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

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Abstract

Size at first sexual maturity (L_{50}) represents an important life history trait in the development of management measures providing fundamental information to avoid the exploitation of younger individuals. L_{50} is known to display variability due to fishing pressure, geographical gradient and environmental features. In this study, in order to investigate L_{50} variability among areas of the Mediterranean and Black Sea, maturity ogives of anchovy (*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 Sub-Areas (GSA) – 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 means of a logistic regression taking into account total length, condition factor, sex and GSA. Obtained results evidenced a significant effect of condition factor, fish in better condition reaching maturity earlier, as well as differences in L_{50} values among areas and between sexes, with males reaching the maturity at lower length than females. Even though the obtained L_{50} estimates are relative to the spawning period only, the observed variability at the Mediterranean basin scale highlights the importance to explicitly consider the habitat peculiarities in order to provide management advices based on an ecosystem approach to fishery.

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 evaluation to provide a sustainable stock exploitation (FAO, 2008; Fogarty, 2013). Knowledge on 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 direct impact on productivity fluctuation in many populations, with implications for fisheries management (Morgan, 2018). Some even suggested that for a sustainable exploitation, fish species should be caught only within a specific window of their size, with a lower size limit excluding the immature individuals and an upper size limit excluding fishes with the greatest reproductive potential (Coleman *et al.*, 2000), although this is quite debated (Conover & Munk 2002). Having accurate, up-to-date information on the maturity at 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, the reproductive traits, including the size at maturity, often display plasticity, generally related to environmental conditions as well as to a geographical gradient (Somarakis *et al.*, 2004; Basilone *et al.*, 2006; Ganiats *et al.*, 2015). For instance, fishes 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 ability to adapt to large-scale patterns in environmental conditions (Winton *et al.*, 2014; Ferreri *et al.*, 2019). Previous studies 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 the population reaches the sexual maturity) could be crucial to develop specific management advices (Morgan, 2018), particularly when addressed to populations inhabiting different geographical areas.

Environmental factors such as photoperiod, temperature and food availability have been shown to influence fish internal factors and trigger maturation, mainly affecting growth. Poor somatic condition (usually associated with poor feeding), may compromise the 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 fishes in better condition (Marteinsdottir & Begg, 2002; Morgan, 2004).

The European anchovy (*Engraulis encrasicolus*) is a pelagic fish widely distributed in the northeast 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 Ionian Sea, South of Sicily and Malta, while the Northwestern Mediterranean stock should incorporate also the Ligurian Sea population (Fiorentino *et al.*, 2014). Finally, separate stocks are detectable in the Alboran Sea (Ventero *et al.*, 2017), a segregation of the Adriatic Sea stock in two main populations, one in the north-eastern and one in the western (Ruggeri *et al.*, 2016), as well as in the Black Sea. In the latter case, the geographic configuration of this almost completely isolated basin strongly contributes to isolating it (Magoulas *et al.*, 2006).

Within the Mediterranean basin, the riverine fallout (e.g., Northwestern Mediterranean) and the presence of local upwellings (e.g., South of Sicily), as well as additional nutrient inputs from marine aquaculture industry (Tičina *et al.*, 2020), cause a 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 anchovy in the Mediterranean and Black Seas starts in spring and protracts 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, and particularly food availability (e.g., zooplankton density, riverine outflows, upwelling phenomena; Somarakis *et al.*, 2000; Basilone *et al.* 2013, 2020; Malavolti *et al.*, 2018). Moreover, L_{50} in

income breeders such as anchovy may display variability also on short time scales (McBride *et al.*, 2015). This might explain the existence of several maturity 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 of the Mediterranean and Black Sea by comparing L_{50} estimated with a single coherent methodological framework. Obtained results should be useful to develop management measures taking into account ecosystem effects on anchovy reproductive traits.

Materials and Methods

Study areas

Within the Mediterranean and Black Sea, several Geographical Sub-Areas (GSAs; Fig. 1) were identified for management purposes (GFCM, 2009).

The Northern Spain (GSA 06), which includes the Balearic Sea and the Gulf of Valencia, is connected with the Gulf of Lions through the Northern Current flowing to the South-West (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 needing 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). The 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 Sub-Areas namely the GSA 9 (including the Ligurian Sea and the Northern Tyrrhenian Sea) and GSA 10 (Central and Southern Tyrrhenian Sea). The surface circulation is characterised by a fresher water of Atlantic origin (Atlantic Water) flowing in the Tyrrhenian Sea along the northern Sicily and the Italian peninsula coasts (Millot & Taupier-Letage, 2005). Moreover, the central areas are strongly influenced by the outflow of numerous medium and large-sized 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 a permanent coastal upwelling along the southern coast of Sicily despite characterized by inter-annual variability in terms of shape, position, and strength (Bonanno *et al.*, 2014).

The Adriatic Sea is split in two GSA with different oceanographic features: the Northern Adriatic Sea (GSA 17) and the Southern Adriatic Sea (GSA 18). The Northern part of Adriatic Sea mainly shows shallow depths and high river discharge, particularly due to Po River, which determines high nutrient inputs influencing the 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. Indeed, 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 accordingly with season (Zavatarelli *et al.*, 1998). In the GSA 17, two acoustic surveys were carried out separately, one in the western part of Northern Adriatic (GSA 17W) along the Italian coast, and the other one in the eastern part of 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 Bosphorus Strait, but the shallow sills in the Strait strongly reduce the exchange between the basin and the Mediterranean. The Northwestern part is mostly characterised by freshwater inputs from rivers, a large continental shelf, and high productivity due to the run-off (Özsoy & Ünlüata, 1997).

Field sampling

Individuals of European anchovy sampled from 2013 to 2018 were considered. In order 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 annual basis in the framework of the MEDiterranean International Acoustic Surveys (MEDIAS) a specific action of the European Data Collection Framework (DCF). During the surveys, aimed to evaluate abundance and distribution of small pelagic fish stocks, acoustic data were collected along parallel transects, mostly perpendicular to the coast. In order 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). Position of each trawl was identified by geographical coordinates (i.e., latitude and longitude) of its starting point.

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

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

Body condition and maturity estimates

The relative somatic condition factor (CF) was also estimated in order to evaluate possible effects on maturity ogives. For the CF computation, 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), while a and b are the parameters of the weight-length regression (i.e., TW vs. TL).

The evaluation of both ovaries and testes was carried out by identification of 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 post-spawning; VI) spent. Phase I was considered immature (spawning not imminent this season) and phases II to VI were considered mature (they are contributing to the reproduction during the sampling season). Based on literature evidence (Silva *et al.*, 2013; Basilone *et al.*, 2021) maturity ogive fitting suffers upon the low proportion of immature fishes in the lower size classes, as well as due to the unbalanced proportion of mature and immature individuals among years. Consequently, in order to avoid possible bias in the maturity ogive estimation, for each considered area only the years showing similar proportion of immature fish were retained (i.e., were excluded years where the number of immatures were very low or absent). Moreover, generally, macroscopic evaluation does not permit accurate distinction between immature and spent individuals, as the oocytes are not visible at neither stage (Costa, 2009; Ferreri *et al.*, 2009). Since this misclassification has an impact in the estimation of the mature proportion of the stock and fish in stage VI should not be considered as actively spawning individuals (ICES, 2008), the spent anchovies have not been included in further estimates.

