)	7.00 (55)	2.20 (16)	50.13 (394)	58.68 (426)	8.02 (63)	11.02 (80)
GSA29	1.64 (2)	42.31 (11)	6.56 (8)	7.69 (2)	4.10 (5)	26.92 (7)	45.90 (56)	11.54 (3)	17.21 (21)	3.85 (1)	24.59 (30)	7.69 (2)

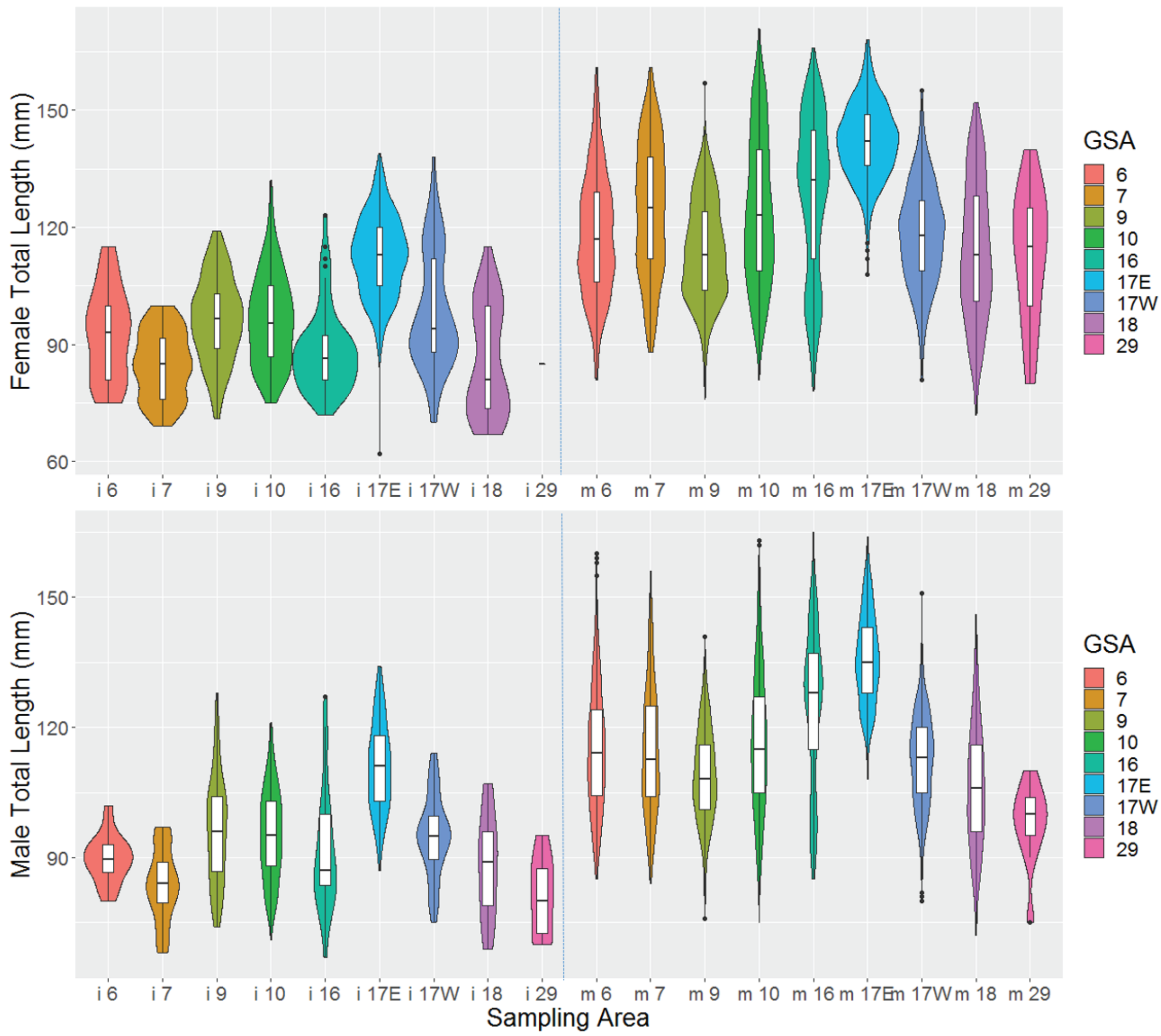


Fig. 2: Female (upper panel) and male (lower panel) size distribution (Total Length, mm) per maturity state (i.e., immature, or mature) within each study area (geographical sub-area, GSA). Dotted line separates immature (i; left of the panels) and mature (m; right of the panels) fish.

