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Life history traits and spatial patterns of five mid-size pelagic fish species of the Gulf of Cadiz



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Máster en Acuicultura y Pesca. Recursos Marinos y Sostenibilidad

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**Life history traits and spatial patterns of five mid-size pelagic fish species of the
Gulf of Cadiz**

Memoria presentada por José Antonio Canseco Rodríguez para la obtención del
Título de Máster en Acuicultura y Pesca
(Perfil Investigador)

Firma del Alumno

A handwritten signature in blue ink, consisting of several overlapping, fluid strokes that form a cursive representation of the name José Antonio Canseco Rodríguez.

Fdo.: José Antonio Canseco Rodríguez

Puerto Real, a 30 de Noviembre de 2016

TESIS DE MASTER (PERFIL INVESTIGADOR)
MASTER ACUICULTURA Y PESCA

María Ángeles Torres Leal, Doctora en Ciencias del Mar, Fernando Ramos, Licenciado en Biología y Antonio Medina, Doctor en Biología, como Tutores del Trabajo Fin de Máster titulado "Life history traits and spatial patterns of five mid-size pelagic fish species of the Gulf of Cadiz", realizada por "José Antonio Canseco Rodríguez",

INFORMAN: que el trabajo presentado en la presente memoria se ha llevado a cabo bajo nuestra tutorización en las dependencias del Instituto Español de Oceanografía, Centro Oceanográfico de Cádiz

Y para que así conste firmamos el presente informe en Cádiz, a 30 de Noviembre de 2016

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Abstract/Resumen

In the last decades, there has been an increasing interest on mid-size pelagic fish species (MSPFS) based on their economic and ecological importance in the marine ecosystems. The main goal of the present is to report novel information on the life history traits (size composition, reproductive aspects, condition status, age structure and growth) and spatial distribution (latitude, longitude and depth) of five MSPFS, belonging to the genus *Scomber* and *Trachurus*, in the Gulf of Cadiz shelf waters analyzing summer survey data (2007-2015). The main findings showed that their respective populations make a different use of the surveyed area, showing different population structures and reproductive and condition states. *Scomber scombrus* and *Trachurus mediterraneus* had the more restricted spatial distribution. It is hope that these new insights will contribute to the implementation of ecosystem-based approaches aimed to reach sustainable fisheries in the study area.

En las últimas décadas, se ha incrementado el interés por los peces pelágicos de mediano tamaño debido a su importancia económica y ecológica en los ecosistemas marinos. El principal objetivo del presente trabajo es presentar información inédita acerca de la historia de vida (composición de tallas, aspectos reproductivos, estado de condición, estructura demográfica y crecimiento) y la distribución espacial (en función de la longitud, latitud y profundidad) de cinco especies de peces pelágicos de mediano tamaño del Golfo de Cádiz, pertenecientes a los géneros *Scomber* y *Trachurus*, analizando datos de campañas realizadas en verano (2007-2015). Los resultados más relevantes mostraron que cada población hace un uso diferente del área, mostrando diferentes estructuras poblacionales y estados reproductivos y de condición. *Scomber scombrus* y *Trachurus mediterraneus* presentaron una distribución espacial más restringida. Se espera que estos nuevos hallazgos contribuyan a la implementación de enfoques ecosistémicos que permitan una gestión sostenible de la pesca en el área de estudio.

Keywords: demographic structure, age, center of gravity, Scombridae, Carangidae, length-weight relationships, growth pattern, maturity, distribution range

1. Introduction

Mid-size pelagic fish species (MSPFS) comprise a group of teleost families that share common characteristics such as inhabiting the pelagic habitat, feeding primarily on planktonic preys, showing common coloration patterns and forming schools aimed to avoid predation by top-predators (Ben Tuvia, 1995; Hemelrijk et al., 2005; Zheng et al., 2005). These fishes are usually speedy swimmers, which allow them to migrate long distances. In most exploited marine ecosystems, their contribution to the global fishery catch is of great relevance (Ben Tuvia, 1995). For example, in 2014 seven of the top ten most fished species were MSPFS (FAO, 2016). Therefore, fluctuations in the MSPFS populations might have important economic impacts in addition to ecological consequences in the structure and functioning of any marine ecosystem.

The Gulf of Cadiz (GoC) is an Atlantic marine ecosystem located at the South of the Iberian Peninsula including both Portuguese and Spanish waters. It corresponds to Subdivision 9.a-South established by the International Council for the Exploration of the Sea (ICES, 2016a; www.ices.dk). In this region, fisheries are an important socio-economic supply (Sobrino et al., 1994; Ramos et al., 2012; Leitão et al., 2014). Nevertheless, they have been also recognized to exert overall negative impacts on marine biodiversity (Torres et al., 2013). In general, the main fisheries operating in the area include trawling, purse seining and artisanal. MSPFS including mackerel *Scomber scombrus* (Linnaeus, 1758), Atlantic chub mackerel *Scomber colias* (Gmelin, 1789), horse mackerel *Trachurus trachurus* (Linnaeus, 1758), Mediterranean horse mackerel *Trachurus mediterraneus* (Steindachner, 1868) and blue jack mackerel (*Trachurus picturatus* (Bowdich, 1825)) are exploited, almost exclusively, by trawling and purse seining fisheries (Millán, 1992; Silva et al., 2007; ICES, 2010). In the area, this latter fishery targets mainly European anchovy (*Engraulis encrasicolus*), but also sardine (*Sardina pilchardus*) but additionally both mackerels (*S. scombrus* and *S. colias*) are also caught, primarily in the summer (Millán, 1992; Silva et al., 2007). On the other hand, the Atlantic horse mackerel (*T. trachurus*) is a target species for certain bottom trawling *metiers* and by-catch for the purse seining fishery whereas the

Mediterranean horse mackerel (*T. mediterraneus*) is considered as by-catch for the bottom trawling and purse seining fisheries, respectively. In addition, blue jack mackerel (*T. picturatus*) is caught mainly by Portuguese purse seiners in the coastal Southern Portugal and the Azores islands (ICES, 2016). The contribution of each species targeted to the total fishery catch in the area varies in relation to seasonality (IEO Database).

The information regarding the main pelagic fishes in the area is focused mostly on the small pelagic fish species (SPFS) anchovy and sardine (Rodríguez-Roda, 1970, 1977; Millán, 1999; Bellido et al., 2000; Ruíz et al., 2006; Ruíz et al., 2009; Catalán et al., 2014). More recently, studies on trophic ecology of tuna (*Thunnus thynnus*) (Valera, 2012), and its interaction with the fishery and the killer whales (*Orcinus orca*) near the Strait of Gibraltar have been also published (Esteban et al., 2014). However, knowledge on the life history traits and spatial distribution of MSPFS remains scarce in the area, despite these species have been identified as important resources both economically and within the GoC food-web (Rodríguez-Roda, 1982; Ramos et al., 2005; Martins, 2007; Velasco et al., 2011; Ramos et al., 2012; Torres et al., 2013). Up-to-date, the only existing data of such species derives from the local summer surveys (ECOCADIZ: acoustic assessment and BOCADEVA: Daily Egg Production Method (DEPM)). However, these datasets generated have not been so far analyzed. Therefore, the coming information would provide novel insights on the biology and ecology of the MSPFS in the area.

Currently, stocks management units have already been established for *S. scombrus* (North Eastern Atlantic Mackerel Stock; ICES, 2016b), *T. trachurus* (South Horse Mackerel Stock; ICES, 2016c) and *T. picturatus* (Blue Jack Mackerel Azores Stock; ICES, 2016d). The ICES Working Groups involved in the annual assessment of these three stocks have recently concluded that only *T. trachurus* has shown stability over time. However, assessment outputs regarding *S. scombrus* are contradictory, establishing a precautionary approach to its management. The basis of this precautionary approach to its management is to exercise cautious predictions aimed to avoid overfishing. Finally, *T. picturatus* is exploited under the F_{msy} (Fishing mortality for a Maximum Sustainable Yield) as a precautionary

measure (ICES, 2016d). However, the remaining species (i.e. *S. colias* and *T. mediterraneus*) have not yet been assigned as management units, underlying the importance of addressing studies aimed to unraveling their importance in a fisheries management perspective.

Stocks discrimination has important implications in fisheries management as allows defining the structure and functioning of fish populations (Begg et al., 1999a; Abaunza, 2008a). For example, fisheries managers recognize the importance of characterizing the habitat of the fish stocks by means of accurate maps (Rubec et al., 1998; Friel, 2000). Therefore, an accurate mapping showing the spatial distribution including temporal variation is requested for achieving biodiversity and conservation goals as well as more sustainable fishing (Rubec et al., 1996; Ault et al., 1999). On the other hand, in the context of stock assessment modelling, age and growth estimates are requested as inputs (Hilborn et al., 1992). Therefore, this information is often required together with other life history traits to proper evaluate fish stocks.

In the last decades, the scientific community has encouraged the need of integrating knowledge of biology, ecology and environment drivers (both natural (e.g. oceanographic parameters such as temperature, salinity and dissolved oxygen concentration) and anthropogenic stressors (e.g. fishing) to reach operational ecosystem-based fisheries management (EBFM) of marine living resources (Garcia et al., 2003). This framework is known to account for the major ecosystem components and services to reach sustainable fisheries. The key goal of this new style of management is to rebuild marine ecosystems at high levels of productivity and biological diversity (Garcia et al., 2003). In Europe, the Marine Strategy Framework Directive (MSFD) aims to achieve 'good environmental status (GES)' of European marine waters by 2020 (EU Directive 2008/56/EC). This Directive promotes the ecosystem approach to the management of human activities having an impact on the marine environment, integrating the concepts of environmental protection and sustainable use. To achieve GES, the Directive lists 11 Descriptors associated to specific criteria and indicators, requesting information of biological and ecological traits of

MSPFS for Descriptor 1 (Biodiversity is maintained) and Descriptor 3 (The population of commercial fish species is healthy).

Hence, the overall aim of this study is to provide novel information of life history traits and spatial patterns of five mid-size pelagic fish species (i.e. *S. colias*, *S. scombrus*, *T. trachurus*, *T. mediterraneus* and *T. picturatus*) aimed to contribute to the implementation of ecosystem-based approaches and the MSFD in the Gulf of Cadiz. To this end, time-series of the ECOCADIZ and BOCADEVA summer surveys covering the continental shelf were analyzed for the period 2007-2015. Therefore, the results obtained will be analyzed and presented for this spatial-temporal window. In particular, two objectives are addressed in this study:

- 1) To characterize the demographic structure of the populations of the five selected MSPFS inhabiting the Gulf of Cadiz shelf waters in summer in terms of size composition, reproductive and condition status, age structure and growth patterns.
- 2) To describe spatial patterns of distribution over time of the five selected MSPFS to better understand their habitat preferences.

2. Material and methodology

2.1. Study area

The GoC is the southernmost European Atlantic marine ecosystem (Figure 1) (see Ramos et al. (2012) for a complete review of the Spanish waters). From an assessment management perspective, it is the southernmost part of the ICES Ecoregion *Bay of Biscay and Iberian coasts* Ecoregion, which coincides with the OSPAR convention *Region IV* (www.ospar.org). The continental shelf east of Cabo de Santa María is between 30 and 50 km wide while to the west is much narrower (15 km) where very abrupt bottoms in which submarine canyons are the main geo-morphological characteristic (Criado-Aldeanueva et al., 2006). The main oceanographic feature in the Gulf of Cadiz is the continuous exchange of water masses between the Atlantic Ocean and the Mediterranean Sea through the

Strait of Gibraltar (Bryden et al., 1994; Bellanco and Sánchez-Leal, 2016), which allows the formation of diverse biological communities and an increased primary production in the area (Ramos et al., 2012 and references therein).

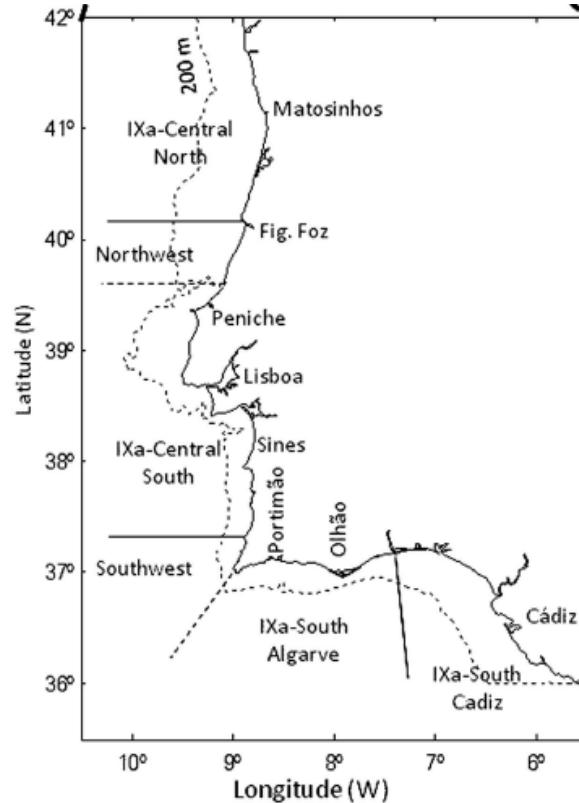


Figure 1: Map of the study area: Gulf of Cadiz (ICES, IXa South).

2.2. Data collection

2.2.1. Biological data

The biological data used in this study were taken after each fishing station during five ECOCADIZ surveys (2007, 2009, 2013, 2014 and 2015) and two BOCADEVA surveys (2008 and 2011), carried out by the Instituto Español de Oceanografía (IEO) (Figure 2). ECOCADIZ acoustic surveys take place yearly in summer (July-August) and are aimed to assess the Gulf of Cadiz SPFS and MSPFS populations through eco-integration (Nakken et al., 1975; Simmonds and MacLennan, 2005). The ECOCADIZ fishing stations for echo trace ground-truthing followed an opportunistic sampling scheme according to the echogram

information. The sampled depths comprised the Gulf of Cadiz continental shelf waters between 20 and 200 m depth. On the other hand, the BOCADEVA survey fishing stations also followed an opportunistic sampling scheme, but the objective of this sampling was to gather information of the anchovy adult population. The fishing hauls were carried out using either a 16 m- mean vertical opening (“Tuneado gear”) or a 20 m-mean vertical opening (“Gran Hermano gear”) trawl at a mean speed of 4 knots; all the fishing hauls were performed during daytime. Length frequency distributions (LFD) measured at 0.5 cm size classes were obtained for all the fish species. Finally, a sub-sample was measured (150-200 individuals) whenever possible (Ramos et al., 2014). The BOCADEVA Series Gulf of Cadiz Anchovy DEPM surveys are undertaken every three years; while the ECOCADIZ acoustic surveys take place once a year. Both surveys do not overlap the same year, therefore they take place alternatively. Despite both surveys are designed for different purposes, the ground trawling fishing hauls are always opportunistic. In 2010, the ECOCADIZ survey was restricted from Cabo de Trafalgar to Cabo de Santa Maria, reason why these data were excluded from the analyses. In 2012, unfortunately the survey did not take place.