Data from selected years for each GSA were joined to obtain a single dataset, which was used for any further computations for all the GSAs. In order to evaluate the influence of different factors on sexual

maturity, generalized linear models (GLM) 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. 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 multicollinearity was evaluated by computing the Generalized Variance Inflation Factor (GVIF; Fox and Monette, 1992). The presence of severe multicollinearity problems was evaluated using 10 as threshold value for GVIF (Borcard *et al.*, 2012). The importance of each term retained in the final model was assessed by computing the average contribution of each predictor based on the general dominance computation 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) for assessing the relative importance of explanatory variables.

Results

Sampling was performed during summer in most areas (Table 1), which coincided with the main spawning period, as displayed by the presence and abundance of stages representing the actively spawning phases (i.e., III - imminent spawning, IV – spawning, and V - partially post-spawning) in almost all the GSAs (Table 2). In the Northeastern Adriatic (GSA 17E), the 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 extended from 6 cm to 14 cm total length, with mean values around 10 cm in all the study areas except for the 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 other areas, although in the Strait of Sicily (GSA 16) mature males displayed a similar distribution and median TL pattern as in GSA 17E, despite a little wider size range (Fig. 2). Even if the sampling in the Black Sea (GSA 29) took place at different seasons (summer and fall) among years, the size distribution of mature females resulted in the same range as in other GSAs (Fig. 2), while males displayed a narrower TL distribution, resulting in lower median TL, than other GSAs. Moreover, it proved difficult to obtain exhaustive information on size distribution within the Black Sea due to the very low number of caught fish, particularly immature (Table 2).

Therefore, due to the different sampling periods that particularly affected the distribution patterns of maturity stages, the logistic regression model was applied removing Northeastern Adriatic (GSA17E) and Black Sea (GSA29) from the dataset. In a 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 significant but they only marginally reduced the residual deviance (~4%) and were thus excluded. All fixed terms were found significant and by considering a threshold value of 10 for GVIF no severe multicollinearity problems were evidenced (Table 3). According to the McFadden index, the most important variable in the model was TL (McFadden index: 0.318), followed by GSA (McFadden index: 0.026), CF (McFadden index: 0.013), sex (McFadden index: 0.007) and latitude (McFadden index: 0.004). Analysis of deviance also evidenced the weak contribution of trawl latitude (Table 3), consequently this variable was removed from the model. 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. Model results showed that higher TL values lead to higher proportion of mature individuals, and similarly, greater CF values lead to a larger estimated proportion of mature at TL (Fig. 4 and 5). Predicted values based on the average CF values by area showed coherent differences between the two sexes in both maturity ogive pattern for all considered GSAs (Fig. 3).

For both sexes, increased CF generated higher probability to find 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 (Fig. 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). Anchovy males reached maturity at little smaller length than females, 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 including Gulf of Lion (GSA 07), Tyrrhenian Sea (GSAs 9 and 10) and Northwestern Adriatic (GSA 17W) where half of anchovy appeared mature at higher size, and a second group including Northern Spain (GSA 06), South of Sicily (GSA 16) and Southern Adriatic (GSA 18) displaying lower size at maturity.

Discussion

The spatial monitoring of small pelagics inhabiting the Mediterranean basin, in the framework of MEDIAS, provides the opportunity to obtain a dataset spread over a wide geographic and habitat parameter range, by the application of the same sampling protocol, including the same procedure and

gears for collecting fishes in all the study areas, according to the MEDIAS handbook (MEDIAS, 2019). Even if a sampling performed once per year would not be representative of the whole population, the present study provides for the first time in several Mediterranean areas a standardized dataset allowing to compare the maturity patterns as well as the size at first maturity uniformly estimated.

Although the histology was recognized as the most accurate method, the macroscopic recognition of reproductive phase by visual examination of gonads is a rapid, inexpensive method for determining the reproductive status in fishes, even though the subjective judgment intrinsic of such method may reduce the data accuracy, particularly for distinguishing between female immature (phase I) and spent (phase VI, non-active but mature), 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 poorly present in partial spawner species especially during the spawning peak (ICES, 2008), which justify the very low number of immature individuals collected in some study area as observed in Northern Spain (GSA 06) and Strait of Sicily (GSA 16) (Table 2). Otherwise, the high proportion of spent fish in Gulf of Lion (GSA 07) may be explained by the common misclassification between phase I and phase VI, inducing to remove spent individuals 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 in the other study areas confirmed the sampling took place during the main spawning period (Table 2). In the case of eastern part of the Adriatic Sea (GSA 17E), where the sampling was carried out after the spawning peak (Table 1), the bigger total length recorded for immature fishes may be linked to difficulties in separating immature and spent fish by naked eye evaluation.

The unbalanced distribution of immature individuals is a well-known source of poor accuracy (Silva *et al.*, 2013; Basilone *et al.*, 2021), which resulted in larger confidence limits and less accurate L_{50} estimates. This 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 to improve accuracy and inter-comparability of the operators, even if a common sampling protocol and maturity scale are used.

Present results showed a 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 along the whole year reported L_{50} of about 10 cm (Lucio & Uriarte, 1990), while in the Mediterranean L_{50} was found between 10 cm and 11 cm (Tsiliras & Stergiou, 2013 and references therein), with the exception of the Adriatic Sea showing L_{50} values spanning between 8 cm and 10 cm (Sinovčić & Zorica, 2006 and references

therein). Lower maturity sizes probably derive from a difference in sampling protocol, as past studies 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, when considering as in the present study only samples from the main spawning season rather than from all months of the year (Motos, 1996; Somarakis, 1999). Over-exploitation of stocks as well as a change 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-life species with slow-growing strategy, which is not the case of anchovy that is a short-living species; however, such evidences from literature highlight the importance to include L_{50} as potential indicator for the impact of fisheries.