index: 0.026), CF (McFadden index: 0.013), sex (McFadden index: 0.007) and latitude (McFadden index: 0.004). Analysis of deviance also showed the weak contribution of trawl latitude (Table 3); consequently, this variable was removed from the model. The GVIF values, relative to the final model, accounting for all fixed effects except for trawl latitude (null deviance: 6669.7; residual deviance: 4224.9 on 11459 degrees of freedom), were all lower than 1.8, highlighting the absence of multicollinearity problems. The model results showed that higher TL values led to a higher proportion of mature individuals, and similarly, greater CF values led to a larger estimat-

Table 3. Analysis of deviance table, significance and GVIF values relative to the model accounting for study area (geographical sub-area, GSA), sex, condition factor (CF), total length (TL; mm), and trawl latitude. $GVIF^{(1/(2*Df))}$ allows to compare GVIF values among explanatory variables by correcting for Df.

	Df	%explained deviance	Df	Resid. Dev	LR Chisq	Pr(>Chisq)	GVIF	GVIF^(1/(2*Df))
NULL			11459	6669.7				
TL	1	31.35	11458	4578.5	2146	<0.001	1.19	1.09
GSA	6	34.20	11452	4388.4	85.43	<0.001	8.82	1.20
CF	1	35.99	11451	4269.1	87.03	<0.001	1.77	1.33
Sex	1	36.66	11450	4224.9	40.7	<0.001	1.09	1.04
Trawl Latitude	1	36.82	11449	4214.1	10.77	0.00103	5.67	2.38

ed proportion of mature individuals at TL (Figs. 4 and 5). Predicted values based on the average CF values by area showed consistent differences in both maturity ogive patterns between the two sexes for all considered GSAs (Fig. 3).

For both sexes, an increased CF generated a higher probability of finding mature individuals: in each area, at fixed increasing CF values (i.e., CF=0.7, CF= 1; CF=1.3), a smaller length at maturity was obtained (Figs. 4 and 5). The L_{50} values of females ranged between 7.8 cm (northern Spain, GSA 06) and 9.1 cm (southern Tyrrhenian, GSA 10) (Table 4 and Fig. 6). In comparison to anchovy females, anchovy males reached maturity at a slightly smaller length, ranging from 7.3 cm (northern Spain, GSA 06) to 8.4 cm (southern Tyrrhenian, GSA 10) (Table 4 and Fig. 6).

The obtained L_{50} values suggested the presence of two distinct groups (Fig. 6): one group including the Gulf of Lion (GSA 07), Tyrrhenian Sea (GSAs 09 and 10) and northwestern Adriatic (GSA 17 W), where half of the anchovies appeared mature at a larger size, and a second group including northern Spain (GSA 06), south of Sicily (GSA 16) and southern Adriatic (GSA 18), where the anchovies displayed lower sizes at maturity.

Discussion

In the framework of MEDIAS, the spatial monitoring of small pelagic species inhabiting the Mediterranean basin provides the opportunity to obtain a dataset covering wide geographic and habitat parameter ranges by applying the same sampling protocol, including the same procedure and gear for collecting fishes in all the study areas, according to the MEDIAS handbook (MEDIAS, 2019). Even if sampling performed once per year would not be representative of the whole population, for the first time in several Mediterranean areas, the present study provides a standardized dataset allowing us to estimate and compare the maturity patterns as well as the size at first maturity in a uniform manner.

Although histology is recognized as the most accurate method, macroscopic recognition of the reproductive phase by visual examination of gonads is a rapid, inexpensive method for determining the reproductive status of fish; however, the subjective judgement intrinsic to such a method may reduce the data accuracy, particularly in terms of distinguishing between immature (phase I) and spent (phase VI, nonactive but mature) females because in both cases, the ovaries are very small, without visible oocytes (Costa, 2009; Ferreri *et al.*, 2009). Generally, both immature and spent fish are minimally present in partial spawner species, especially during the spawning peak (ICES, 2008), which justifies the very low number of immature individuals collected in some study areas, as observed in northern Spain (GSA 06) and the Strait of Sicily (GSA 16) (Table 2). Otherwise, the high proportion of spent fish in the Gulf of Lion (GSA 07) may be explained by the common misclassification between phase I and phase VI, inducing the removal of spent individu-