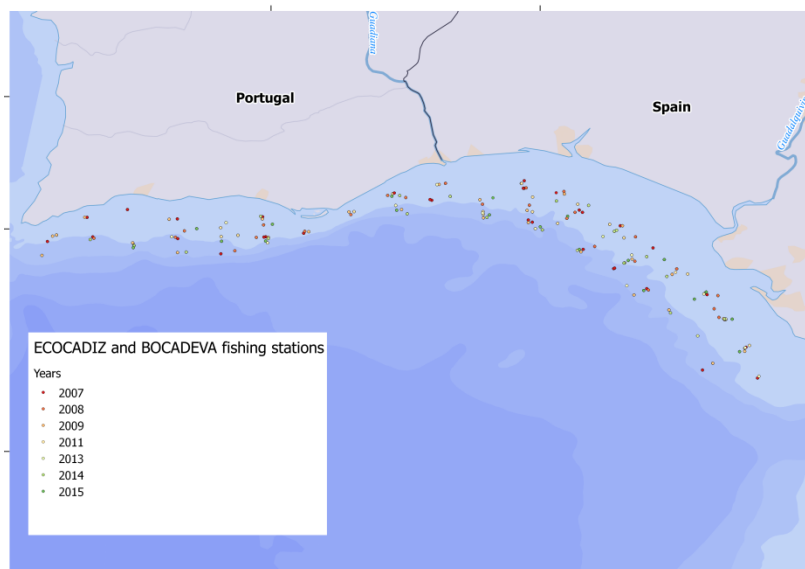


Figure 2: Fishing stations of the ECOCADIZ and BOCADEVA surveys series (2007-2015) in the Gulf of Cadiz.

During the surveys, the biological sampling is performed onboard in two stages. The first stage consists in randomly sampling 50 specimens after each fishing haul. The second stage involves gathering, for both Portuguese and Spanish waters, as many specimens as necessary by size class to complete the size distribution tails. This sampling strategy allows to characterize the overall population by size class. The parameters measured per each specimen were: a) total length (LT, mm), b) wet weight (WW, gr), c) maturity stage (MS) according to a 6-step macroscopical scale (1-virgin or resting, 2-maturing, 3-pre-spawning, 4-spawning, 5-partial post spawning, 6-final post-spawning), based on color, morphology and turgidity of the gonads as well as the oocyte size (in females) and presence of fluent sperm (in males), d) stomach repletion (Sr) using a visual scale (1-empty, 2-almost empty, 3-medium, 4-almost full, 5-full, 6-evaginated), e) sex (S) defined by visual inspection of the gonads (1-male, 2-female, 3-indetermined, 4-hermafrodite), f) gonad wet weight (GWW, gr), and g) eviscerated wet weight, i.e. by removing intestine, stomach, gonads and liver (EWW, gr). Finally, this information was used to estimate the life history traits of the five MSPFS.

2.2.1.1. Size composition

- Length-frequency distribution (LFD)

Length-frequency distributions were represented for the species and both sexes separately. All statistical analyses were conducted and coded in R (v 3.1.1) using the t-series library (Trapletti and Hornik, 2016). Length distribution histograms were plotted using the ggplot2 package (Wickham, 2016). Sexual differences by size were statistically tested within each survey by Kruskal-Wallis tests.

2.2.1.2. Reproductive parameters

- Sex ratio (SR)

Sex ratio of the five MSPFS was calculated based on the equation (Eq. 1):

$$SR = (\text{number of females} / \text{number of males}) * 100 \quad (\text{Eq. 1})$$

To test significant deviation from a 1:1 sex-ratio, Chi-square tests were applied with a significance level set at 0.05.

- Maturity stage and Length at First Maturity (LFM)

The reproductive state of the sampled populations of each analyzed species was assessed from the percentage of occurrence of the maturity stages in the pooled samples from each survey.

The possibility of estimating the species' length at first maturity (i.e. size at which 50% of the individuals sampled are mature) was further explored according to the reproductive condition exhibited by the species during the survey season. When LFM was possible to be computed, this size was estimated by fitting the proportion of mature specimens by size class to a logistic function (Eq. 2):

$$P(L) = 1 / (1 + \exp(-aL + b)) \quad (\text{Eq. 2})$$

where P is the proportion of mature specimens, a and b are the parameters estimated of the logistic function and L is the total length of the fish. LFM is then calculated from such proportion (Eq. 3):

$$\text{LFM} = a/b \quad (\text{Eq. 3})$$

Kruskal Wallis non-parametric analyses of variance were conducted to test significant differences in length by maturity stage. The power analysis was conducted using an alpha of 0.05.

2.2.1.3. Relative growth and condition status

- Length-weight relationship (LWR)

The LWR parameters were calculated using the classical equation (Eq. 4):

$$W = a L^b \quad (\text{Eq. 4})$$

where W is body weight, L length, and a is the intercept and b the slope (Ricker, 1973). The relationships between length and weight were calculated using the least-squares linear regression method (Ricker, 1973, 1975). The patterns of relative growth of each species were further examined by looking at the coefficient b . When $b=3$ the type of growth is assigned as isometric (i.e. length and weight increases proportionally), $b>3$ is positively allometric (i.e. weight increases faster than length) and, $b<3$ is negatively allometric (i.e. length increases faster than length) (Tesch, 1968).

- Le Cren's relative condition factor (K_{rel})

Le Cren's (1951) relative condition factor, which compares the observed weight of an individual with the mean weight for such length was used to assess proximate individual fish's health using standard weight (Froese, 2006) (Eq. 5):

$$K_{rel} = TW/TL^b \quad (\text{Eq. 5})$$

where TW is the total wet weight, TL is the total length and b is the slope estimated from the LWR.

- Stomach repletion

Stomach repletion was used to describe the stomach fullness and it is essential to understand the feeding intensity of a fish population (Hyslop, 1980). The proportion of stomach repletion in the different stages by sex was represented using the ggplot2 library in R (v 3.1.1) (Wickham et al., 2016).

2.2.1.4. Age structure and growth determination

In order to assign ages to the species selected in this study without age readings from hard structures such as otoliths, the Von Bertalanffy Growth Function (VBGF) parameter estimates were calculated through iterative procedures using two length-based methods: 1) ELEFAN I (Pauly and David, 1981) and 2) Length Frequency Analysis (LFA), based on

modal progression analysis (MPA; Petersen, 1982). Such routines were performed using the FiSAT software (Gayanilo et al., 2005).

The base of the method 1 relies in the best fit of the non-seasonal VBGF to a set of length frequency data using the ELEFAN I method, which uses fixed start parameters (L_{∞} , asymptotic length), and provides a “goodness of fit index” (R_n) value; which is useful to obtain the best parameters. This method provides direct estimates of the growth rate (K).

Conversely, modal progression analysis (MPA) infers growth by observing an apparent modal shift in the LFD’s throughout the time series. This is achieved by separating graphically the observed normal components (Bhattacharya method; Bhattacharya, 1967). Afterwards and using modal components obtained the Bhattacharya method as initial guesses, the NORMSEP computerized method is applied (Abrahamson, 1971). This method uses maximum likelihood techniques and allows us to compare our input data with the computed data from the NORMSEP method. Once the results from NORMSEP are estimated (mean lengths, population sizes (in numbers), standard deviations and separation index (SI) for the groups identified), a *Linking of Means* method is used to link the mean lengths belonging to the same cohort through the samples considered. Finally, the FiSAT routine *Analysis of length at age data* is applied; this estimates the VBGF parameters K and L_{∞} through a non-linear fit of the (relative) age-length pairs of data applying Marquardt algorithm (Gayanilo et al., 1997, 2005).

Finally, to calculate ages from the estimated growth parameters considered, the inverse Von Bertalanffy Growth Function (VBGF) (Mackay et al., 1990) was followed (Eq. 6):

$$t = t_0 - 1/K * (1 - \ln(L/L_{\infty})) \quad (\text{Eq. 6})$$

where t_0 is the age at which length is zero, K is the growth rate, L is total length and L_{∞} is the asymptotic length at which growth is zero. Given the lack of information in the study area, the average of species-specific hatching lengths taken from literature was considered in the present study as a proxy of t_0 (Table 1).

Table 1: Length at hatch of the five MSPFS selected and the mean values calculated as a proxy of the age at which length is zero (t0)

Species	Length (mm)	References	Mean (mm) ~ t0
<i>Scomber scombrus</i>	6.0	Sette (1943)	3.8
	3.2	Studholme et al. (1999)	
	3.5	Miller et al. (1997)	
	2.3	Villamor et al. (2000)	
<i>Scomber colias</i>	4.6	Hwang et al. (2005)	4.6
<i>Trachurus trachurus</i>	2.5	Pipe et al. (1987)	3.3
	2.5	Russel (1976)	
	5.0	Muus and Nielsen (1999)	
<i>Trachurus mediterraneus</i>	2.9	Yandi and Altinok (2015)	2.9
<i>Trachurus picturatus</i>	2.0	Ahlstrom et al. (1951)	2.0

2.2.2. Spatial data

2.2.2.1. Acoustic data

Inferences on the summer distribution pattern exhibited by the analyzed species in the Gulf of Cadiz shelf were based on the exploratory analysis of the geo-referenced acoustic energy data attributed to each of these species sampled during the ECOCADIZ acoustic surveys (years 2007, 2009, 2013, 2014 and 2015).

The survey design consisted in a systematic parallel grid with transects equally spaced by 8 nm, normal to the shoreline (Figure 3). Echo-integration was carried out over such transects with a *Simrad™ EK60* echo sounder working in the multi-frequency fashion (18, 38, 70, 120, 200 kHz). Average sampling speed was about 10 knots and the acoustic signals were integrated over 1-nm intervals (elemental standard distance unit, ESDU). The total of sampled ESDU by survey is c.a. 300 nm. Raw acoustic data were stored for further post-processing using *Echoview™* software package (at present by *Echoview Software Pty. Ltd.*). Acoustic equipment was previously calibrated following the standard procedures (Demer et al., 2015).

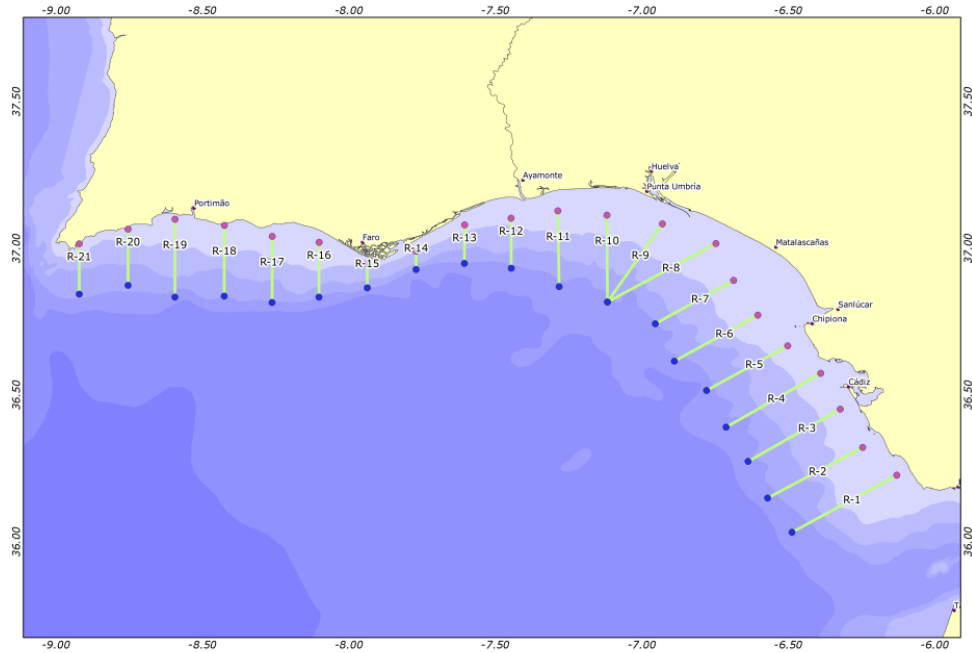


Figure 3: Acoustic transects of the ECOCADIZ surveys time-series (Source: Jorge Tornero, IEO).

As described in section 2.2.1, ground-truthing haul samples provided biological data on species and they were also used to identify fish species and to allocate the total back-scattering values (nautical area scattering coefficients, NASC, in $\text{m}^2 \text{nm}^{-2}$) into fish species according to the proportions found at the fishing stations (Nakken and Dommasnes, 1975). The species-specific NASC values by ESDU were considered as a proxy of the fish density and constituted the dataset to be analyzed from a spatial perspective.

Survey execution and abundance estimation followed the methodologies firstly adopted by the ICES Planning Group for Acoustic Surveys in ICES Sub-Areas VIII and IX (ICES, 1998) and the recommendations given more recently by the Working Group on Acoustic and Egg Surveys for Sardine and Anchovy (WGACEGG) in ICES areas VIII and IX (ICES, 2011a,b, 2012a).

2.2.2.2. Spatial patterns

To represent the spatial distribution of the focused MSPFS, two complementary techniques were applied. First, Single Parameter Quotient (SPQ) analyses (Bonnano et al.,

2014; Raya et al., 2015) were performed to explore species-specific preferences across spatial variables such as Depth (m), Latitude (°), and Longitude (°).

This method evaluates the 'mean spatial behavior' of any selected species during a specific time lapse (Bonnano et al., 2014; Raya et al., 2015). In this study, the frequency of occurrence of the NASC values in each sampling station was calculated and grouped. The spatial variables were assigned into categories (0.2° for latitude and longitude, and 0.5 m for log-transformed data of depth). Finally, the SPQ is estimated based on the different categories assigned in each station (Drapeau, 2005) using the formula (Eq. 7):

$$\text{SPQ} = \% \text{ observed NASC for each station} / (\text{Spat. Var. freq}_i * 100) \quad (\text{Eq. 7})$$

where % observed NASC is the frequency of occurrence of the NASC value in each station and Spat. Var. freq_i is the frequency of appearance of each spatial variable (i). The curves illustrated in the corresponding histograms represent the relative NASC value over each spatial variable. For instance, quotient values >1 mean significant selection, whereas a value <1 indicate rejection (Raya et al., 2015).

Aimed to better visualize the spatial distribution patterns over time and complement the information obtained from the SPQ analyses, the center of gravity (CG) representing the mean location of a population was also calculated (Barra et al., 2015; Saraux et al., 2014; Casini et al., 2014). In addition to CG, other spatial indices were summarized such as inertia and isotropy. Inertia refers to the dispersion of the population around its CG while isotropy indicates if the population distribution is homogeneous (i.e. isotropy) or heterogeneous (i.e. anisotropy) (Woillez et al., 2009; Saraux et al., 2014; Barra et al., 2015). The three spatial indices were calculated and mapped using the library RGeostats to represent the spatial patterns of the five MSPFS across the GoC. The plotted maps contain the CG and the patches showing the location where the NASC comprised more than 10% of the maximum recorded value of each population (Saraux et al., 2014; Barra et al., 2015).

3. Results

3.1. Life history traits

Life history traits including size composition of the population, sex ratio, reproductive status and LFM, LWR, condition status, stomach repletion, age structure and growth pattern are presented for each of the selected MSPFS.