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

Spatial variability in L_{50} estimates identified mainly two groups (Table 3; Fig. 6): the first one includes Northern Spain, Strait of Sicily and Southern Adriatic where anchovy reached maturity at smaller sizes, compared to the second group including the Gulf of Lion, the Tyrrhenian Sea (both GSA 09 and GSA 10) and 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; Feuilloy *et al.*, 2020). Fish maturity, among other life history traits, is linked to the environmental productivity in each region (McBride *et al.*, 2015). The effects on reproductive behavior and traits may be explained by habitat peculiarity at 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, have been shown to induce changes in both the size at maturity and the fish condition (Duntill & Lambert, 2000; Wertheimer *et al.*, 2004). In the Strait of Sicily, gonad development has been associated to the chlorophyll amount variability (Basilone *et al.*, 2006), which appeared mainly driven by the oceanic circulation (Bonanno *et al.*, 2013; Rinaldi *et al.*, 2014). Differently to Sicilian waters, in the Northern Adriatic Sea a strong link has been observed between primary production and river inputs as well as in the Tyrrhenian Sea, particularly in central and Northern areas where the small pelagic are particularly concentrated (Santojanni *et al.*, 2014; Bonanno *et al.*, 2016). Similarly, in the Gulf of Lion anchovy biomass and spawning were positively affected by rivers runoff (Lloret *et al.*, 2004). In the Northern Spain, due to the wide extension of the GSA (Fig. 1), the Ebro river only partially influenced the water enrichment, while the water and nutrient circulations are mainly driven by the Northern current (Ospina-Alvarez *et al.*, 2012). The lower size at maturity in Southern Adriatic may be linked to the oligotrophic condition 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 up to the Gulf of Lion provided new insights on the maturity ecology of MEDIAS monitored anchovy stocks. Environmental variability experienced by fish in their own area (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 labs within the MEDIAS framework, present results highly suggest to increase the standardization level of collected data, specially trying to harmonize sampling periods as well as maturity stage assignment among areas/operators. Indeed, 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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References

- Abaunza, P., Fariña, A.C., Carrera, P., 1995. Geographic variations in sexual maturity of the hors mackerel, *Trachurus trachurus*, in the Galician and Cantabrian shelf. *Scientia Marina*, 59 (3–4), 211–222.
- Artioli, Y., Friedrich, J., Gilbert, A.J., McQuatters-Gollop, A., Mee, L.D., *et al.*, 2008. Nutrient budgets for European seas: a measure of the effectiveness of nutrient reduction policies. *Marine Pollution Bulletin*, 56, 1609–1617.
- Azen, R., and Traxel, N., 2009. Using Dominance Analysis to Determine Predictor Importance in Logistic Regression. *Journal of Educational and Behavioral Statistics*, 34(3), 319–347.
- Bănar, D., Mellon-Duval, C., Roos, D., Bigot, J.-L., Souplet, A., *et al.*, 2013. Trophic structure in the Gulf of Lions marine ecosystem (northwestern Mediterranean Sea) and fishing impacts. *Journal of Marine Systems*, 111–112, 45–68.
- Basilone, G., Guisande, C., Patti, B., Mazzola, S., Cuttitta, A., *et al.*, 2006. Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. *Fisheries oceanography*, 15 (4), 271–280.
- Basilone, G., Bonanno, A., Patti, B., Mazzola, S., Barra, M., *et al.*, 2013. Spawning site selection by European anchovy (*Engraulis encrasicolus*) in relation to oceanographic conditions in the Strait of Sicily. *Fisheries oceanography*, 22, 309–323.
- Basilone, G., Ferreri, R., Barra, M., Bonanno, A., Pulizzi, M., *et al.*, 2020. Spawning ecology of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily: Linking variations of zooplankton prey, fish density, growth, and reproduction in an upwelling system. *Progress in Oceanography*, 184, 102330.
- Basilone G, Ferreri R, Aronica S, Mazzola S, Bonanno A, *et al.*, 2021. Reproduction and Sexual Maturity of European Sardine (*Sardina pilchardus*) in the Central Mediterranean Sea. *Frontiers in Marine Science*, 715846.
- Bonanno, A., Zgozi, S., Cuttitta, A., ElTurki, A., Di Nieri, A., *et al.*, 2013. Influence of environmental variability on anchovy early life stages (*Engraulis encrasicolus*) in two different areas of the Central Mediterranean Sea. *Hydrobiologia*, 701 (1), 273–287.
- Bonanno, A., Placenti, F., Basilone, G., Mifsud, R., Genovese, S., *et al.*, 2014. Variability of water mass properties in the Strait of Sicily in summer period of 1998–2013. *Oceanographic Science*, 10, 759–770.
- Bonanno, A., Barra, M., Basilone, G., Genovese, S., Rumolo, P., *et al.*, 2016. Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. *Fisheries oceanography*, 25 (5), 471–490.

- Borcard, D., Gillet, F., Legendre, P., 2012. Numerical ecology with R. *Journal of Agricultural, Biological and Environmental Statistics*, 17 (2), 308-309.
- Brosset, P., Lloret, J., Muñoz, M., Fauvel, C., Van Beveren, E., *et al.*, 2016. Body reserves mediate trade-offs between life-history traits: new insights from small pelagic fish reproduction. *Royal Society Open Science*, 3, 160202.
- Coleman, F.C., Koenig, C.C., Huntsman, G.R., Musick, J.A., Eklund, A.M., *et al.*, 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries*, 25(3), 14–20.
- Conover, D.O., Munch, S.B., 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297, 94–96.
- Costa, A. M., 2009. Macroscopic vs. microscopic identification of the maturity stages of female horse mackerel. *ICES Journal of Marine Science* 66, 509–516.
- Darnaude, A.M., Salen-Picard, C., Polunin, N.V.C., Harmelin-Vivien, M.L., 2004. Trophodynamic linkage between river runoff and coastal fishery yield elucidated by stable isotope data in the Gulf of Lions (NW Mediterranean). *Oecologia*, 138, 325–332.
- Domínguez-Petit, R., Saborido-Rey, F., 2010. New bioenergetic perspective of European hake (*Merluccius merluccius* L.) reproductive ecology. *Fishery Researcher*, 104, 83–88.
- Dutil, J-D., Lambert, Y., 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 826-836.
- FAO, 2006. General Fisheries Commission for the Mediterranean/Commission générale des pêches pour la Méditerranée. Report of the ninth session of the Scientific Advisory Committee. Rome, 24–27 October 2006/Rapport de la neuvième session du Comité scientifique consultatif. Rome, 24-27 octobre 2006. FAO Fisheries Report/FAO Rapport sur les pêches, No 814, 106 pp.
- FAO, 2008. Fisheries management. 2 The ecosystem approach to fisheries. 2.1 Best practices in ecosystem modelling for informing and ecosystem approach to fisheries. FAO Technical Guidelines for Responsible Fisheries, 4(2) Add. 1, 78 pp.
- FAO, 2020. The State of Mediterranean and Black Sea Fisheries 2020. General Fisheries Commission for the Mediterranean. Rome. 175pp.
- Ferreri, R., Basilone, G., D'Elia, M., Traina, A., Saborido-Rey, F., *et al.*, 2009. Validation of macroscopic maturity stages according to microscopic histological examination for European anchovy. *Marine Ecology* 30, 181–187.
- Ferreri, R., McBride, R.S., Barra, M., Gargano, A., Mangano, S., *et al.*, 2019. Variation in size at maturity by horse mackerel (*Trachurus trachurus*) within the central Mediterranean Sea: Implications for investigating drivers of local productivity and applications for resource assessments. *Fisheries Research*, 211, 291–299.
- Feuilloley, G., Fromentin, J-M., Stemmann, L., Demarcq, L., Estournel, C., *et al.*, 2020. Concomitant changes in the environment and small pelagic fish community of the Gulf of Lions. *Progress in Oceanography*, 186, 102375.