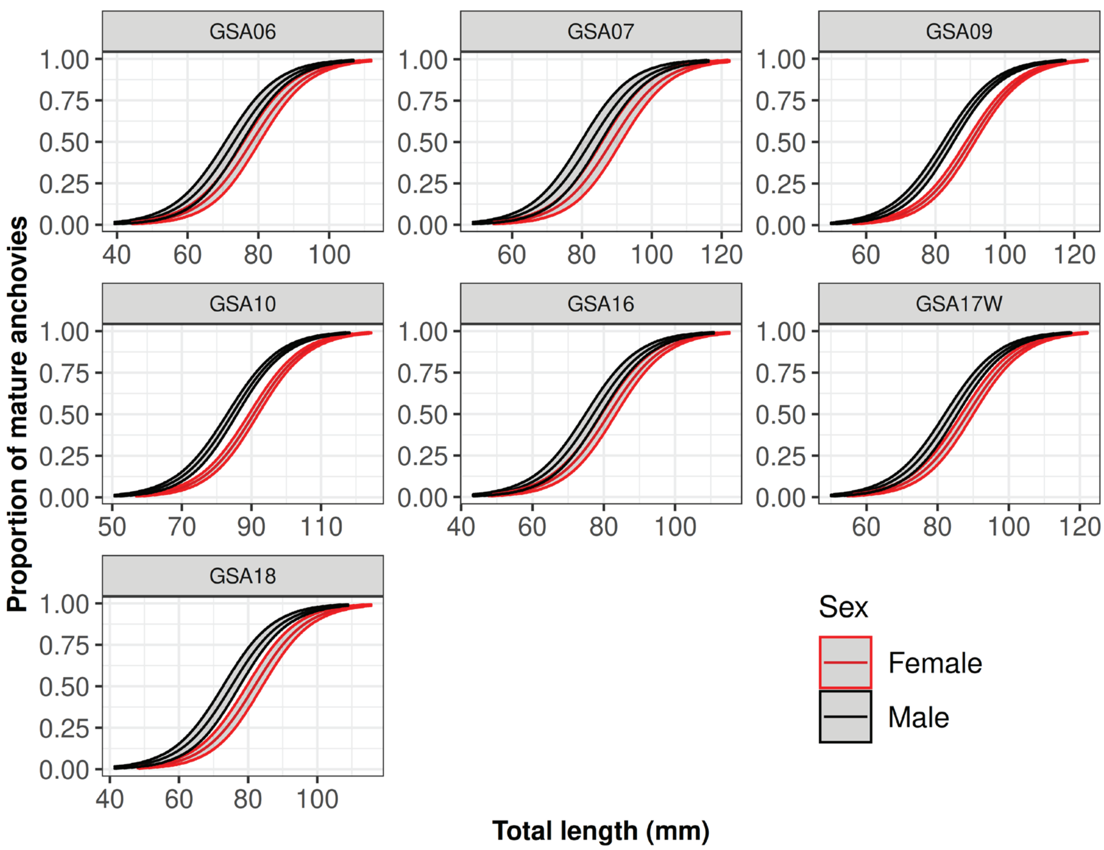


Fig. 3: Maturity ogives (solid line) for each study area (geographical sub-area, GSA) with 95% confidence intervals (shadow area) for both male (M) and female (F) anchovies.