A. *Scomber scombrus*

S. scombrus showed an overall size range between 13 and 39 cm (Table 1S, SM), with a mean size (\pm SD) of 26.0 (\pm 3.6) cm, and modal size classes at 19 and 27 cm for the whole period studied (Figure 5B). The 27 cm modal size class comprised the majority of the population while the smaller contained a low number of specimens. Minimum sizes were higher for males (16.8 cm) than for females (12.6 cm), although females presented larger sizes than males. Significant differences between males and females mean size (Kruskall-Wallis test, $p < 0.05$) were found in 2007 and 2015.

Sex ratio showed significant differences in the beginning of the time series analyzed, females significantly outnumbering to males during the survey season (Chi-square test: $p < 0.05$; Figure 5A). However, in recent years, a 1:1 sex ratio has remained except for 2014. This result might be related to the time when the surveys took place. The first three surveys (2007-2009) were performed at the beginning of the summer (June-July) while the more recent were carried at the middle of the summer (July- August).

The percentage of reproductively active population was close to 50 % during the whole period (Figure 5C) except in 2013, year in which almost the entire population (~90%) remained resting. Maturity stages analyzed indicated that, maturity stage varied with length (Figure 1S, SM). Statistical significant differences between size classes accounting for the maturity stage were observed (Kruskal-Wallis test: $p < 0.05$). Therefore, smaller sizes were mostly resting while the larger specimens were spawning. Length at first maturity ranged between 25.6 and 30 cm (Table 1S, SM), although the estimates could be

somewhat overestimated because of the high proportion in the population of maturity stage 1 individuals (considered as immature) which includes both truly immature and (adult) resting fishes. In addition, the smallest size matched the first sampled year (2007) while the largest size matched the last sampled year (2015).

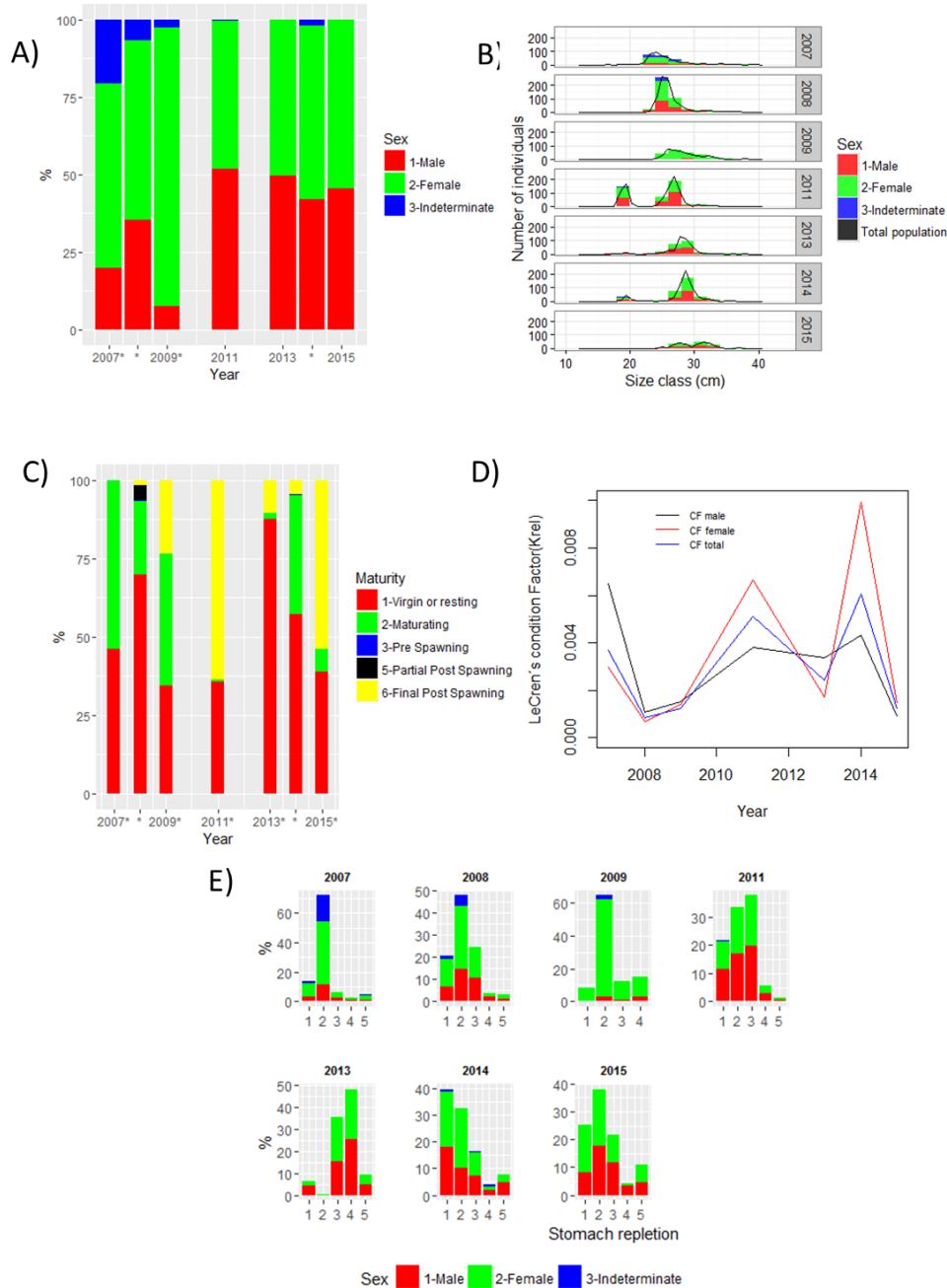


Figure 5: *Scomber scombrus* in the Gulf of Cadiz under summer conditions (2007-2015) a) Sex proportion, b) length-frequency distribution by sex, c) maturity stage, d) Fulton's condition factor variation, and e) stomach repletion by sex (1-empty, 2-almost empty, 3-medium full, 4-almost full, 5-full, 6-evaginated). The symbol * indicates significant differences.

Regarding relative growth, this species showed a positive allometric growth for the whole population. However, the coefficient b ranged interannually between 3.06 and 3.63 in males and between 2.92 and 3.71 in females (Table 1S, SM). In general, this interannual variation of the coefficient b for both sexes was also found for the whole population, with higher values obtained at the beginning of the time series (2008-2009) while lower b values were present in the more recent years (2014-2015).

Le Cren's condition factor for the total population showed a clear variation over time with a poor condition in 2008 and a better condition in 2014, reaching the maximum value (Figure 5D). Both sexes presented interannual variation on the condition factor, with females showing a similar trend to those illustrated for the whole population, with the maximum value reached in 2014. The maximum value for males was showed in 2007. Conversely, minimum values were presented in 2015 for males and in 2008 for females. A relationship between the condition and the coefficient b was detected in 2014, both presenting high values.

A large proportion of stomachs empty, almost empty, or medium full were found for *S. scombrus* (20-40 %) throughout the whole period analyzed. However, in 2013 over 50% of the specimens sampled presented almost full stomachs (Figure 5E), an observation which, in some extent, confirms a diurnal active feeding. Both sexes followed the similar pattern of stomach repletion.

Results on the *S. scombrus* population age structure during the survey season were found to be similar using both estimation methods. NORMSEP-based MPA estimation method (MPA) showed more putative age groups (0 to 10 age groups) than those obtained from ELEFAN I method (1 to 8 age groups; Table 6S, SM). Goodness of fit of the VBGF parameters as estimated by ELEFAN I was very low ($R_n=0.21$) evidencing that this method was unable to find more accurate values. In any case, the L_∞ which yielded the best fit was 44 cm, which resulted in an estimated K of 0.24 year^{-1} . NORMSEP-based MPA estimates of L_∞ (38.2 cm) and K (0.51 year^{-1}) differed from the ones estimated by the ELEFAN I method. As expected, the most reliably identified cohorts ($S.I. >2$) were the youngest cohorts with

highlighted modal classes, while the oldest cohorts overlapped each other (S.I.<2). Beyond the 3rd normal component in the LFD, the remaining modal components should be included in a plus (+) age group.

B. *Scomber colias*

The size composition of *S. colias* in the Gulf of Cadiz shelf waters in summer for the whole analyzed period and both sexes combined was comprised of individuals ranging from 13 to 34.6 cm (modal size classes at 21 and 24 cm; mean size (\pm SD): 22.4 (\pm 2.9) cm; Table 2S, SM). The dominant modal size class corresponded to 24 cm, while juveniles mostly composed the smaller size class. The larger specimens of *S. colias* were present in 2009 while the smaller individuals were found in 2015 (Table 2S, SM). Both sexes showed wider size ranges in the earlier years, while more recently their size ranges became narrower (Figure 6B). The mean size by sex showed significant differences from 2007 to 2009 as well as in 2014 (Kruskal-Wallis test; $p < 0.05$).

Sex ratio of *S. colias* only showed no statistical deviations from a 1:1 ratio in 2011 and 2013 (Chi-square test: $p > 0.05$) (Figure 6A). During the first surveys series, sex ratio significantly was dominated by females whereas in the more recent years the proportion was the opposite.

The total population presented a high proportion of resting specimens (60-90 %; Figure 6C) during the time series analyzed with a small fraction of the population reproductively active (10~30%). The number of reproductively active individuals decreased over the years (Figure 2S, SM).

Maturity stage by size class showed significant differences over time, except in 2009 and 2013 (Kruskal-Wallis test: $p > 0.05$) (Figure 6C). LFM ranged between 22.0 and 24.6 cm (Table 2S, SM), although the same abovementioned problems of overestimation for *S. scombrus* are also valid for *S. colias*.

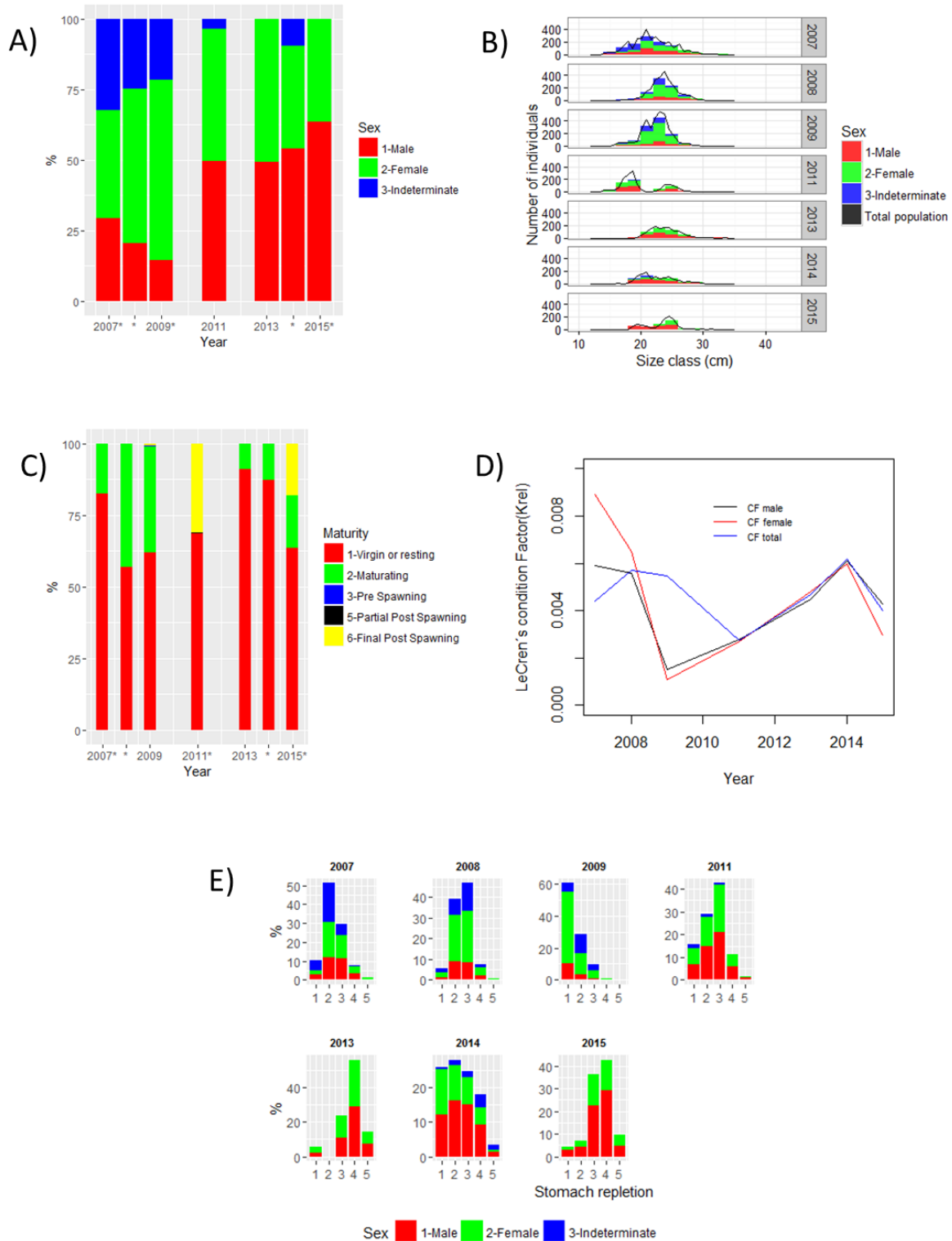


Figure 6: *Scomber colias* in the Gulf of Cadiz under summer conditions (2007-2015) a) Sex proportion, b) length-frequency distribution by sex, c) maturity stage, d) Fulton's condition factor variation, and e) stomach repletion by sex (1-empty, 2-almost empty, 3-medium full, 4-almost full, 5-full, 6-evaginated). The symbol * indicates significant differences.

The allometric coefficient b showed a wider range for females than for males, although both showing an overall positive allometric pattern of relative growth (Table 2S, SM). This coefficient fluctuated during the analyzed time, with lower values in 2008 and 2014 whereas higher values were found in 2009, 2011 and 2013. Females presented isometric growth and negative allometric patterns in 2007 and 2015 respectively, while the males showed a positive allometric pattern during the whole period analyzed.

Le Cren's condition factor (Figure 6D) for the overall population showed a clear interannual variation, reaching maximum values in 2007 and 2014. In 2008, the K_{rel} values show a declining trend until the more recent years, when the condition factor started to show an increasing trend. Both sexes followed the same pattern as the whole population. The steep decline from 2008 to 2010 coincided with the occurrence of a high number of sexually indeterminate juvenile individuals sampled those years. This fact may suggest that the individuals achieve a better condition close to the onset of the maturation process. Condition and coefficient b seemed to be inversely related, showing high condition values paired with low coefficient b values.

The stomach repletion is showed in Figure 6E. Although the species shows some diurnal feeding behavior, in the beginning of the survey series, almost 50% of the population had empty or almost empty stomachs, particularly in 2009. Conversely, a higher proportion of individuals with medium full, almost full and full stomachs was recorded in the last years, coinciding with the abovementioned increasing trend in the condition in the last analyzed years. This increased active feeding, as reflected by an increased stomach repletion, might be favoring a better condition (Figures 6D and 6E).