- Fiorentino, F., Massuti, E., Tinti, F., Somarakis, S., Garofalo, G., *et al.*, 2014. Stock units: Identification of distinct biological units (stock units) for different fish and shellfish species and among different GFCM-GSA. STOCKMED Deliverable 03: Final Report. September 2014, 310 p.
- Fogarty, M., 2013. The art of ecosystem-based fishery management. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(3), 479–490.
- Fox, J., Monette, G., 1992. Generalized collinearity diagnostics. *Journal of American Statistical Association*, 87, 178–183.
- Ganias, K., Lowerre-Barbieri, S. K., Cooper, W., 2015. Understanding the determinate – indeterminate fecundity dichotomy in fish populations using a temperature dependent oocyte growth model. *Journal of Sea Research*, 96, 1–10.
- GFCM, 2009. Establishment of Geographical Sub-Areas in the GFCM area amending the resolution GFCM/31/2007/2, RES-GFCM/33/2009/2.
- Giraldez, A., Abad, R., 1995. Aspects on the reproductive biology of the western Mediterranean anchovy from the coasts of Málaga (Alboran Sea). *Scientia Marina*, 59, 15–23.
- Gücü, A.C., Inanmaz, Ö.E., Ok, M., Sakinan, S., 2017. Recent changes in the spawning grounds of Black Sea anchovy, *Engraulis encrasicolus*. *Fisheries Oceanography*, 25, 67–84.
- Huret, M., Tsiaras, K., Daewel, U., Skogen, M.D., Gatti, P., 2019. Variation in life-history traits of European anchovy along a latitudinal gradient: a bioenergetics modelling approach. *Marine Ecology Progress Series*, 617, 95-112.
- ICES, 2008. Report of the Workshop on Small Pelagics (*Sardina pilchardus*, *Engraulis encrasicolus*) maturity stages (WKSPMAT). ICES CM 2008/ACOM, 40. 82 pp.
- Lappalainen, A., Saks, L., Šuštar, M., Heikinheimo, O., Jürgens, K., *et al.*, 2016. Length at maturity as a potential indicator of fishing pressure effects on coastal pikeperch (*Sander lucioperca*) stocks in the northern Baltic Sea. *Fisheries Research*, 174, 47–57.
- Le Cren, E. D., 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the Perch (*Perca fluviatilis*). *Journal of Animal Ecology*, 20, 201–219.
- Leonori, I., Tičina, V., De Felice, A., Vidjak, O., Grubišić, L., *et al.*, 2012. Comparisons of two research vessels' properties in the acoustic surveys of small pelagic fish. *Acta Adriatica*, 53(3), 389-398.
- Lisovenko, L.A., Andrianov, D.P., 1996. Reproductive biology of anchovy (*Engraulis encrasicolus ponticus* Alexandrov 1927) in the Black Sea. *Scientia Marina*, 60 (Supl. 2), 209-218.
- Lloret, J., Palomera, I., Salat, J., Sole, I., 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). *Fisheries Oceanography*, 13, 102– 110.
- Lucio, P., Uriarte, A., 1990. Aspects of the reproductive biology of the anchovy (*Engraulis encrasicolus*, L. 1758) during 1987 and 1988 in the Bay of Biscay. ICES Document, CM 1990/H: 27.

- Magoulas A., Castillob, R., Caetano, S., Marcato, S., Patarnello, T., 2006. Mitochondrial DNA reveals a mosaic pattern of phylogeographical structure in Atlantic and Mediterranean populations of anchovy (*Engraulis encrasicolus*). *Molecular Phylogenetics and Evolution*, 39, 734–746.
- Malavolti, S., De Felice, A., Costantini, I., Biagiotti, I., Canduci, G., *et al.* 2018. Distribution of *Engraulis encrasicolus* eggs and larvae in relation to coastal oceanographic conditions (the South-western Adriatic Sea case study). *Mediterranean Marine Science*, 19(1), 180-192.
- Marteinsdottir, G., Begg, G. A., 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, 235, 235-256.
- McBride, R.S., Somarakis, S., Fitzhugh, G.R., Albert, A., Yaragina, N.A., *et al.*, 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, 16, 23-57.
- MEDIAS, 2019. MEDIAS handbook. Common protocol for the Pan-Mediterranean Acoustic Survey (MEDIAS): Athens, Greece, April 2019, 24 pp. <http://www.medias-project.eu/medias/website>
- Millot, C., 1990. The Gulf of Lions' hydrodynamics. *Continental Shelf Research*, 10, 885–894.
- Millot, C., Taupier-Letage, I., 2005. Circulation in the Mediterranean Sea. *The Handbook of Environmental Chemistry*, K, 29–66.
- Morgan, M. J., 2004. The relationship between fish condition and the probability of being mature in American plaice (*Hippoglossoides platessoides*). *ICES Journal of Marine Science*, 61: 64-70.
- Morgan, M. J., 2018. Understanding biology to improve advice for fisheries management. *ICES Journal of Marine Science*, 75(3), 923–931.
- Motos, L., 1996. Reproductive biology and fecundity of the Bay of Biscay anchovy population (*Engraulis encrasicolus* L.). *Scientia Marina*, 60 (Suppl. 2), 195-207.
- Navarrete, C. B., Soares, F. C., 2020. dominanceanalysis: Dominance Analysis. R package <https://CRAN.R-project.org/package=dominanceanalysis>
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., *et al.*, 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428, 932–935.
- Ospina-Alvarez, A., Parada, C., Palomera, I., 2012. Vertical migration effects on the dispersion and recruitment of European anchovy larvae: from spawning to nursery areas. *Ecological Modelling*, 231, 65–79.
- Özsoy, E., Ünlüata, Ü., 1997. Oceanography of the Black Sea: a review of some recent results. *Earth-Science Reviews*, 42, 231–272.
- Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., *et al.*, 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Progress in Oceanography*, 74, 377–396.
- Pešić, A., Regner, S., Mandić, M., Ikica, Z., Đurović, M., *et al.*, 2013. Biological characteristics of anchovy (*Engraulis encrasicolus*) in Bokakotorska Bay (Montenegro). *VI International Conference "Water & Fish"*, 197-203.

- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rahmani, K., Koudache, F., 2020. Reproductive biology of horse mackerel, genus *Trachurus* Rafinesque, 1810 (Perciformes Carangidae), caught in Béni-Saf Bay, W-Mediterranean Sea (Algeria). *Biodiversity Journal*, 11 (2), 389–398.
- Rinaldi, E., 2012. Satellite and in Situ Data Integrated Analysis to Study the Upper Ocean and Coastal Environment of the Italian Seas. PhDthesis. Alma Mater Studiorum Università di Bologna.
- Rinaldi, E., Buongiorno Nardelli, B., Volpe, G., Santoleri, R., 2014. Chlorophyll distribution and variability in the Sicily Channel (Mediterranean Sea) as seen by remote sensing data. *Continental Shelf Research*, 77, 61-68.
- Robinson, A. R., Sellschopp, J., Warn-Varnas, A., Leslie, W. G., Lozano, C. J., *et al.*, 1999. The Atlantic Ionian Stream, *Journal of Marine Systems*, 20, 129–156.
- Ruggeri, P., Splendiani, A., Occhipinti, G., Fioravanti, T., Santojanni, A. *et al.*, 2016. Biocomplexity in populations of European anchovy in the Adriatic Sea. *PLoS ONE*, 11 (4), 1–21.
- Santojanni, A., Arneri, E., Bernardini, V., Cingolani, N., Di Marco, M., *et al.*, 2006. Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. *Climate Research*, 31, 181–193.
- Silva, A., Santos, M. B., Caneco, B., Pestana, G., Porteiro, C., *et al.*, 2006. Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and the western Mediterranean. *ICES Journal of Marine Science*, 63, 663-676.
- Silva, A., Faria, S., Nunes, C., 2013. Long-term changes in maturation of sardine, *Sardina pilchardus*, in Portuguese waters. *Scientia Marina*, 77, 429–438.
- Sinovčić, G., Zorica, B., 2006. Reproductive cycle and minimal length at sexual maturity of *Engraulis encrasicolus* (L.) in the Zrmanja River estuary (Adriatic Sea, Croatia). *Estuarine, Coastal and Shelf Science*, 69, 439-448.
- Somarakis, S., 1999. Ichthyoplankton of the NE Aegean with emphasis on anchovy, *Engraulis encrasicolus* (Linnaeus, 1758) (June 1993, 1994, 1995, 1996). PhD thesis, University of Crete.
- Somarakis, S., Maraveya, E., Tsimenides, N., 2000. Multispecies ichthyoplankton associations in epipelagic species: is there any intrinsic adaptive function? *Belgian Journal of Zoology*, 130, 125-129.
- Somarakis, S., Palomera, I., Garcia, A., Quintanilla, L., Koutsikopoulos, C., *et al.*, 2004. Daily egg production of anchovy in European waters. *ICES Journal of Marine Science*, 61, 944-958.
- STECF, 2016. Reports of the Scientific, Technical and Economic Committee for Fisheries (STECF) - Methodology for the stock assessments in the Mediterranean Sea (STECF-16-14). JCR102680. 168 pp.
- Tičina V., Katavić, I., Dadić, V., Marasović, I., Kršinić, F., *et al.*, 2006. Acoustic estimates of small pelagic fish stocks in the eastern part of Adriatic Sea. Proceedings of GFCM-SAC WG on Identification of

- Reference Points for the management of fishery resources, Roma, 20-21 April 2004, *Biologia Marina Mediterranea*, 13(3), part 2, 124-136.
- Tičina, V., Katavić, I., Grubišić, L., 2020. Marine Aquaculture Impacts on Marine Biota in Oligotrophic Environments of the Mediterranean Sea - A Review. *Frontiers in Marine Science*, 7:217.
- Tsikliras, A.C., Koutrakis, E.T., 2013. Growth and reproduction of European sardine, *Sardina pilchardus* (Pisces: Clupeidae), in northeastern Mediterranean. *Cahiers de Biologie Marine*, 54, 365-374.
- Tsikliras A. C., Stergiou, K. I., 2013. Size at maturity of Mediterranean marine fishes. *Reviews in Fish Biology and Fisheries*, 20, 499-538.
- Ventero, A., Iglesias, M., Villamor, B., 2017. Anchovy (*Engraulis encrasicolus*) otoliths reveal growth differences between two areas of the Spanish Mediterranean Sea. *Scientia Marina*, 81, 327-337.
- Wertheimer A.C., Heard W.R., Maselko J.M., Smoker W.W., 2004. Relationship of size at return with environmental variation, hatchery production, and productivity of wild pink salmon in Prince William Sound, Alaska: does it matter? *Reviews in Fish Biology and Fisheries*, 14,321–334.
- Winton, M. V., Wuenschel, M. J., McBride, R. S., 2014. Investigating spatial variation and temperature effects on maturity of female winter flounder (*Pseudopleuronectes americanus*) using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 1279-1290.
- Zavatarelli, M., Raicich, F., Bregant, D., Russo, A., Artegiani, A., 1998. Climatological biogeochemical characteristics of the Adriatic Sea. *Journal of Marine Systems*, 18, 227–263.

Table

Table 1: Area (Geographical Sub-Area, GSA) and sampling period. Sampling months were abbreviated as follows: 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

1 **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
 2 individuals is provided in parenthesis.
 3

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)

4 Table 3: Analysis of Deviance Table, terms significance and GVIF values relative to the model accounting
 5 for study area (Geographical Sub-Area, GSA), sex, condition factor (CF) and total length (TL; mm) and
 6 trawl latitude. $GVIF^{(1/(2*Df))}$ allows to compare GVIF values among explanatory variables by correcting for
 7 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

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Table 4. Size (in 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)

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15 **Figure Captions**

16 **Figure 1.** The geographical subareas (GSAs) identified by the General Fisheries Commission for the
17 Mediterranean (GFCM) (source: <http://www.fao.org/gfcm/about/area-of-application/ru/>), including the
18 study areas (from West to East): Northern Spain (GSA 06); Gulf of Lion (GSA 07); Northern Tyrrhenian
19 Sea (GSA 09); Southern Tyrrhenian Sea (GSA10); South of Sicily (GSA 16); Adriatic Sea (GSA 17); Southern
20 Adriatic Sea (GSA 18); Black Sea (GSA 29). Black stars identified the study area.

21
22 **Figure 2.** Female (upper panel) and male (lower panel) size distribution (Total Length, mm) per maturity
23 state (i.e., immature or mature) within each study area (Geographical Sub-Area, GSA). Dotted line
24 separates immature (i; left of the panels) and mature (m; right of the panels) fish.

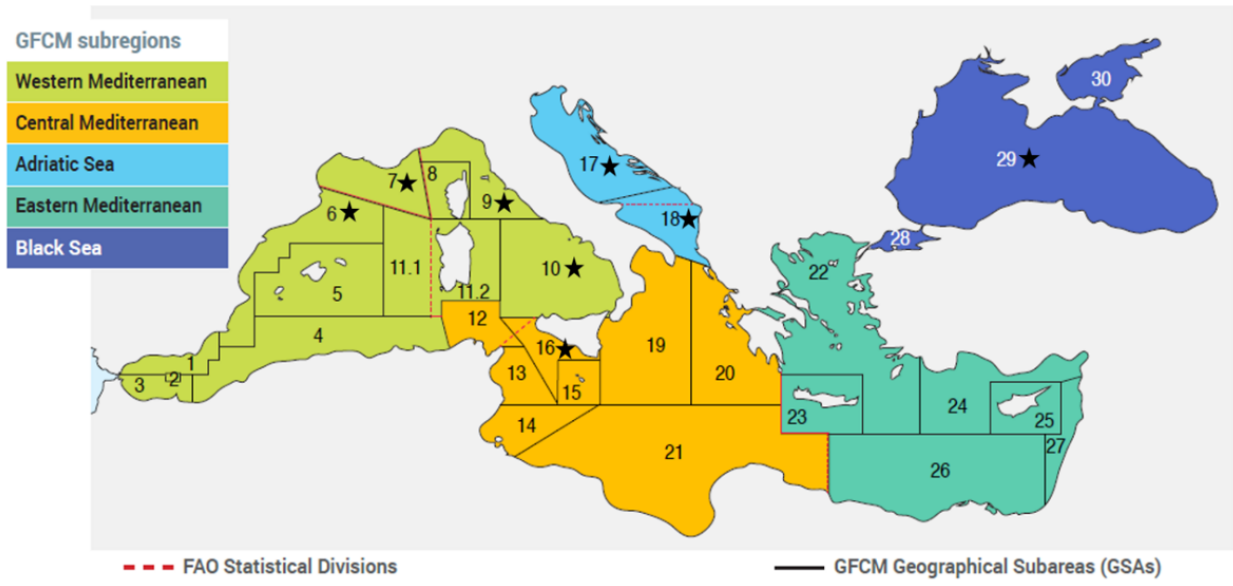
25
26 **Figure 3.** Maturity ogives (solid line) for each study area (Geographical Sub-Area, GSA) with 95%
27 confidence intervals (shadow area) for both male (M) and female (F) anchovies.