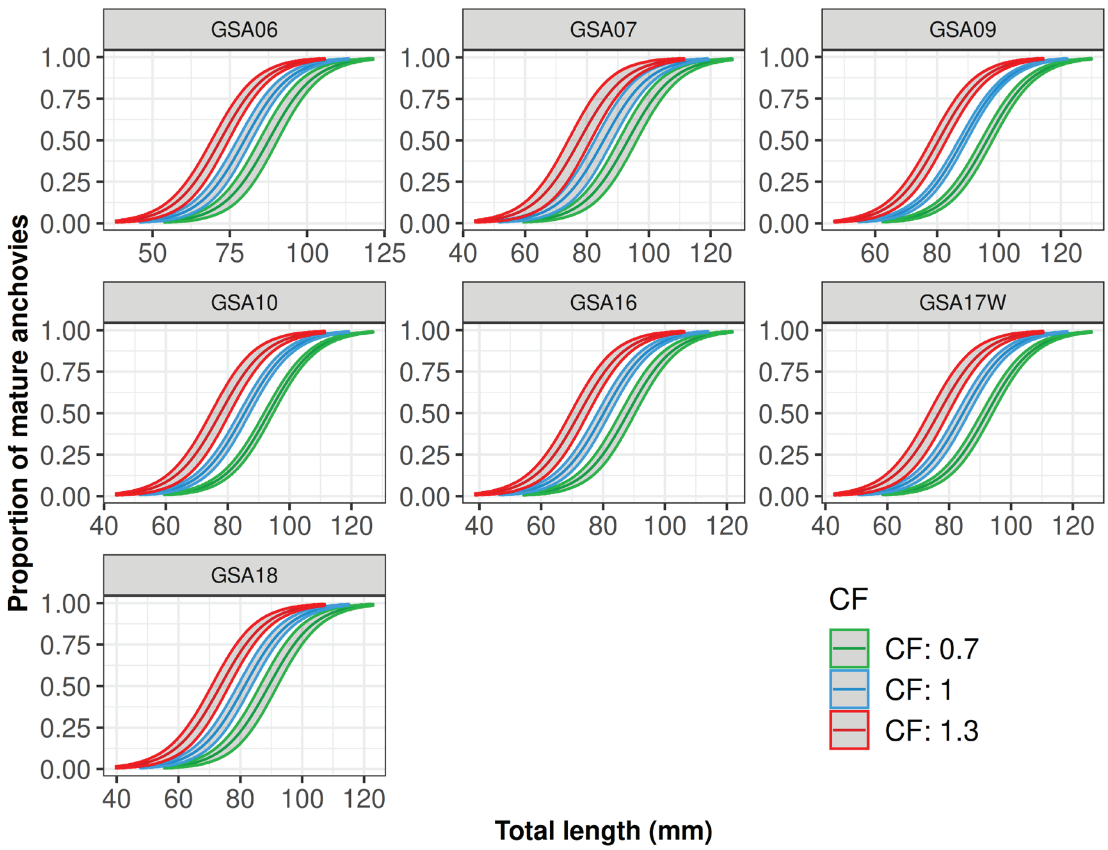


Fig. 4: Predicted values of proportion of mature females at length assuming different condition factor values (i.e., CF=0.7; CF=1; CF=1.3) for each study area (geographical sub-area, GSA). The shadow area represents the 95% confidence intervals for each maturity ogive.