Age estimates showed a similar age interval estimated using both methods (NORMSEP-based MPA: 2 to 8 year groups; ELEFAN 1: 1 to 5 year groups; Table 6S, SM). ELEFAN I goodness of fit index ($R_n = 0.30$) was somewhat higher than in *S. scombrus*, but is still low, with estimates of L_∞ of 39.0 cm and a K of 0.40 year^{-1} . NORMSEP VBGF parameter estimates were quite different from those obtained using the ELEFAN I method; the L_∞ was estimated at 51.5 cm and K was set at 0.14 year^{-1} . Such estimates were based on

clearly identifiable cohorts in the samples as it was indicated by high Separation Index values ($SI > 2$).

C. *Trachurus trachurus*

Length frequency distribution ranged from 9 to 33 cm (Figure 7B, Table 3S, SM), with a mean (\pm SD) value of 17.0 (\pm 4.2) cm and modal size classes of 12, 17 and 23 cm, with the most abundant modal size class being that found at 23 cm. In the most recent years, however, the modal size class of 12 cm achieved a great relevance in the population indicating the occurrence of a recruitment pulse during the survey season (Table 3S, SM). Males presented larger sizes than females but both showing similar minimum sizes. Mean sizes between sexes were statistically different during the period studied ($p < 0.05$), except in 2007.

Sex ratio of *T. Trachurus* showed significant differences in 2007, 2013 and 2014, with females being dominant in 2007 and 2013 while males in 2014 (Figure 7A). The proportion of individuals assigned as indeterminate increased over time (Figure 7B), reaching the maximum value in 2015, corresponding to the year with the occurrence of the smallest size classes.

In general, the whole population presented a great proportion of individuals showing some spawning activity, although differences between years were detected. In 2007 and 2013, the proportion of resting specimens was $>70\%$. On the contrary, in 2009 and 2011 there were a higher proportion of reproductively active specimens (Figure 7C).

The results of *T. trachurus* detected significant differences (Kruskal-Wallis test: $p < 0.05$) between maturation stages and size classes over time (Figure 7C). Specimens of smaller size classes corresponded to stage 1 (virgin or resting) while those belonging to larger size classes were found in stage 4 (spawning) (Figure 4S, SM). LFM showed a wide range over the years with the smallest value found in 2013 (17.7 cm) and the largest value in 2009 (22.0 cm) (Table 3S, SM).

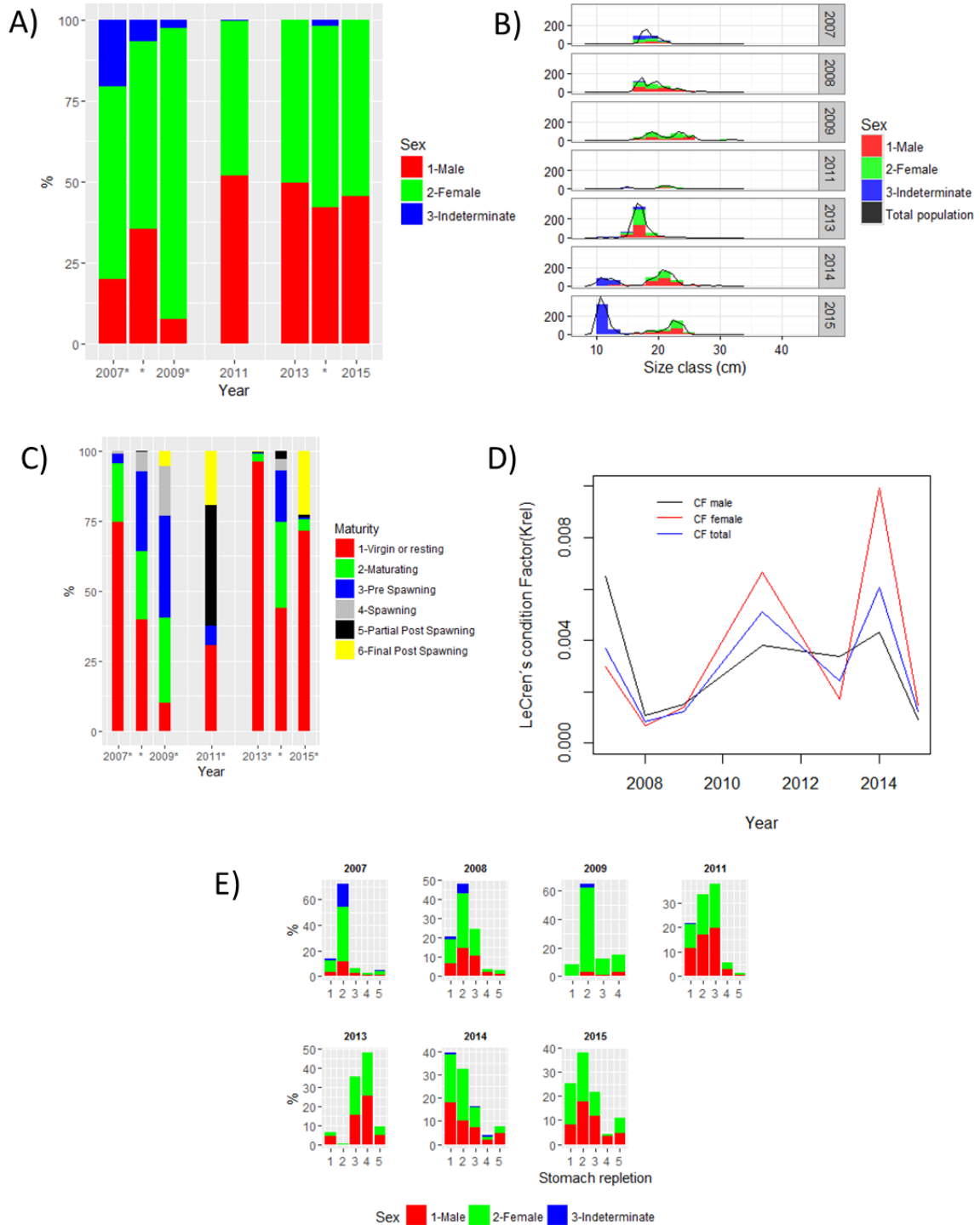


Figure 7: *Trachurus trachurus* in the Gulf of Cadiz under summer conditions (2007-2015) a) Sex proportion, b) length-frequency distribution by sex, c) maturity stage, d) Fulton's condition factor variation, and e) stomach repletion by sex (1-empty, 2-almost empty, 3-medium full, 4-almost full, 5-full, 6-evaginated). The symbol * indicates significant differences.

The results of *T. trachurus* detected significant differences (Kruskal-Wallis test: $p < 0.05$) between maturation stages and size classes over time (Figure 7C). Specimens of smaller size classes corresponded to stage 1 (virgin or resting) while those belonging to larger size classes were found in stage 4 (spawning) (Figure 4S, SM). LFM showed a wide range over the years with the smallest value found in 2013 (17.7 cm) and the largest value in 2009 (22.0 cm) (Table 3S, SM).

The whole population presented the three types of growth patterns, with negative allometry at the beginning of the time series and positive allometry in 2015. Similar growth pattern was observed for both sexes. The b coefficients ranged between sexes (2.27-3.07 for males and 1.64-3.12 for females) (Table 3S, SM), showing different patterns of relative growth throughout the period analyzed.

Le Cren's Condition Factor fluctuated over time, showing a decreasing trend for males and a slightly increasing trend for females (Figure 7D). The coefficient b and the condition did not show any relationship. A large proportion of the population (> 50%) showed both empty or almost empty stomachs except for 2013 when 50 % of the population had almost full stomachs (Figure 7E). No relationship between stomach repletion and condition was observed.

Unfortunately, the small number of cohorts in the samples did not allow the estimation of the VBGF parameters using the NORMSEP-based MPA method. VBGF parameters estimated using ELEFAN I method were: $K = 0.23 \text{ year}^{-1}$ and $L_{\infty} = 42.0 \text{ cm}$ with a coefficient of goodness of fit R_n of 0.20. A relatively complex population age structure composed by age groups 1 to 6 years was estimated (Table 6S, SM).

D. *Trachurus mediterraneus*

Size composition of *T. mediterraneus* ranged from 12 cm to 40 cm with a mean size (\pm SD) of 24.6 (\pm 4.3) and modal size classes at 21 and 28 cm for the whole survey series (Table 4S, SM). The dominant modal size class was 21 cm, however a large number of individuals were present in the larger size class (28 cm), suggesting that the population is mainly

comprised of adults. Males showed larger maximum sizes than females while minimum sizes were the same for both sexes. An increase in the modal size classes was detected throughout the time series. No statistical significant differences in mean sizes by sex were recorded in 2008, 2009, 2011 and 2014 (Kruskal Wallis test; $p < 0.05$). Those years showing significant differences were characterized by larger males than females, except for 2015.

Males outnumbered significantly females in 2008, 2009, 2011 and 2013. In the remaining years, the sampled population showed a relatively balanced sex ratio (Chi-square test: $p < 0.05$; Figure 8A).

A high proportion of the population were either in a pre-spawning or spawning stage, indicating that the spawning season occurs when the surveys took place (Figure 8C). During the first years (2007-2009), a high proportion of the population was spawning (40-70%) while between 2011 and 2014, the population seemed to be reproductively active but with most of the individuals pre-spawning or post-partial spawning (50-70% for the more recent years)

Significant differences ($p < 0.05$) between mean size at maturation stage were found in 2007 and 2013 (Figure 8C). LFM estimates ranged between 22.2 and 28.6 cm with a maximum value reached in 2015 and the minimum value at the beginning of the time series (Table 4S, SM).

Allometric coefficient b ranged for the whole population between 1.12 and 2.80. The lowest values were present in 2009 and 2014, with wider ranges for females than for males (Table 4S, SM). The whole population had a negative allometric pattern of growth.

Le Cren's condition factor (Figure 8D) fluctuated throughout the years. Males seemed to be in better condition in 2009. However, the results fluctuated during the analyzed period with years of decreasing condition (2007, 2011 and 2013) and increasing condition in 2014 and 2015. For this species, a positive relationship between condition and coefficient b , with higher values of condition the years with higher coefficient b values was visually detected.

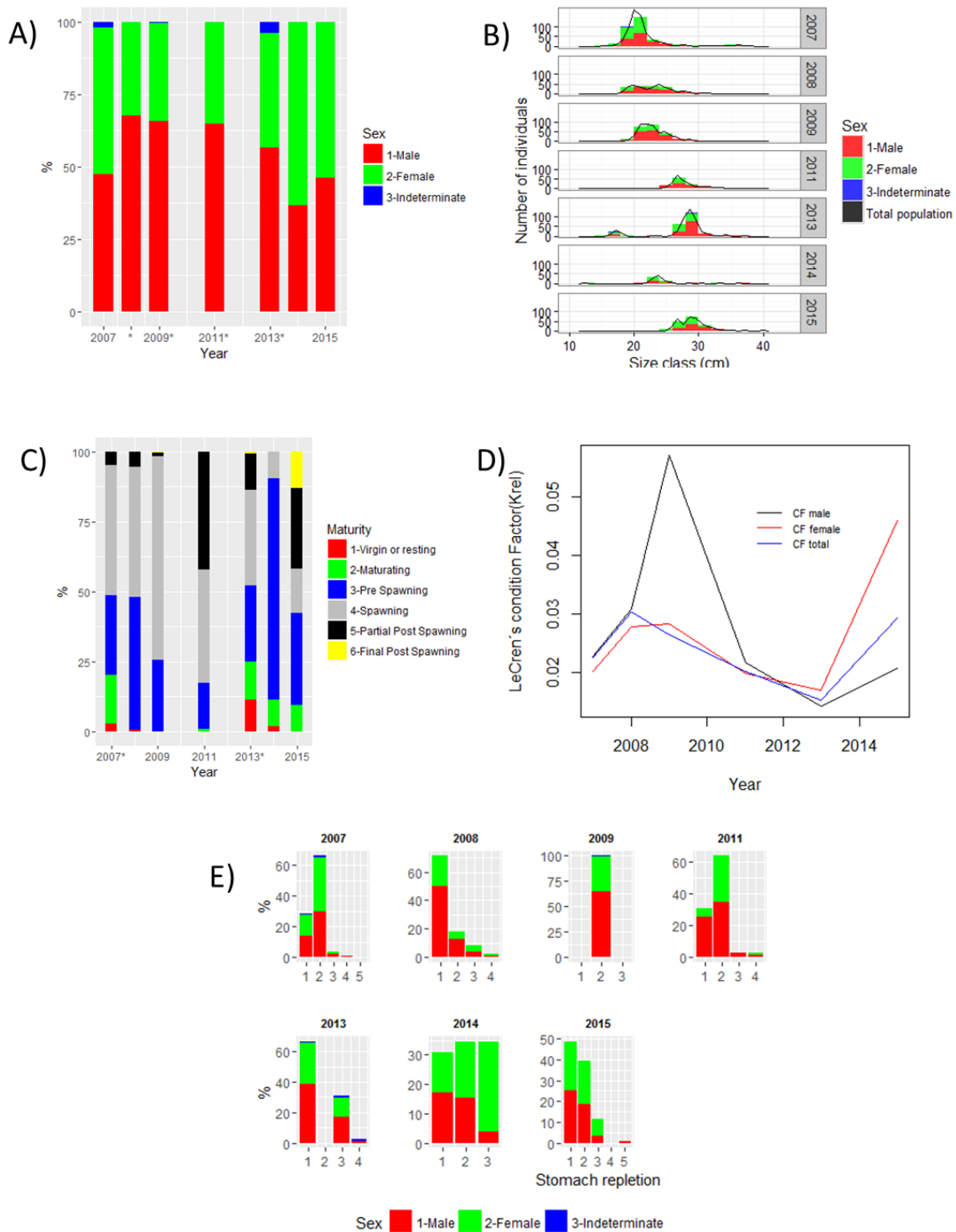


Figure 8: *Trachurus mediterraneus* in the Gulf of Cadiz under summer conditions (2007-2015) a) Sex proportion, b) length-frequency distribution by sex, c) maturity stage, d) Fulton's condition factor variation, and e) stomach repletion by sex (1-empty, 2-almost empty, 3-medium full, 4-almost full, 5-full, 6-evaginated). The symbol * indicates significant differences

Stomach repletion (Figure 8E) showed clearly that most of the sampled individuals had empty, almost empty, or medium full stomachs during the survey series. However, in 2009 the whole population showed almost empty stomachs (100 %). Also in 2014, females presented a higher proportion of medium full stomachs while males showed empty or almost empty stomachs. No relationship between condition and stomach repletion was identified for this species.

Unfortunately, age estimates of *T. mediterraneus* were not estimated using NORMSEP based MPA method based on the small number of cohorts found in the sample. ELEFAN I method estimated a large complex age structure (Table 6S, SM) with age groups ranging from 2 to 15 years. VBGF parameters estimated using ELEFAN I showed a low R_n (0.25) with a K estimate of 0.14 year^{-1} and a L_∞ of 46 cm.