28
29 **Figure 4.** Predicted values of proportion of mature females at length assuming different condition factor
30 values (i.e., CF=0.7; CF=1; CF=1.3) for each study area (Geographical Sub-Area, GSA). The shadow area
31 represent the 95% confidence intervals for each maturity ogive.

32
33 **Figure 5.** Predicted values of proportion of mature males at length assuming different condition factor
34 values (i.e., CF=0.7; CF=1; CF=1.3) for each study area (Geographical Sub-Area, GSA). The shadow area
35 represent the 95% confidence intervals for each maturity ogive.

36
37 **Figure 6.** Comparison of male and female length at maturity (L_{50} , mm) for the study areas (Geographical
38 Sub-Area, GSA) sampled during the spawning peak: Northern Spain (GSA 06); Gulf of Lion (GSA 07);
39 Northern Tyrrhenian Sea (GSA 09); Southern Tyrrhenian Sea (GSA10); South of Sicily (GSA 16);
40 Northwestern Adriatic Sea (GSA 17W); Southern Adriatic Sea (GSA 18). Bars displayed the 95%
41 confidence limits.

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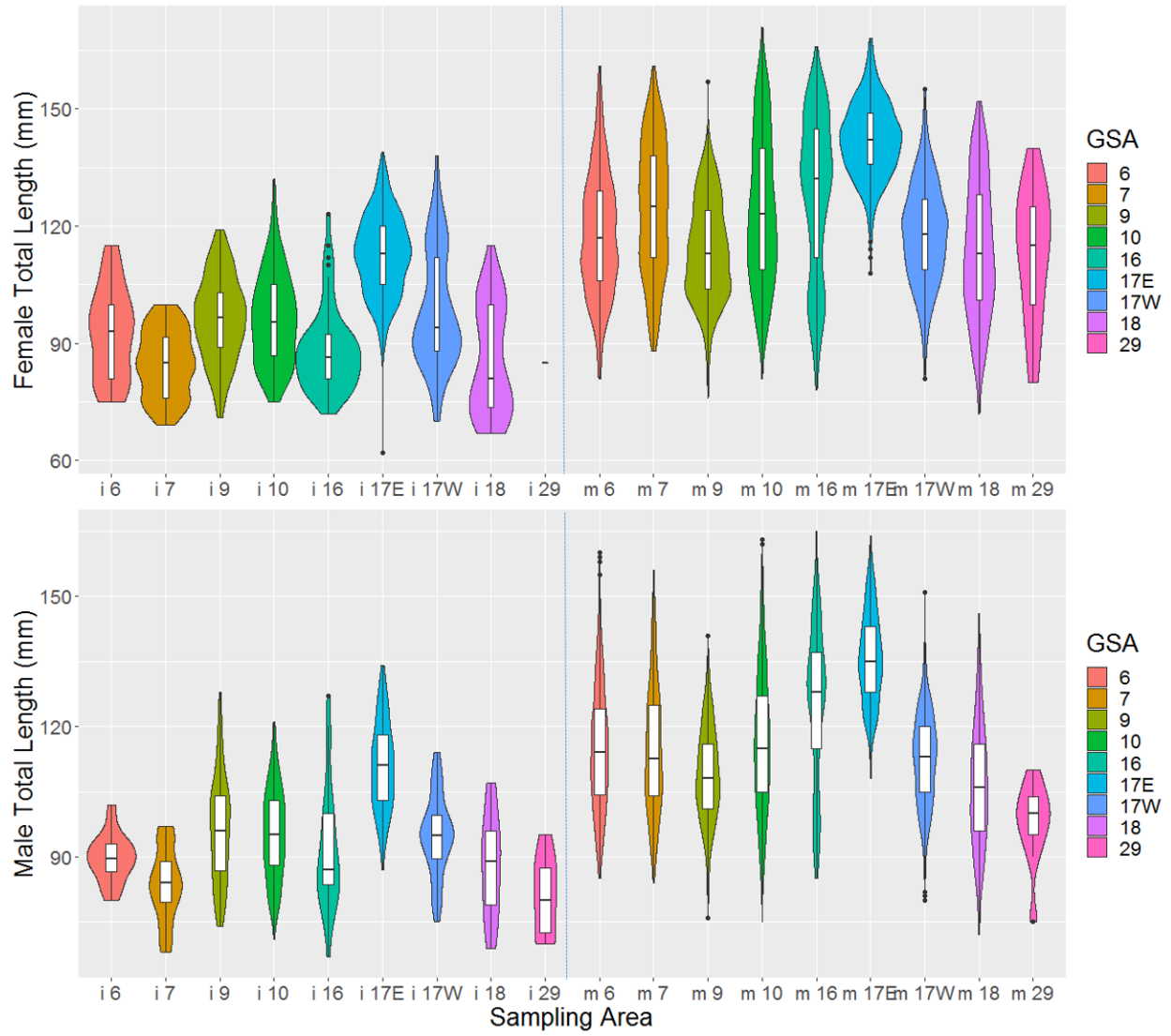