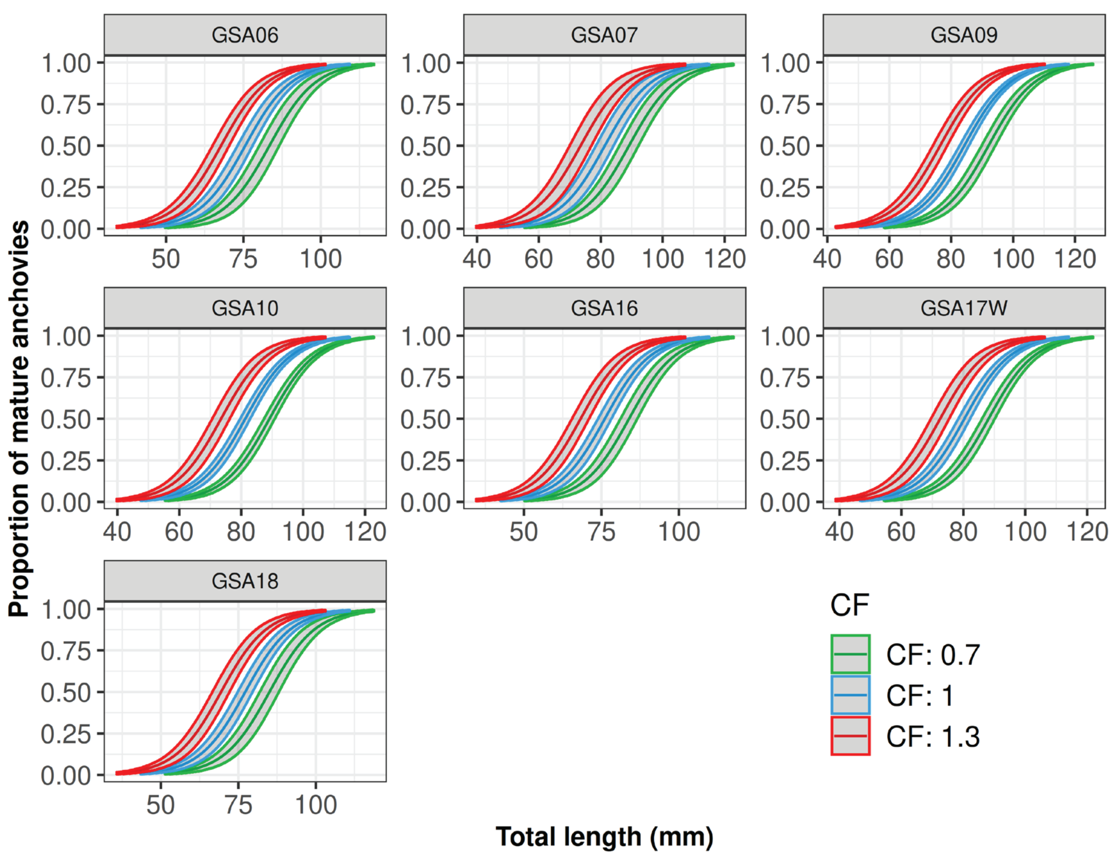


Fig. 5: Predicted values of proportion of mature males at length assuming different condition factor values (i.e., CF=0.7; CF=1; CF=1.3) for each study area (geographical sub-area, GSA). The shadow area represents the 95% confidence intervals for each maturity ogive.

Table 4. Size (total length, mm) at which 5% (L_5), 50% (L_{50}) and 95% (L_{95}) of anchovy females (F) and males (M) are mature within each study area (geographical sub-area, GSA). Confidence limits are provided in brackets.

GSA	Sex	L_5 (95% CI)	L_{50} (95% CI)	L_{95} (95% CI)
GSA06	F	56.2 (53.6 - 60)	78 (75.7 – 80.5)	99.4 (97.3 - 102.2)
GSA07	F	66.5 (63.6 - 70.8)	88.4 (85.6 - 91.4)	110.3 (106.7 - 113.2)
GSA09	F	68.1 (66 - 70.8)	90 (89.1 - 92.5)	111.9 (110.2 - 113.6)
GSA10	F	68.9 (66.5 - 71.3)	90.5 (89.1 - 92.1)	112.4 (110.7 – 114.1)
GSA16	F	59.5 (56.9 - 62.8)	81.3 (79.3 - 83.6)	103.3 (100.8 - 105.4)
GSA17W	F	66.5 (64.3 - 69.6)	88.3 (86.6 - 90.2)	110.2 (108.3 - 112.1)
GSA18	F	59.9 (57.3 - 63.5)	81.7 (79.4 - 84.2)	103.6 (100.8 - 106.2)
GSA06	M	51.2 (48.2 - 55.2)	73 (70.5 - 75.6)	94.9 (92.3 – 97.1)
GSA07	M	60.6 (57.6 - 65)	82.4 (79.6 - 85.5)	104.3 (100.7 - 107.3)
GSA09	M	61.7 (59.6 - 64.6)	83.6 (82 - 85.3)	105.5 (103.8 - 107.1)
GSA10	M	62.5 (60.3 - 65.4)	84.3 (82.8 - 86)	106.2 (104.6 - 107.9)
GSA16	M	55.1 (52.5 - 58.8)	76.9 (74.7 – 79.4)	98.9 (96.5 - 101)
GSA17W	M	61.9 (59.4 - 65.2)	83.7 (81.9 - 85.7)	105.6 (103.7 - 107.4)
GSA18	M	53.2 (50.6 - 57)	75 (72.6 - 77.6)	96.9 (94.1 - 99.5)