E. *Trachurus picturatus*

Length distribution of *T. picturatus* had an overall size range between 11.4 and 26.3 cm (Table 5S, SM), with a mean size (\pm SD) of $17.0 (\pm 2.6)$ cm, and modal size classes at 11, 14 and 18 cm for the whole period studied (Figure 9B). The main modal size class was 18 cm although many individuals were present in the other modal size classes. Modal size classes were smaller than the other Carangidae family species. Minimum sizes were higher for females (13.8 cm) than for males (11.8 cm). Significant differences in the mean sizes by sex were detected for all the years except for 2007 and 2008 (Kruskal Wallis test; $p > 0.05$).

Sex ratio of *T. picturatus* in 2007, 2008, 2009 and 2014 did not show any statistical significant deviance from the 1:1 ratio (Chi-square test: $p > 0.05$). However, for the remaining years when no 1:1 ratio was obtained, males were dominant (Figure 9A).

In general, the population inhabiting the Gulf of Cadiz was comprised almost exclusively of immature specimens (80-95%). Occasionally, in 2008 50 % of the individuals sampled were separated into males and females. Kruskal Wallis test results indicated statistical evidences ($p < 0.05$) between maturation stage and length in 2009 and 2015 (Figure 9C).

LFM estimated ranged from 17.3 to 20.7 cm (2007-2009). From 2013 to 2015 the population sampled was composed of immature individuals.

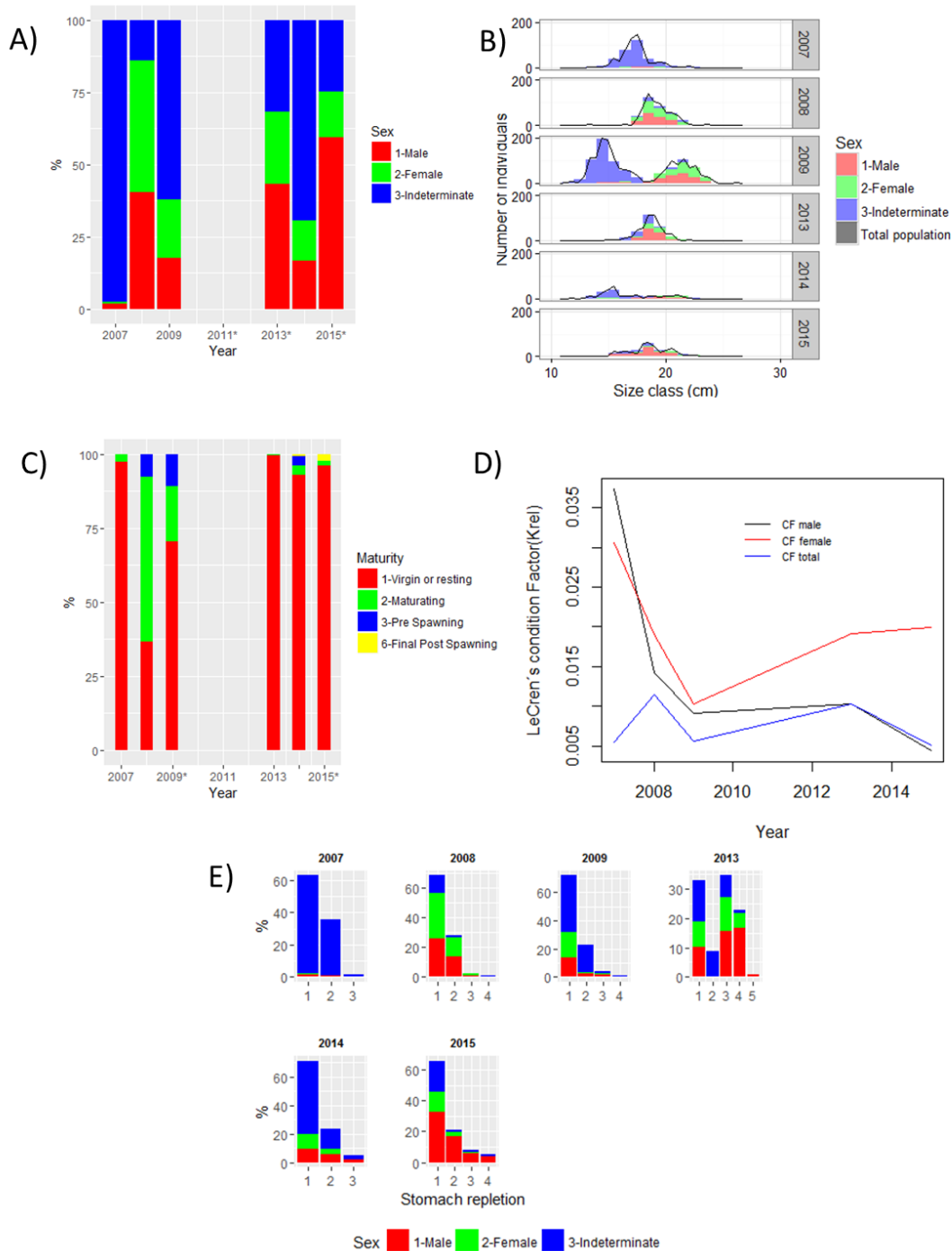


Figure 9: *Trachurus picturatus* in the Gulf of Cadiz under summer conditions (2007-2015) a) Sex proportion, b) length-frequency distribution by sex, c) maturity stage, d) Fulton's condition factor variation, and e) stomach repletion by sex (1-empty, 2-almost empty, 3-medium full, 4-almost full, 5-full, 6-evaginated). The symbol * indicates significant differences.

T. picturatus experienced during the study period both allometric and isometric relative growth depending on the year and sex (Table 5S, SM). The species showed a declining trend in its condition status since 2013, although males showed a better condition overall (Figure 9D).

Le Cren's condition factor for the whole population fluctuated with a maximum and minimum values in 2007 and 2009, respectively. The more recent years showed a different pattern for females (increasing condition) than for males and the rest of the population (decreasing condition). There was no visual evidence of a direct relationship between condition and coefficient b .

T. picturatus showed an overall high proportion of empty stomachs (~50%) (Figure 9E). However, in 2013 there was a higher proportion of specimens with almost empty (35 %) or medium full stomachs (25 %).

As described previously for *T. mediterraneus*, ages groups were only estimated using the ELEFAN 1 method (Table 6S, SM) and ranging from 0 to 3 years. The goodness of fit ($R_n=0.26$) indicated a large uncertainty in the data. The parameters estimated were: $K=0.66 \text{ year}^{-1}$ and $L_\infty=29.0 \text{ cm}$.

3.2. Spatial distribution

The quotient analyses and the centers of gravity (CG) calculated for the five MSPFS selected in this study are presented in this section.

A. *Scomber scombrus*

S. scombrus showed preferences for the mid-shelf (50-100 m) throughout the time series, although in 2014 was also recorded in the outer-shelf (100-200 m) (Figure 9S, SM). *S. scombrus* population showed an overall preference for latitude and longitude referring to the Guadiana river estuary and Algarve waters (37° N, -8° W) (Figures 10 and 11). In 2014, the population was displaced towards Portuguese waters as shown by the CG (Figure 14S, SM). The CG of *S. scombrus* matched the results obtained in the quotient analyses. In the

beginning of the ECOCADIZ surveys series, its distribution was well represented near the Guadiana river estuary, in the Portuguese region. However, in 2014, the CG of *S. scombrus* moved close to Cabo de San Vicente, the westernmost part of the GoC. In 2015, the CG was restricted to the estuaries of the rivers Tinto and Odiel. The distribution range and shape indicated anisotropy, i.e. heterogeneous distribution. Inertia followed a reduction pattern from a widely-dispersed species to appearing in a restricted area CG (Figure 14S, SM).

B. *Scomber colias*

The overall results from the quotient analysis presented for *S. colias* indicated that its preferred depths ranged between 20 and 90 m (i.e. inner- and mid-shelf waters). However, more recently (2014-2015), the specimens sampled were found in the outer-shelf waters (~115 m). In general, latitudinal and longitudinal preferences of this species ranged from South of Portugal waters to the Guadiana river estuary (36.9° to 37.4° and -8.5° to -7°) (Figure 10). In 2014, there was an increase in acoustic abundance in the westernmost longitudes as evidenced by both the quotient analysis and the resulting CG (Figure 10S and 14S, SM).

The spatial distribution of *S. colias* (Figure 10) reflected the same pattern observed from the Quotient Analyses (Figure 11), showing interannual variation. In 2007, the CG described a distribution closer to Portuguese waters (Figure 14S, SM). However, in 2009 the population exhibited a displacement towards Spanish waters with patches distributed all over the GoC. In the more recent years, the trend showed an increase in patchiness near the estuaries of the rivers Tinto and Odiel. In 2013, the CG indicated that the population was distributed across the whole GoC including Portuguese and Spanish waters, with no clear pattern, but inhabiting deeper waters in comparison to previous years. In 2014, this species showed preferences in its distribution pattern for Portuguese waters with an increase in patchiness near Cabo de San Vicente. In fact, its CG was present exclusively in the Portuguese area of the GoC. Finally, in 2015 the distribution was restricted to the Portuguese waters with a CG occupying the central area.

C. *Trachurus trachurus*

T. trachurus individuals were found across the whole shelf, without any depth preferences. Latitude and longitude preferences had a great interannual variation with an overall selection for the Algarve waters, Southern Portugal (Figure 10). In 2007 and 2009, this species was distributed all over the GoC (Figure 11S, SM), while more recently a shift towards northern waters was observed (37°).

Quotient analyses results were in agreement with the spatial distribution represented by the CG. The overall species CG was observed in Cabo Santa Maria (Figure 11), although *T. trachurus* showed a shift in its spatial distribution (Figure 15S, SM) moving from the Strait of Gibraltar (2007) to Portuguese waters (2009). More recently, the population showed a wide and heterogeneous distribution throughout the GoC based on the inertia size and isotropy shape. In 2013, the population was aggregated in a more restricted area, comprising exclusively Algarve waters in Portugal (Figure 15S, SM), although its distribution range was dispersed throughout the GoC.

D. *Trachurus mediterraneus*

T. mediterraneus presented an overall depth range from 20 to 120 m (inner and mid-shelf). However, in 2014 a small proportion of individuals were registered in the outer-shelf (180 m; Figure 12S, SM). Latitudinal preferences for the whole population was found closer to the Strait of Gibraltar (36.1°- 36.6°) (Figure 10). In 2007 and 2013, this species exhibited a slightly northward preference. On the other hand, *T. mediterraneus* showed a clear preference near eastern longitudes of the Bay of Cadiz (-6° to -7°).

The overall species distribution, was restricted to the Bay of Cadiz and Cabo de Trafalgar (Figure 11), which matched with the quotient analyses results. Despite of showing a wider range of spatial distribution in 2007, in recent years based on the smaller size of inertia, the population seemed to prefer inhabiting the Spanish waters near the Guadalquivir river estuary (Figure 15S, SM). In general, the population spatial range varied from covering almost all the Spanish GoC to inhabiting areas near the Strait of Gibraltar.

E. Trachurus picturatus

The overall depth preferences of *T. picturatus* comprised the inner- and mid-shelf waters (20-100 m) (Figure 10), although showing a clear interannual variation. In 2013, the species showed a shallower habitat preference. Latitude and longitude quotient described a preference for northwestern areas, i.e. South of Portugal (36.7° - 37.1°, -8° - -7.5°). For the longitude quotient, an increased interannual variation was observed (Figure 13, SM). In 2009 and 2015, this species showed preferences for eastern longitudes (-7.5° to -9°), while no preferred longitudes were found for the remaining years.

The overall species distribution was located at the South of Cabo de Santa Maria (Figure 11). In 2007, the population of *T. picturatus* was distributed near the Guadiana estuary moving slightly towards the border between Portugal and Spain. In 2013, a wider range in its distribution was observed, covering the entire GoC (Figure 15S, SM). The next years, the population backed to waters of Portugal, being restricted to Cabo de San Vicente.

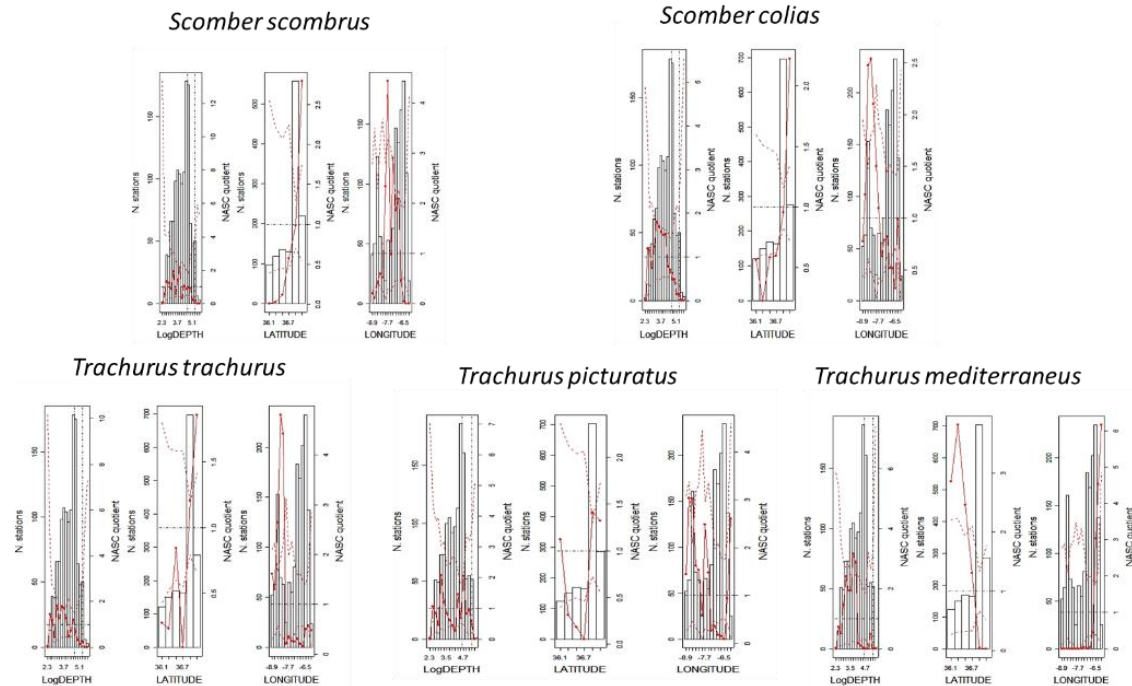


Figure 10: MSPFS quotient analyses representing the spatial variables depth, latitude and longitude for the whole study period (2007-20015). The red lines represent the relative NASC value (nautical area scattering coefficient, i.e. the acoustic energy attributed to species, in $\text{m}^2 \text{mn}^{-2}$) over each spatial variable.