GFCM GSAs

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

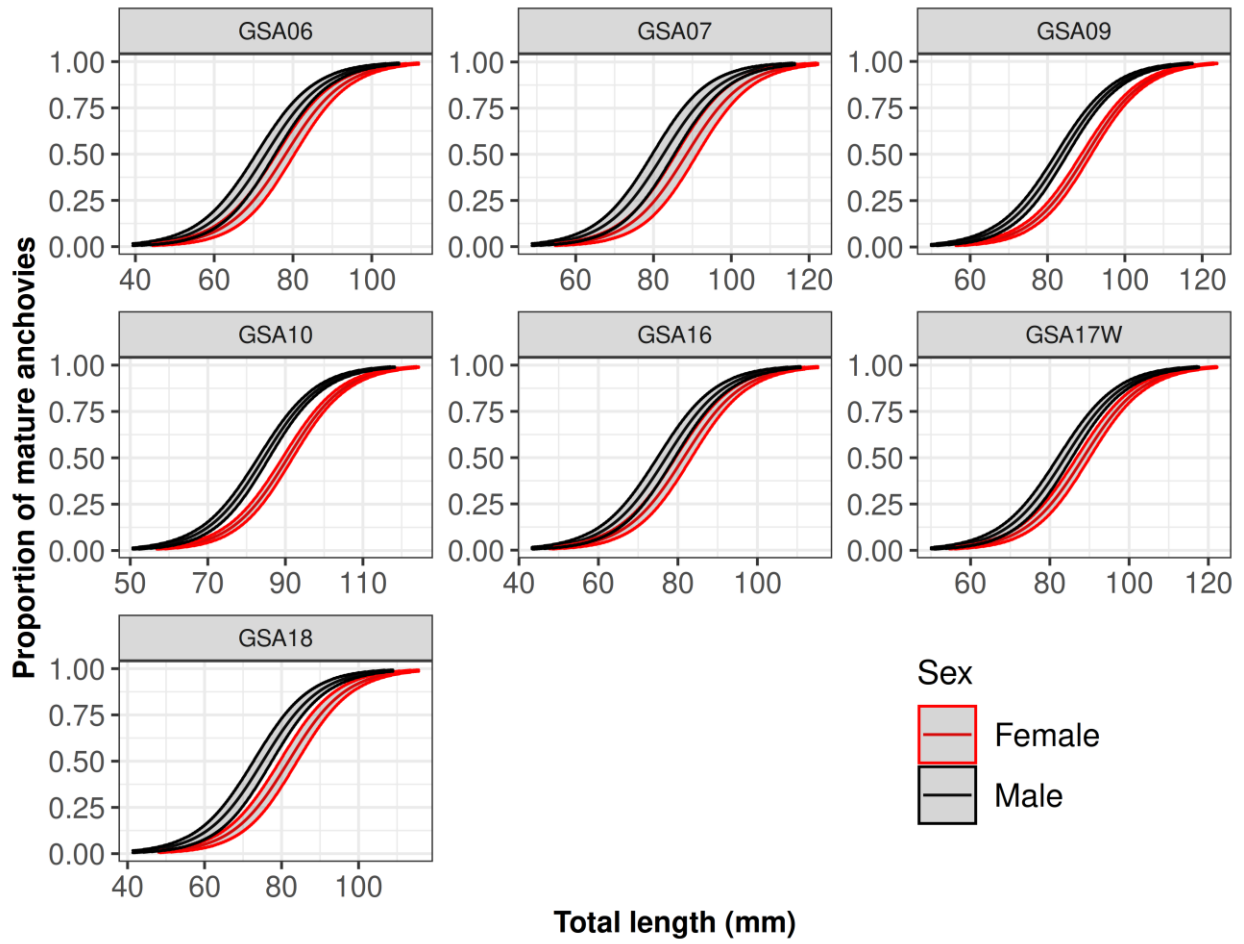
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Fig. 1