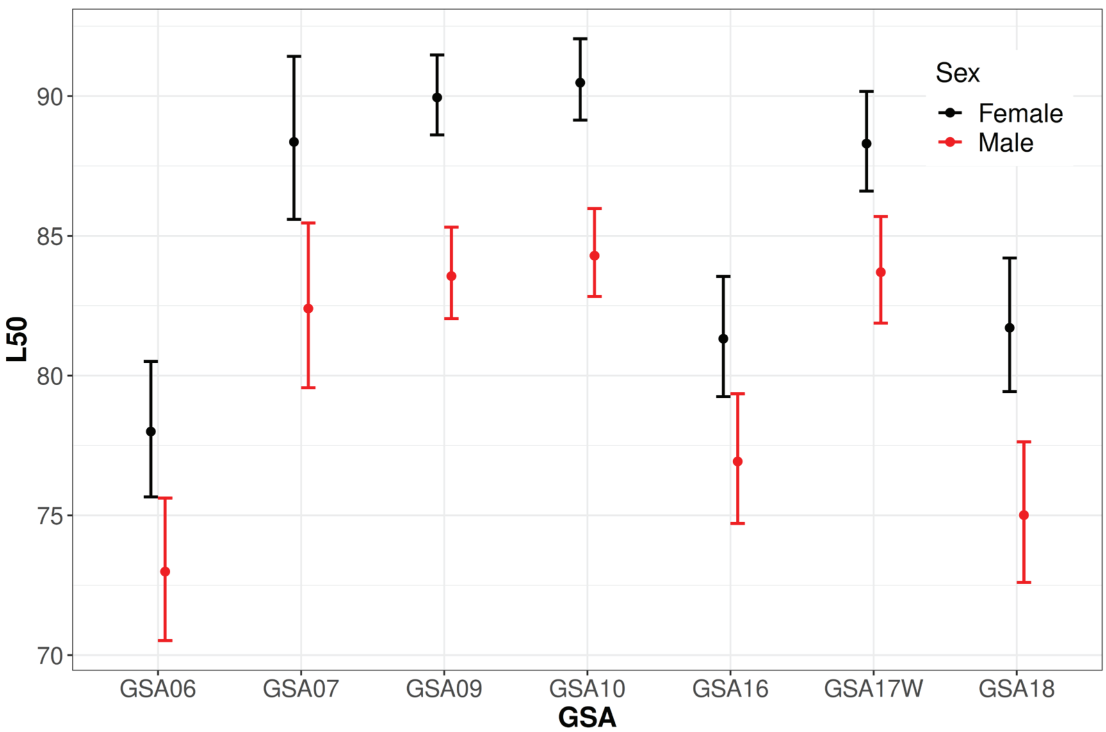


Fig. 6: Comparison of male and female length at maturity (L_{50}, mm) for the study areas (geographical sub-area, GSA) sampled during the spawning peak: northern Spain (GSA 06); Gulf of Lion (GSA 07); northern Tyrrhenian Sea (GSA 09); southern Tyrrhenian Sea (GSA10); south of Sicily (GSA 16); northwestern Adriatic Sea (GSA 17W); southern Adriatic Sea (GSA 18). Bars displayed the 95% confidence limits.

als from the analyses since such misinterpretation deeply affects the estimate of the mature individual proportion within a stock. Otherwise, within the Gulf of Lion, the higher proportion of active spawning fish than those in the other study areas confirmed that sampling took place during the main spawning period (Table 2). In the case of the eastern part of the Adriatic Sea (GSA 17E), where sampling was carried out after the spawning peak (Table 1), the larger total length recorded for immature fishes may have been linked to difficulties in separating immature and spent fish by a naked eye evaluation.

An unbalanced distribution of immature individuals is a well-known source inhibiting accuracy (Silva *et al.*, 2013; Basilone *et al.*, 2021), which results in larger confidence limits and less accurate L_{50} estimates. This scenario could be due to both the low number of collected fishes and the uncorrected maturity assignment, suggesting differences in the macroscopic interpretation despite the adoption of a common maturity scale. The present results thus suggested that periodic intercalibration exercises for both sexes could help improve the accuracy and intercomparability of the operators, even if a common sampling protocol and maturity scale are used.

The present results showed an L_{50} between 7 cm and 9 cm for both sexes, estimates lower than those generally obtained for this species. In the Bay of Biscay, studies including sampling throughout the year reported an L_{50} of approximately 10 cm (Lucio & Uriarte, 1990), while in the Mediterranean, the L_{50} was between 10 cm and 11 cm (Tsikliras & Stergiou, 2013 and references therein), with the exception of the Adriatic Sea, which showed L_{50} values spanning between 8 cm and 10 cm (Sinovčić & Zorica, 2006 and references therein). Lower maturity sizes are probably derived from a difference in sampling protocol, as past studies have highlighted that most recruits are already mature at the peak of the spawning season, thus leading to an apparent reduction of the size at maturity; however, in the present study, only samples from the main spawning season rather than from all months of the year were sampled (Motos, 1996; Somarakis, 1999). Overexploitation of stocks and changes in the environment are also known to generate a decrease in size and age at maturity (Olsen *et al.*, 2004; Brosset *et al.*, 2016; Lappalainen *et al.*, 2016), causing a lower suitable yield. Fishing pressure effects are most commonly recorded for long-lived species with a slow-growing strategy, but anchovy is not a short-living species; however, such evidence from the literature highlights the importance of including L_{50} as potential indicator of the impact of fisheries.