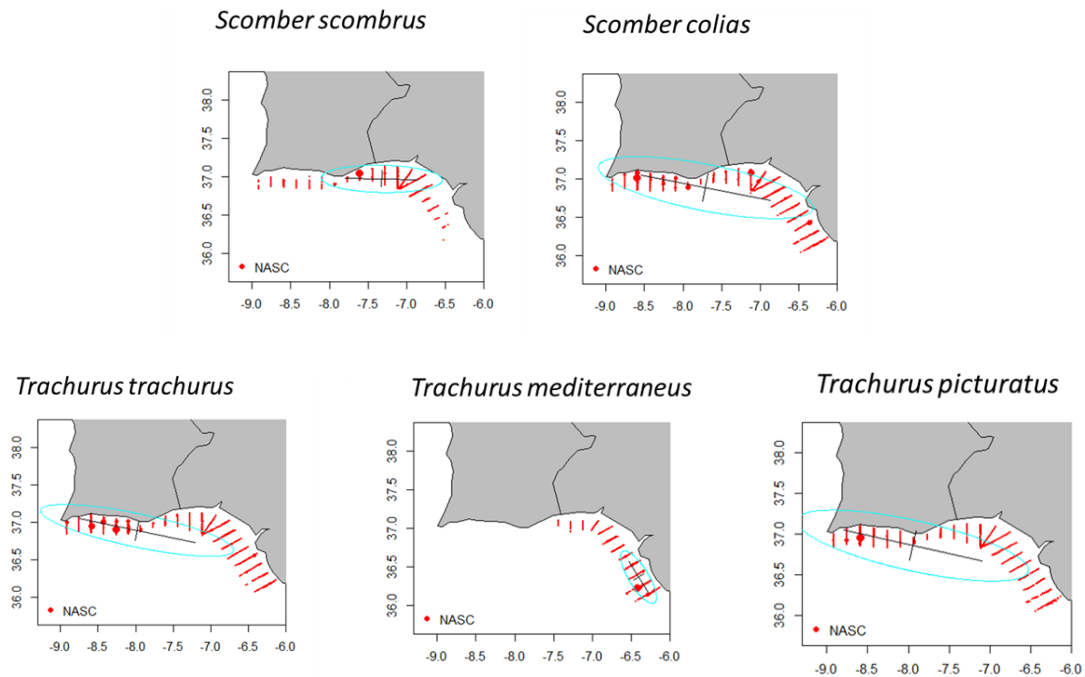


Figure 11: MSPFS center of gravity, inertia and isotropy of the distribution of the acoustic energy attributed to the species (NASC, nautical area scattering coefficient, in $\text{m}^2 \text{mn}^{-2}$) for the whole study period (2007-2015).

4. Discussion

Understanding the life history traits is a fundamental first step to identify stocks, before applying more specific stock identification analyses (Pawson and Jennings, 1996; Begg et al., 1999; Begg, 2005). With life history traits, the stock can be described in terms of the growth, survival and reproduction rates as well as migratory behaviour (Pawson and Jennings, 1996; Wootton, 1998). Life history trade-offs and strategies are also crucial for an increased knowledge of communities ecological structure and population responses to climate and ocean changes (King and McFarlane, 2003; Bonsall et al., 2004). Many commercially exploited species change their habitat over their lives. They actively migrate to use different areas for feeding, wintering, and spawning. It is, therefore, necessary to know the temporal and spatial distribution and variability at different scales of the fish populations for which assessment data are collected (Freon and Misund, 1999).

In Europe, the insights of life history traits and spatial distribution of marine resources, including the MSPFS, are recognized to be key in contributing to the implementation of the Marine Strategy Framework Directive (MSFD). For example, descriptors of habitat and diversity (Descriptor 1, D1) and of commercial species (Descriptors 3, D3) are requested to achieve a 'good environmental state' (GES) in the Gulf of Cadiz (South Atlantic Marine Demarcation for the Spanish waters) by 2020. D1-based GES is assessed by species-based indicators which take into account the species-specific area of distribution and the distribution pattern within this area. Additionally, D1 indicators based on its demographic characteristics such as the population size composition and age structure, sex ratio, fecundity, survival, and genetic structure are also required (Modica et al., 2016). Notwithstanding the above, lack of information regarding the spatial and temporal components of biodiversity and their associated pressures are one of the main limitations for a global assessment of our Demarcation. On the other hand, Descriptor 3, which advises that for well establish stock the use of Stock Spawning Biomass (SSB) and fishing mortality (F) as indicators, has been characterized for the study area with the methods established for stocks without sufficient information (ICES 2012). For fish species exploited in the pelagic ecosystem, particularly MSPFS, acoustic surveys conducted in the South Atlantic Demarcation provide indicators associated to a high uncertainty as the surveys do not cover the whole bathymetric range of these species. Therefore, it would be necessary to explore deeper waters and account for seasonality to provide more reliable indicators for these pelagic components in the study area.

Bearing in mind the above facts, the present study contributes to improve the knowledge of life history traits and spatial distribution of five MSPFS in the Gulf of Cadiz (both Portuguese and Spanish waters) from IEO pelagic ecosystem surveys data. The novelty of this study is the analyses of IEO datasets so far unexplored and show, for the first time, results on the reproductive and condition status, population size and age structure, growth patterns and spatial distribution patterns of these species in the study area under summer conditions. Therefore, it might be considered as a prior step needed for future development of the indicators mentioned above in the frame of the MSFD.

Population structure

Age and growth studies of the analyzed MSPFS have been reported previously for the study area (Rodríguez-Roda, 1982, Velasco et al. (2011) and near systems (Azevedo, 1990; Villamor et al., 2004; Vasconcelos et al., 2011) based on otolith readings and differing from the MPA-based approach used in the present study.

Here, species LFDs indicated inter-species differences with the smallest size classes for *T. picturatus* and the largest size classes for both *T. mediterraneus* and *S. scombrus*. An increased number of modal components were also present for those larger sized species. Note that the acoustic surveys and DEPM surveys do not cover the whole bathymetric range of each species, particularly those belonging to the genus *Trachurus*. For the species, the adult population is known to inhabit deeper depths, contrary to sub adults and juveniles (FAO, 2005; Mytilineou, 2005).

Overall, there are differences in mean length between *S. scombrus* and *S. colias*, having the first one bigger length classes over time. However, the largest size ever caught for *S. colias* in the GoC was 65 cm in length and a total weight of 2.9 kg during the summer of 2007 by a commercial long line (Navarro et al., 2012).

Growth parameters and age estimates of *S. scombrus* calculated by the two methods (i.e. ELEFAN I and MPA) showed differences compared to those estimated by Villamor et al. (2004) in the Northeast Spain. However, ELEFAN I method parameter estimates were quite similar (Villamor et al. (2014); $K=0.24$ and $L_{\infty}=44$ cm).

In the GoC, the only parameters estimated previously corresponded to *S. colias* (Rodríguez-Roda, 1982, Velasco et al., 2011). The growth parameters estimated using ELEFAN I method agreed with those estimated by Velasco et al. (2011) ($K=0.40$ and $L_{\infty}=39$ cm). However, the results differed from those estimated in other further areas, for example in the Hellenic Sea (Kiparissis et al. (2000); $K=0.15$ and $L_{\infty}=47$ cm). Despite the different methods, the growth parameters obtained in this study can be considered as valid since they are in agreement with the authors mentioned above. Nevertheless, ageing

methods based on hard structures (e.g. otoliths) are highly advocated to corroborate and validate the present results.

Length range distribution for *T. trachurus* and *T. mediterraneus* were similar to those observed previously in the area in spring and autumn (Torres et al., 2012), although *T. picturatus* showed smaller sizes. These differences might be related to the different seasons and years when the data were taken.

The results obtained for *T. trachurus* ($K=0.23$, $L_{\infty}=42$ cm) were similar to those obtained by Santic et al. (2002) ($K = 0.23$, $L_{\infty}= 37.68$ cm) in the Adriatic Sea and slightly different from Karlou-Riga et al. (1997) ($K= 0.366$, $L_{\infty}= 30.27$ cm) in the Gulf of Saronikos. Contrary to our expectations, the results differed from those estimated previously in the study area (CREANDA PROJECT, 2005; $L_{\infty}= 45$ cm, $K= 0.1$). However, the estimates were based on otolith readings in the GoC as well as in the Adriatic Sea and Gulf of Saronikos. *T. mediterraneus* growth parameters varied from those obtained of the Eastern Mediterranean Sea (Karlou-Riga, 2000). Finally, *T. picturatus* growth estimates were different from those observed by Vasconcelos et al. (2011) in Madeira waters though this species is less abundant in the GoC than in Madeira waters.

Reproductive status

From a reproductive point of view, the only species using the area as spawning ground were *S. scombrus*, *T. trachurus* and *T. mediterraneus*, although there is no information related to the spawning season for the mentioned species in the GoC except for *T. trachurus*. Borges et al. (1977) reported for *T. trachurus* from southern Portugal two main reproductive periods: one from January to June and a second from July to September. Arruda (1984) reported this reproductive period for the same area from September to May. It was also found that individuals spawning in September were young, when at that time the older individuals were in a “resting season”. Borges and Gordo (1991), working with samples from the entire coast of Portugal, determined the spawning season to last from December to June.

S. scombrus spawns in the North Sea from May to July (Eltnick, 1987; Lockwood, 1988) while *T. mediterraneus* spawning period ranges from May to August in the Mediterranean Sea (Ünlüata et al., 1996; Viette et al., 1997; Karlou-Riga, 2000; Demirel et al, 2013). Results obtained from these authors agreed with those obtained for the GoC. For *S. colias*, Vasconcelos et al. (2011) suggested a spawning season from January to April while the present study utilized data from summer, reason why the proportion of mature individuals was small or none. The proportion of either males or females in *S. scombrus* and *S. colias*, suggested a shift in the sex ratio for the period analyzed. During the earliest years, the proportion of females was higher than males. However, this pattern was found opposite in the more recent years, dominating males in the population analyzed. This fact might be related to the spawning period, for example, at the beginning of the spawning period there is a higher proportion of males while at the middle of the spawning period the proportion of females increases (Eltink A., 1987). Sexual maturity showed differences between species. *S. scombrus* had a higher proportion of pre-spawning and partial post spawning individuals while *S. colias* presented most of specimens analyzed immature or resting which might be related to the pattern described from Vasconcelos et al. (2011). The estimated length at first maturity for *S. colias* in the GoC was higher than that obtained previously in the area (CREANDA Project 2005) and in the Madeira and Canary Islands (Nespereira, 2004; Vasconcelos et al., 2011). On the other hand, the length at first maturity estimated for *S. scombrus* in the Gulf of Cadiz is in agreement with the one reported by Collete (1983).

The proportion of males and females of *T. trachurus* agreed with the results obtained in the Galician and Cantabrian shelf (Abaunza et al., 1995). Conversely, *T. mediterraneus* showed a higher proportion of males at the beginning of the time series analyzed, presenting the biggest specimens of the three species comprising this family. The population of *T. picturatus* was characterized mostly by immature and smaller individuals.

Length at first maturity differed between the three *Trachurus* species; based on the different modal size classes comprising each species in the GoC. The length at first

maturity estimated for *T. trachurus* is within the range observed in the northeast Atlantic (Abaunza et al., 1995; Abaunza et al., 2003). However, this is the first study estimating this parameter in the GoC. In the case of *T. mediterraneus*, there are no studies related to compare with, only the overall estimate reported in Fishbase corresponding to smaller individuals (20 cm) for the Aegean Sea. Finally, *T. picturatus* is comprised in this area of a high proportion of immature individuals, with an overall length of first maturity estimate for the northeast Atlantic of 27 cm (Garcia et al., 2015).

Condition status and feeding behaviour

Both mackerel species presented a positive allometric growth pattern, agreeing with the results reported previously by Torres et al. (2012) in the Gulf of Cadiz and Velasco et al. (2011) in the Southwestern Mediterranean. Relationships between condition, maturity and stomach repletion were identified, although the condition showed great variability throughout the time series. Small pelagic fish species, for example anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), usually are in better condition at the beginning of the spawning season (Millan, 1999; Sinovčić et al., 2008). In this study, the relationship between maturity stage and condition was found for *S. colias*, showing a decrease in condition with a high proportion of maturing individuals. In general, most of individuals of both species of Scombrids analyzed had small quantities of food in their stomachs. Similar results were also found by Torres (2013), sampling individuals of both *Scomber* species caught in spring and autumn during bottom trawling surveys in the study area. According to others studies performed in the Narraganset Bay and Mauritania, both species are nocturnal feeders (Maigret et al., 1986; Macy et al., 1998). In our study, this is a limitation, since the fishing hauls took place at daily hours.

In terms of relative growth, there were differences between the three *Trachurus* species with *T. mediterraneus*, agreeing with the relative growth patterns found by Torres et al. (2012) in the GoC. However, a positive allometric growth was found in the Izmir Bay (Özaydin et al., 2006). The other two species presented variation between the three types of growth describing differences with those presented in the GoC (Torres et al., 2012). It is

known that length-weight relationships may vary according to environmental and biological factors such as temperature, salinity, prey abundance, habitat and maturity, spawning period season, sex, season, juveniles absence and health (Pauly, 1984; Safran, 1992; Froese, 2006). However, none of these factors have been taken into account in the present study, evidencing the necessity of conducting new studies accounting for the factors mentioned above.

Most specimens in *T. mediterraneus* were found to be in their spawning season, corresponding to the largest sizes recorded. *T. trachurus*, on the other hand, showed a great proportion of individuals either in pre-spawning or maturing stages. Finally, *T. picturatus*, showed an almost entirely immature population. A slight relation between maturity and condition was detected. Spawners individuals seemed to be in better somatic condition whereas those pre-spawners and maturing seemed to expend their energy for the maturation process. *T. trachurus* and *T. picturatus* followed the same interannual condition trend whereas *T. mediterraneus* followed an inverse pattern which may be related to its spawning activity when they were analyzed. Stomach repletion also followed a certain interannual trend in the three species with an increase in the repletion those years in which a better condition was observed. The three species from the Carangidae family feed mainly on crustaceans in the study area (Torres, 2013) as well as in north-eastern Atlantic and the Mediterranean systems (Smith-Vaniz, 1986).

Spatial preferences and patterns

The five analyzed MSPFS showed different degrees of spatial co-occurrence possibly related to inter-specific interactions such as competition or predation. *S. scombrus* and *S. colias* showed preferences for Portuguese waters; though *S. colias* had higher abundance and wider spatial distribution. On the other hand, the spatial variables tested in this study showed that *T. trachurus* and *T. picturatus* were located mainly in Portuguese waters while the distribution of *T. mediterraneus* is linked to the Strait of Gibraltar nearby areas.

In general, the spatial patterns observed by the five MSPFS indicated preferences for Portuguese waters or near the Strait of Gibraltar where these species might feed on their main preys such as small crustaceans, polychaetes and eggs of other pelagic fish (Torres, 2013; Garrido et al., 2015). The only species showing a similar distribution pattern over time and space is *T. trachurus*. In this study, the spatial variables analyzed were latitude, longitude, and depth. However, environmental drivers might be also involved in shaping the distribution of these species and establish their essential habitats.

To conclude, despite weaknesses associated to survey design (opportunistic fishing hauls), season (surveys were carried out during the summer season), daily hauls (they were performed during the day, for further studies, nocturnal hauls should be carried out) or lack of hard parts (no otoliths were extracted for the studied species) identified in this study, it is hope that the findings reported of the life history traits and spatial distribution will contribute to increase the knowledge of the MSPFS in the Gulf of Cadiz. Hopefully, these findings will contribute to the implementation of future ecosystem-based approaches in the area aimed to link sustainable fisheries with biodiversity conservation goals.