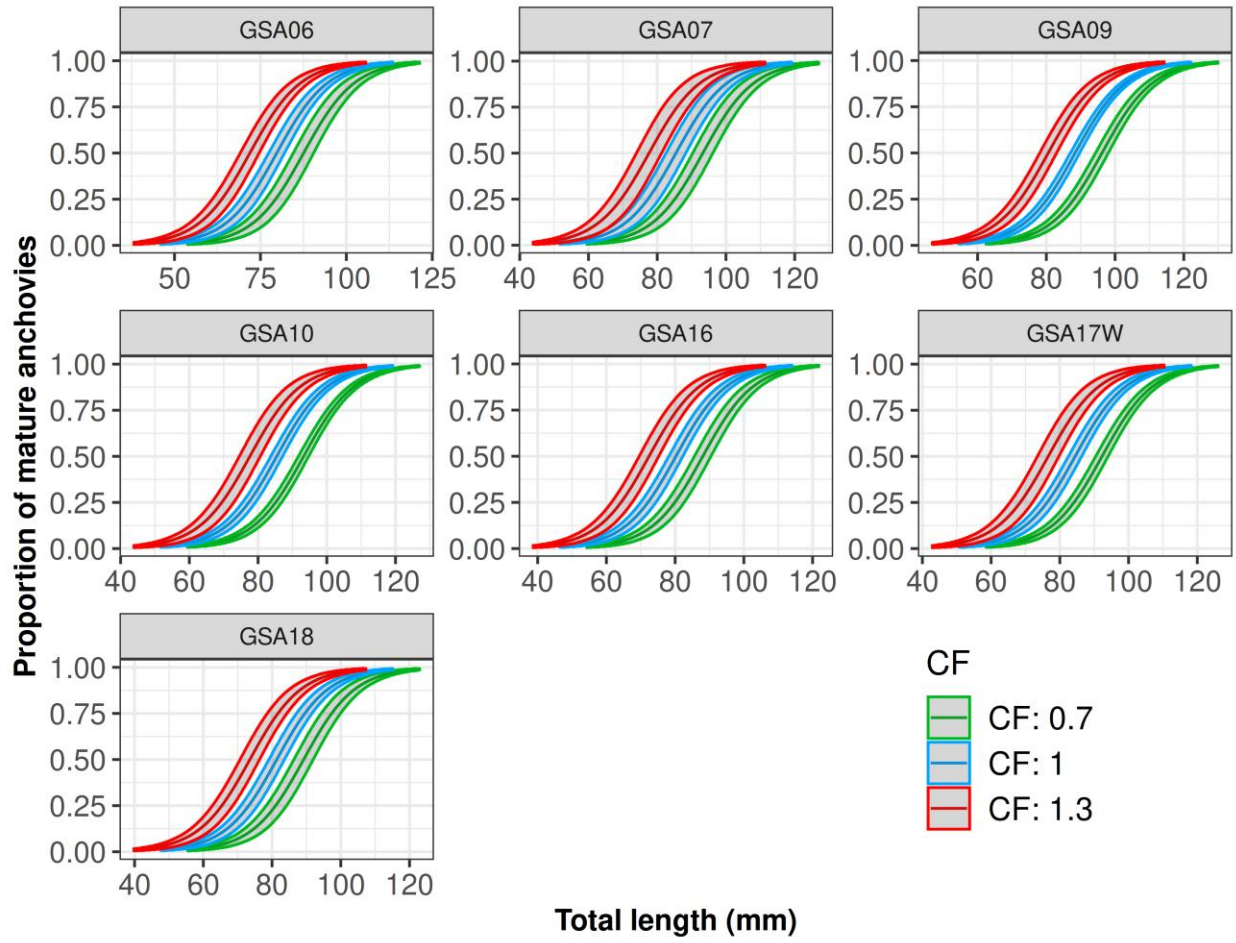


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Fig. 2

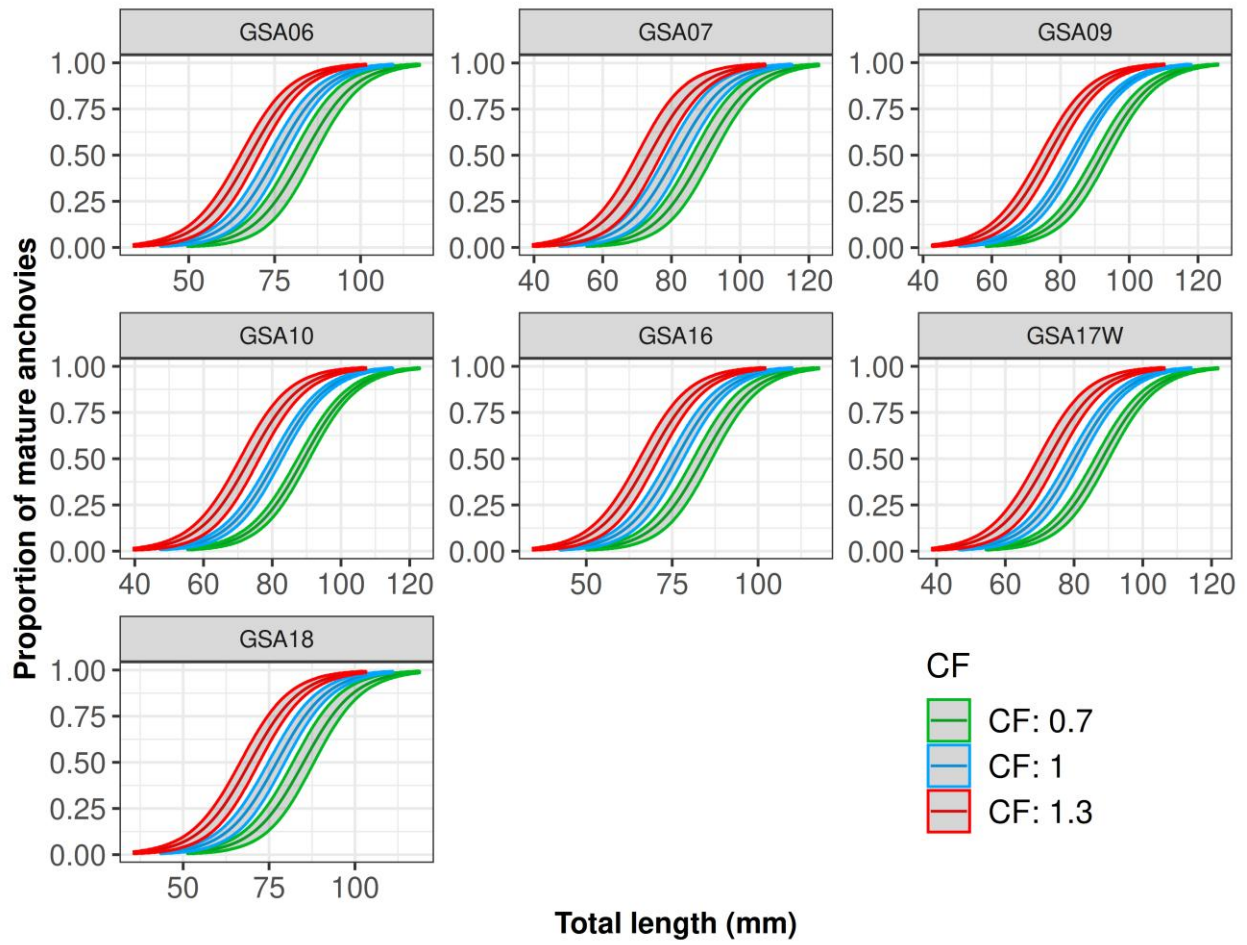


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60 Fig. 3

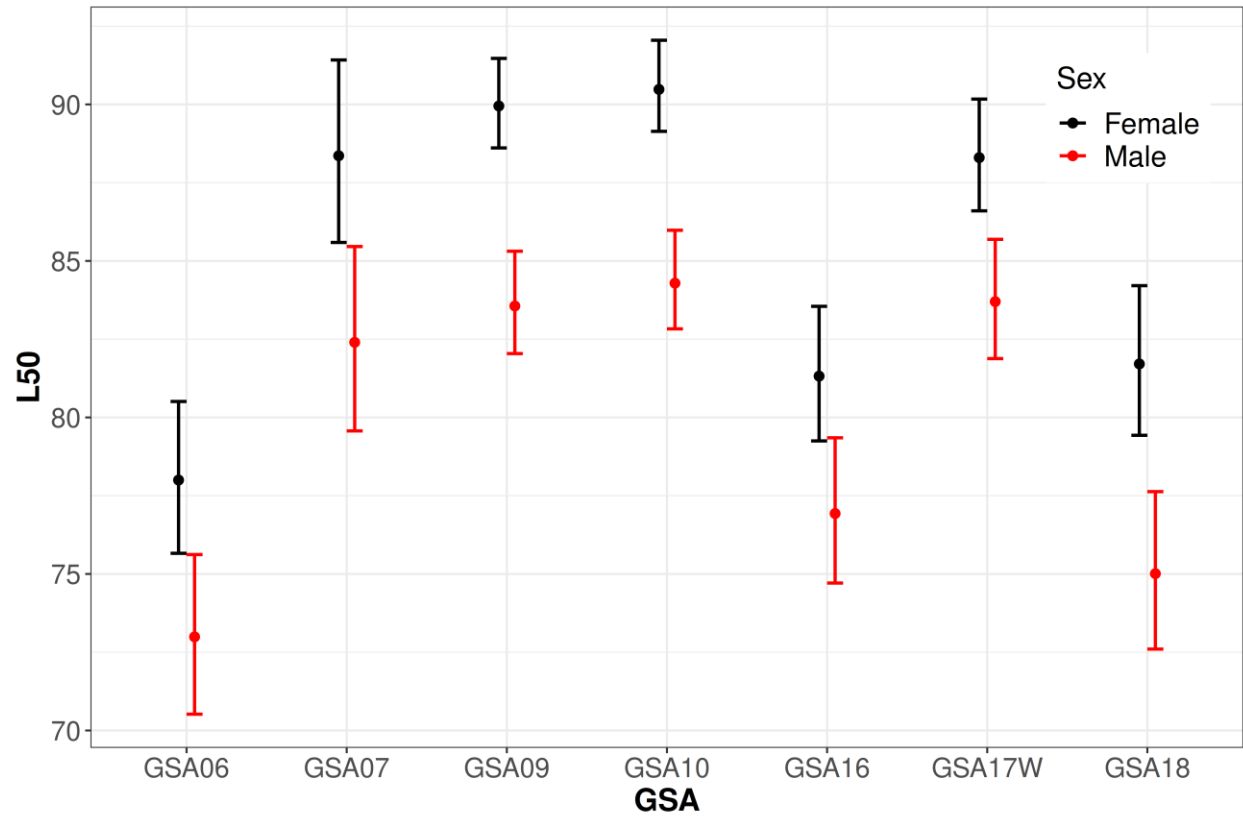


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 62 Fig. 4
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