Generally, in comparison to anchovy females, anchovy males appeared mature at smaller sizes in the same area (Fig. 3), confirming previous results of investigations on both this species (Sinovčić & Zorica, 2006; Pešić *et al.*, 2013) and other pelagic fishes (e.g., Lisovenko & Andrianov, 1996; Rahmani & Koudache, 2020). The literature has shown that some Mediterranean marine fishes also experience differences in age at maturity between sexes, suggesting that in comparison to females, males mature earlier but probably display higher mortalities and shorter lifespans (Tsikliras & Koutrakis, 2013). As observed for both genders in the present study (Fig. 4 and Fig. 5), anchovies displayed a positive effect of fish condition on the probability of maturity, as already observed in different fish species (Marteinsdottir & Begg, 2002; Morgan, 2004), including small pelagic fish (Silva *et al.*, 2006). Fish in better condition may have a surplus of energy to devote to reproduction, making them able to mature at smaller sizes. As the condition of a fish changes over time as well as in relation to poor feeding conditions and environmental variability (Dutil & Lambert, 2000), its effect on the size at which a fish reaches sexual maturity may have a direct impact on stock reproductive potential through a direct effect on spawning stock biomass.

The spatial variability in the L_{50} estimates identified two main groups (Table 3; Fig. 6): the first group includes northern Spain, the Strait of Sicily and southern Adriatic, where anchovies reached maturity at smaller sizes, compared to those in the second group, including the Gulf of Lion, the Tyrrhenian Sea (both GSA 09 and GSA 10) and the northwestern Adriatic. Although the two groups appear to be segregated along a north–south latitudinal gradient, the observed differences could mainly be driven by specific environmental factors since the areas belonging to the "northern" group are all strongly influenced by river runoff (e.g., Artioli *et al.*, 2008; Rinaldi, 2012; Bonanno *et al.*, 2016; Feuilloley *et al.*, 2020). Fish maturity, among other life-history traits, is linked to environmental productivity in each region (McBride *et al.*, 2015). The effects on reproductive behaviour and traits may be explained by habitat characteristics at the local level, thus requiring more attention in spawning stock monitoring (Domínguez-Petit & Saborido-Rey, 2010). Variability in chlorophyll concentration, temperature and food retention, mostly driven by physical processes, has been shown to induce changes in both size at maturity and fish condition (Duntil & Lambert, 2000; Wertheimer *et al.*, 2004). In the Strait of Sicily, gonad development has been associated with chlorophyll amount variability (Basilone *et al.*, 2006), which appeared mainly driven by oceanic circulation (Bonanno *et al.*, 2013; Rinaldi *et al.*, 2014). In contrast to in Sicilian waters, in the northern Adriatic Sea, as well as in the Tyrrhenian Sea, particularly in central and northern areas where small pelagic species are particularly concentrated, a strong link has been observed between primary production and river inputs (Santojanni *et al.*, 2014; Bonanno *et al.*, 2016). Similarly, in the Gulf of Lion, anchovy biomass and spawning were positively affected by river runoff (Lloret *et al.*, 2004). In northern Spain, due to the wide extension of the GSA (Fig. 1), the Ebro River only partially influenced water enrichment, while the water and nutrient circulations were mainly driven by the northern current (Ospina-Alvarez *et al.*, 2012). The smaller size at maturity in the southern Adriatic may be linked to the oligotrophic conditions occurring in this area (Zavatarelli *et al.*, 1998).

The present study offers the first attempt to compare anchovy maturity data from several areas and ecosystems across the whole Mediterranean Sea in summer. Data from the Strait of Sicily to the Gulf of Lion provided new insights on the maturity ecology of MEDIAS-monitored anchovy stocks. Environmental variability experienced by fish in their habitats (e.g., upwelling or river runoff areas) appeared to drive the reproductive potential affecting the maturity process and timing, also through the variability in the fish conditions. Despite the high level of harmonization and agreement achieved among the laboratories within the MEDIAS framework, the present results highly suggest increasing the standardization level of collected data, especially in terms of trying to harmonize sampling periods as well as maturity stage assignments among areas/operators. In fact, a greater standardization of procedures and protocols would further enhance the opportunity to carry out comparative studies over wider ecological conditions, thus providing ecosystem-based management advice.

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