5. Concluding remarks

- 1) The present study reports the estimates of life history traits and spatial patterns of five MSPFS of the Gulf of Cadiz based on data sets collected from IEO summer surveys (2007-2015). For *S. scombrus*, *T. mediterraneus* and *T. picturatus*, this study presents the first references in the study area.
- 2) Size classes varied between species, the largest size classes belonged to *S. scombrus* and *T. mediterraneus*. On the contrary, the smallest size classes were found in *T. picturatus*. The size classes of *T. trachurus* showed a decreasing trend throughout the time series while *S. colias* size classes did not show large variations.

- 3) *Trachurus* spp. did not show a deviation from a 1:1 sex ratio although interannual fluctuations in the number of males and females were observed. On the other hand, *Scomber* spp. showed a high proportion of females during the first years analyzed.
- 4) An assessment of the reproductive status and estimation of the species-specific lengths at first maturity for the five MSPFS indicated that populations of *S. scombrus* and *T. mediterraneus* inhabiting the GoC during summer are mainly composed of sexually active adults which use the GoC shelf waters as a spawning area. Conversely, *S. colias* and *T. picturatus* populations were composed almost entirely of juveniles and sub adults, evidencing a different use of the area for feeding and/or wintering and as nursery or recruitment area. The reproductive status of *T. trachurus* fluctuated through the time series analyzed associated with an increased or decreased maturity stage.
- 5) *S. scombrus* and *S. colias* showed a positive allometric growth pattern while *T. mediterraneus* and *T. picturatus* experienced negative allometric growth. *T. trachurus* however, presented the three types of growth. Condition status presented opposite patterns between *S. scombrus*, *S. colias* and *T. trachurus* and the same between *T. mediterraneus* and *T. picturatus*.
- 6) *S. scombrus* and *S. colias* showed a great variability in the age estimates and VBGF growth parameters using either NORMSEP-based MPA method or ELEFAN I method with the NORMSEP-based MPA method estimating more age groups than the ELEFAN I method. *T. trachurus* and *T. mediterraneus* showed a complex age structure with the identification depending on the year, of 6 and 15 age groups, respectively. The population age structure of *T. picturatus* included 0 age individuals indicating the occurrence and detection of recruitment pulses during the survey season. The reliability and robustness of the age and growth estimation methods should be taken carefully based on the high uncertainty caused by the lack of samples of the remaining seasons. Therefore, the estimated population age structure and growth patterns of the analyzed species in the study area should be

further corroborated and validated by ageing methods based on hard structures (e.g. otoliths).

- 7) From the set of analyzed MSPFS, *S. colias* and *T. trachurus* showed the highest acoustic densities and the most widely distributed populations all over the GoC. *S. scombrus* occurrence in the study area was much lower. *T. mediterraneus* distribution is enclosed near the Strait of Gibraltar while *T. picturatus* has a more western distribution. Spatial distribution range decreased for *S. scombrus*, *S. colias*, *T. mediterraneus* and *T. picturatus* while *T. trachurus* distribution remained the same for all the years. Further modeling studies are advocated including additional environmental variables aimed to identify the main drivers defining the distribution patterns as well as the essential habitats of these MSPFS populations in the Gulf of Cadiz.
- 8) Although these estimates are referred to those fractions of the species populations inhabiting the GoC shelf waters in summer, each life history trait obtained provides a hint of their demographic structure and distribution. Hopefully, these findings will contribute to the implementation of future ecosystem-based approaches in the area aimed to link sustainable fisheries with biodiversity conservation goals.

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Supplementary Material

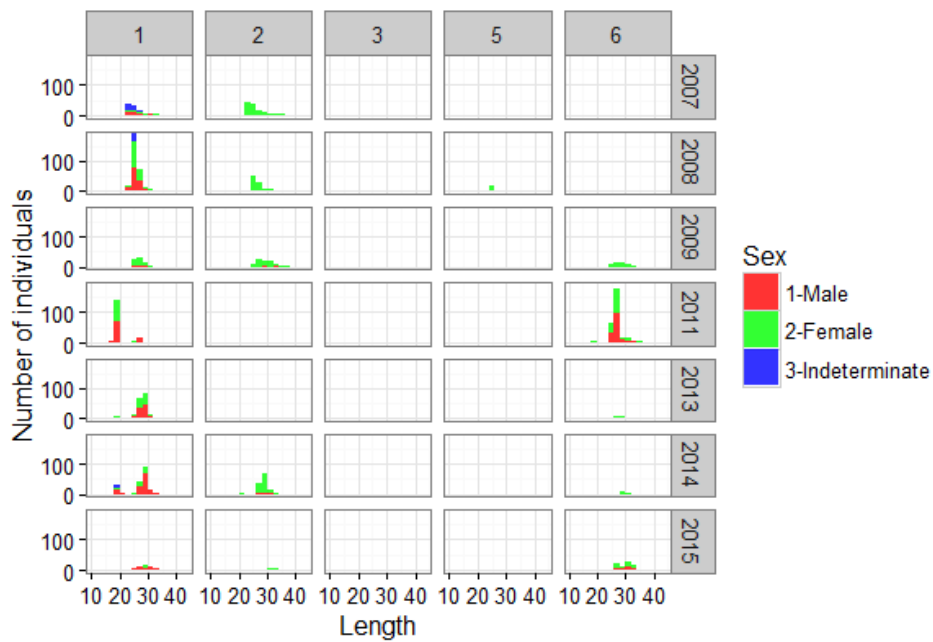


Figure 1S: *Scomber scombrus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Length frequency distribution (cm) represented by sex, year and maturity stage (1: virgin and resting, 2: maturing, 3: pre-spawning, 4: spawning, 5: partial post-spawning and 6: final post- spawning). Note that no individuals were found in stage 4: spawning.

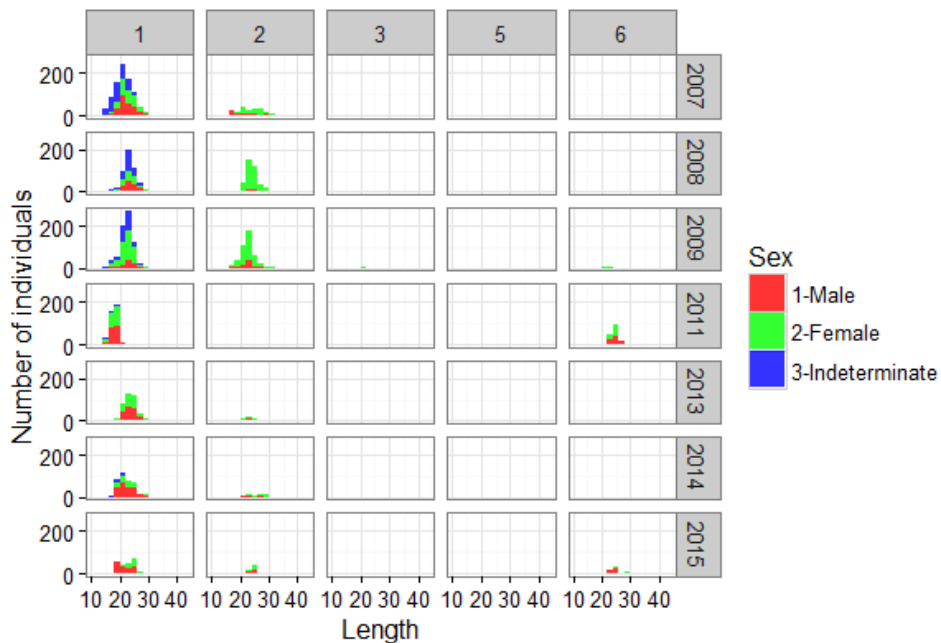


Figure 2S: *Scomber colias* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Length frequency distribution (cm) represented by sex, year and maturity stage (1: virgin and resting, 2: maturing, 3: pre-spawning, 4: spawning, 5: partial post-spawning and 6: final post- spawning). Note that no individuals were found in stage 4: spawning.

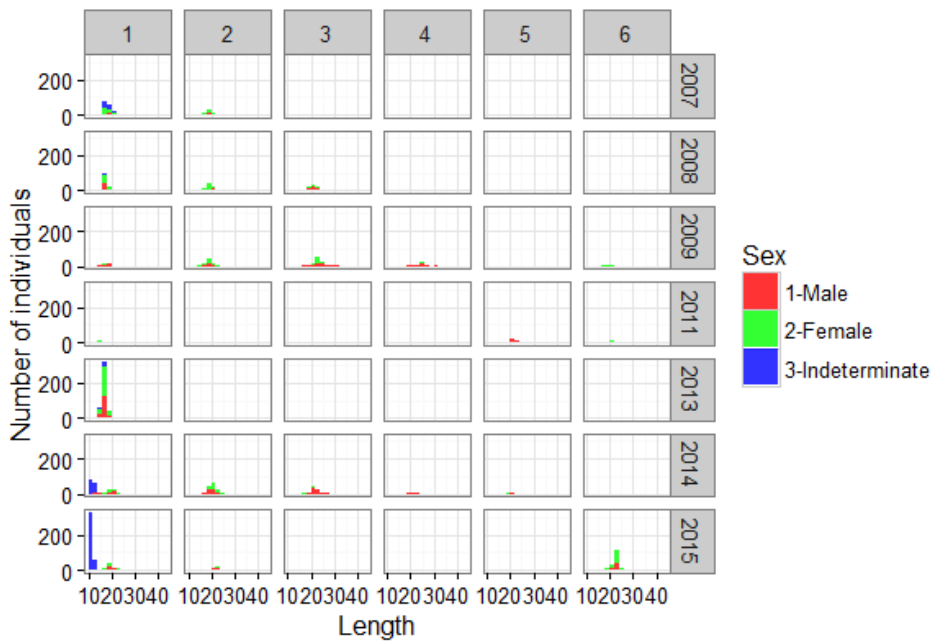


Figure 3S: *Trachurus trachurus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Length frequency distribution (cm) represented by sex, year and maturity stage (1: virgin and resting, 2: maturing, 3: pre-spawning, 4: spawning, 5: partial post-spawning and 6: final post- spawning).

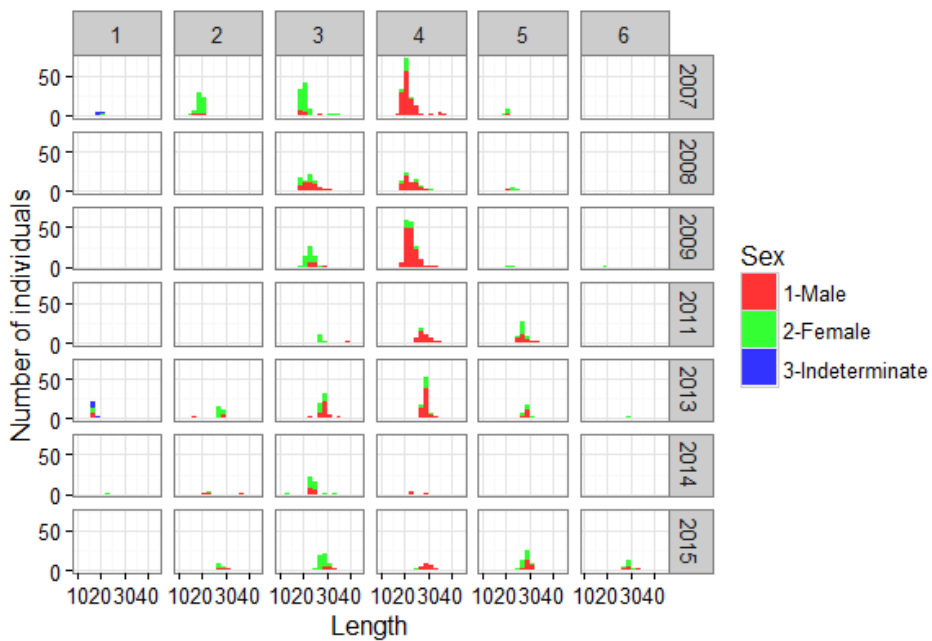


Figure 4S: *Trachurus mediterraneus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Length frequency distribution (cm) represented by sex, year and maturity stage (1: virgin and resting, 2: maturing, 3: pre-spawning, 4: spawning, 5: partial post-spawning and 6: final post- spawning).

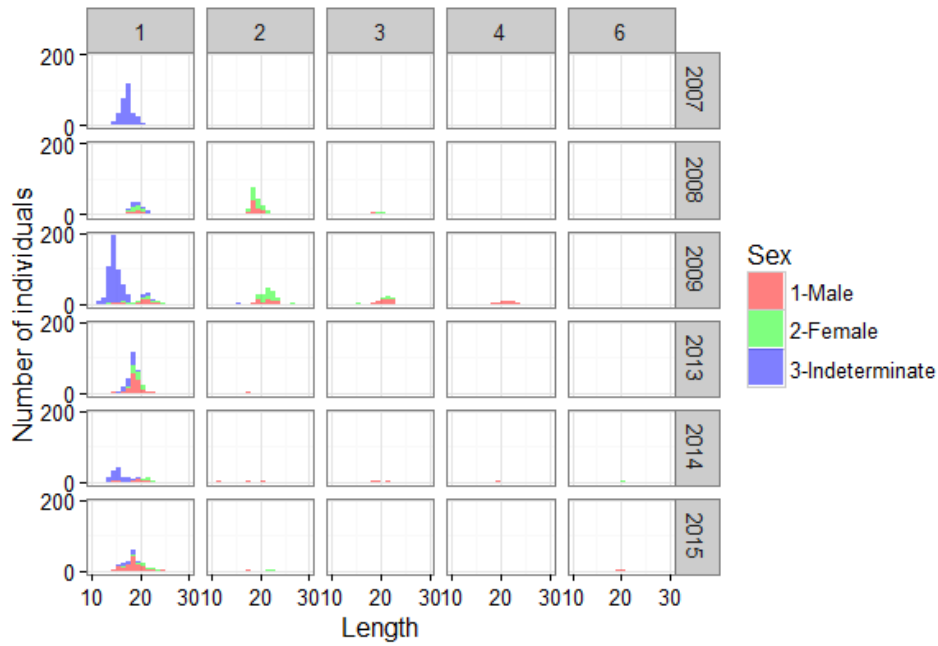


Figure 5S: *Trachurus picturatus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Length frequency distribution (cm) represented by sex, year and maturity stage (1: virgin and resting, 2: maturing, 3: pre-spawning, 4: spawning, 5: partial post-spawning and 6: final post-spawning). Note that no individuals were found in stage 5: partial post-spawning.

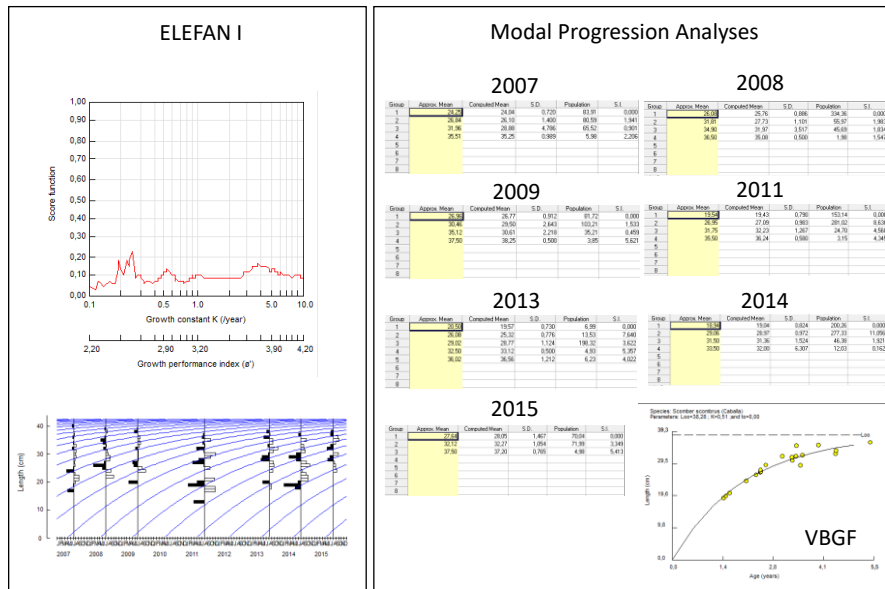


Figure 6S: *Scomber scombrus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Estimation of VBGF parameters based on Length Frequency Analysis (LFA) methods. ELEFAN I (left): K-scan plot (plot of goodness of fit, R_n , values for a range of K values (0.10 to 10) on a log-scale given a fixed estimate of L_{∞}), (top) and resulting VBGF fitted to the restructured length-frequency samples (bottom). Modal Progression Analyses (right): decomposition of the composite LFDs using NORMSEP, with indication of descriptive statistics by normal component and the Separation Index (SI). Group number corresponds to the order of appearance of the normal component and not to the putative age group. The resulting VBGF, with indication of the estimates of k and L_{∞} , is inserted on the bottom right.

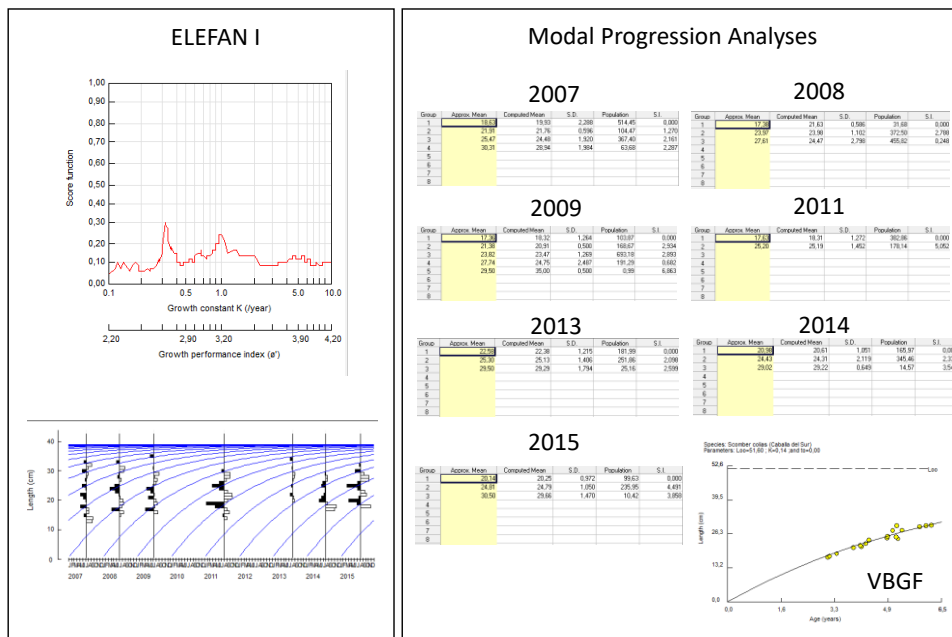


Figure 7S: *Scomber colias* in the Gulf of Cadiz shelf waters (20–200 m depth) under summer conditions (years 2007-2015). Estimation of VBGF parameters based on Length Frequency Analysis (LFA) methods. Same legend as Figure 6S.

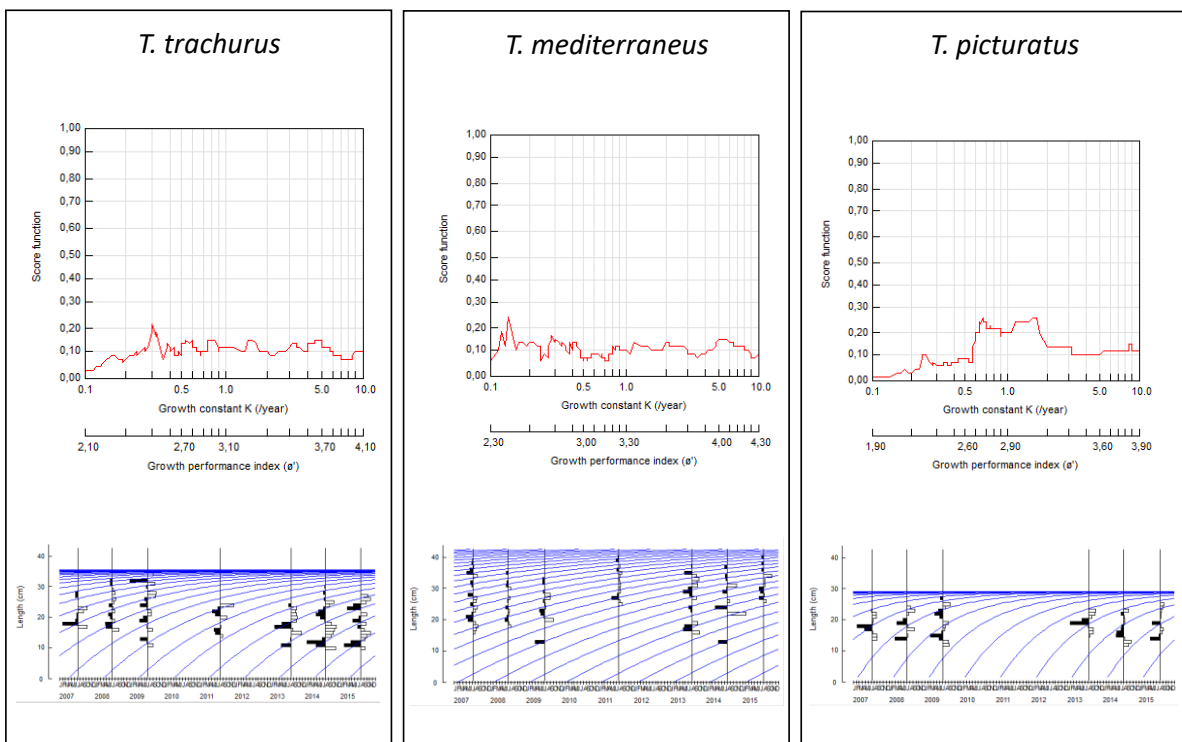


Figure 8S: *Trachurus* spp. in the Gulf of Cadiz shelf waters (20–200 m depth) under summer conditions (years 2007-2015). Estimation of VBGF parameters based on Length Frequency Analysis (LFA) methods. Same legend as Figure 6S. Note that population data did not allow performing Modal Progression Analyses.

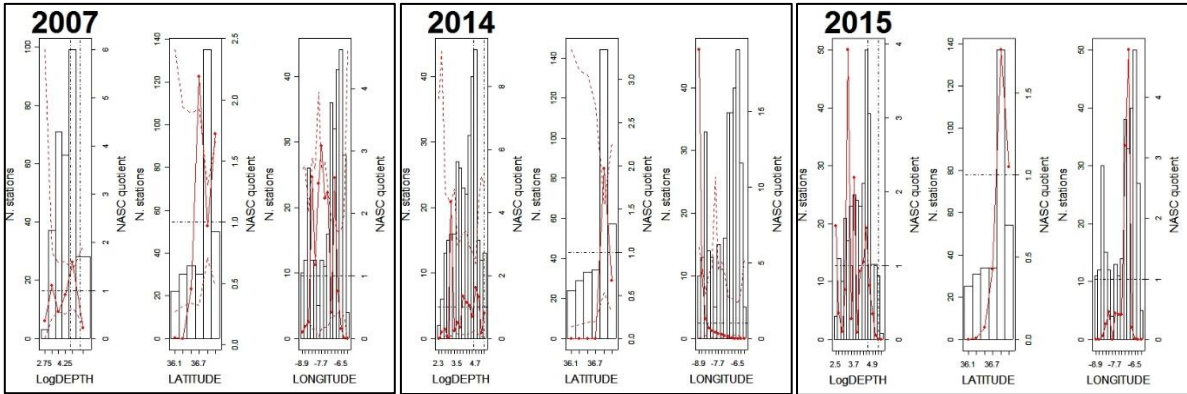


Figure 9S: *Scomber scombrus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Quotient analyses representing the spatial variables depth, latitude and longitude by year when the data were available. The red lines represent the relative NASC value over each spatial variable.

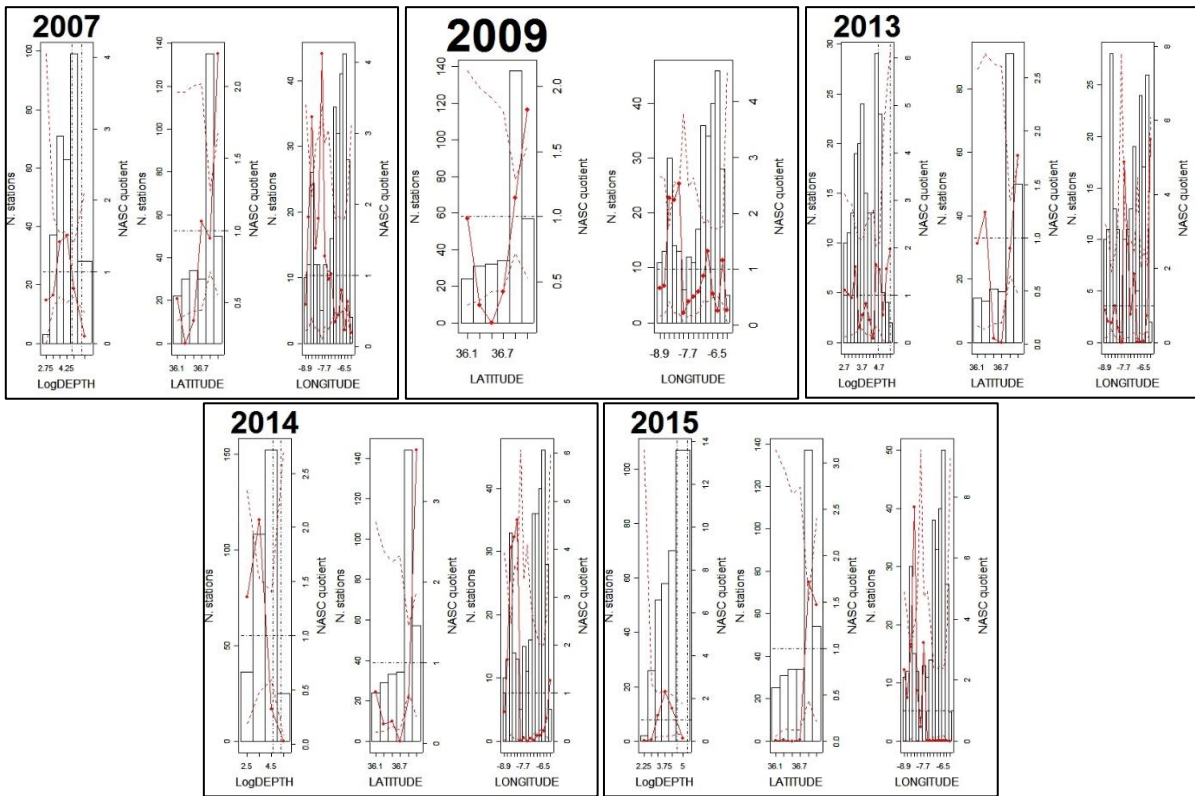


Figure 10S: *Scomber colias* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Quotient analyses representing the spatial variables depth, latitude and longitude by year when the data were available. The red lines represent the relative NASC value (nautical area scattering coefficient, i.e. the acoustic energy attributed to species, in $m^2 mn^{-2}$) over each spatial variable.

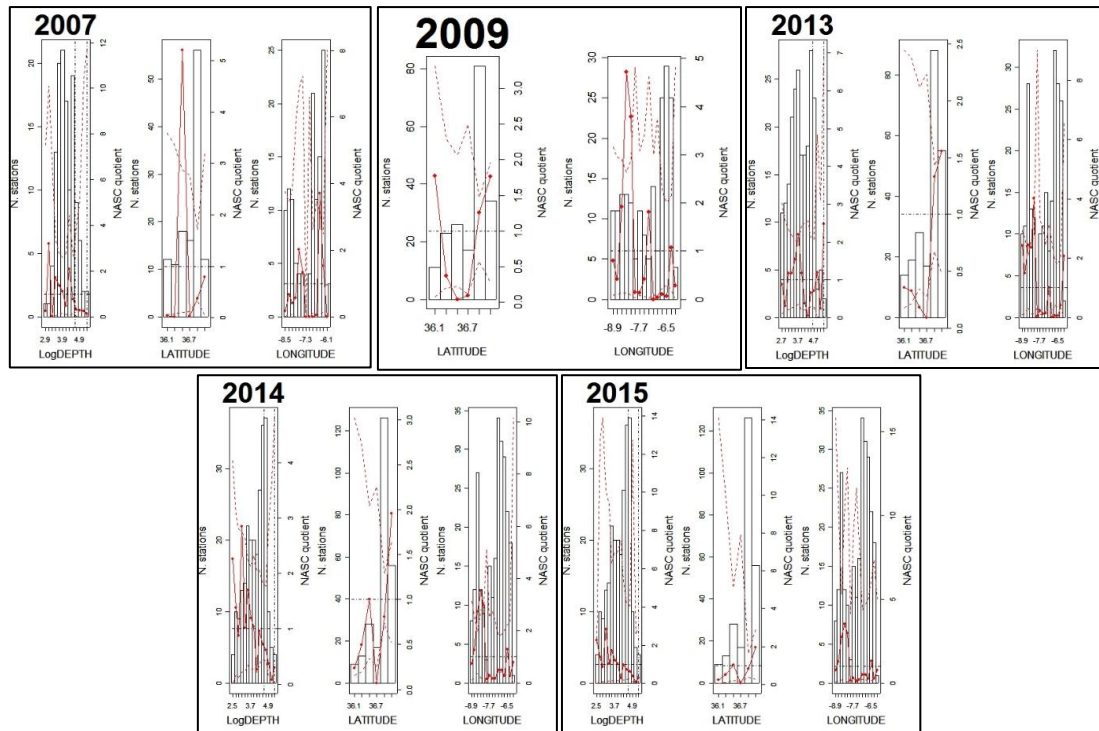


Figure 11S: *Trachurus trachurus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Quotient analyses representing the spatial variables depth, latitude and longitude by year when the data were available. The red lines represent the relative NASC value (nautical area scattering coefficient, i.e. the acoustic energy attributed to species, in $m^2 mn^{-2}$) over each spatial variable. Note that in 2009, the variable depth was not available.

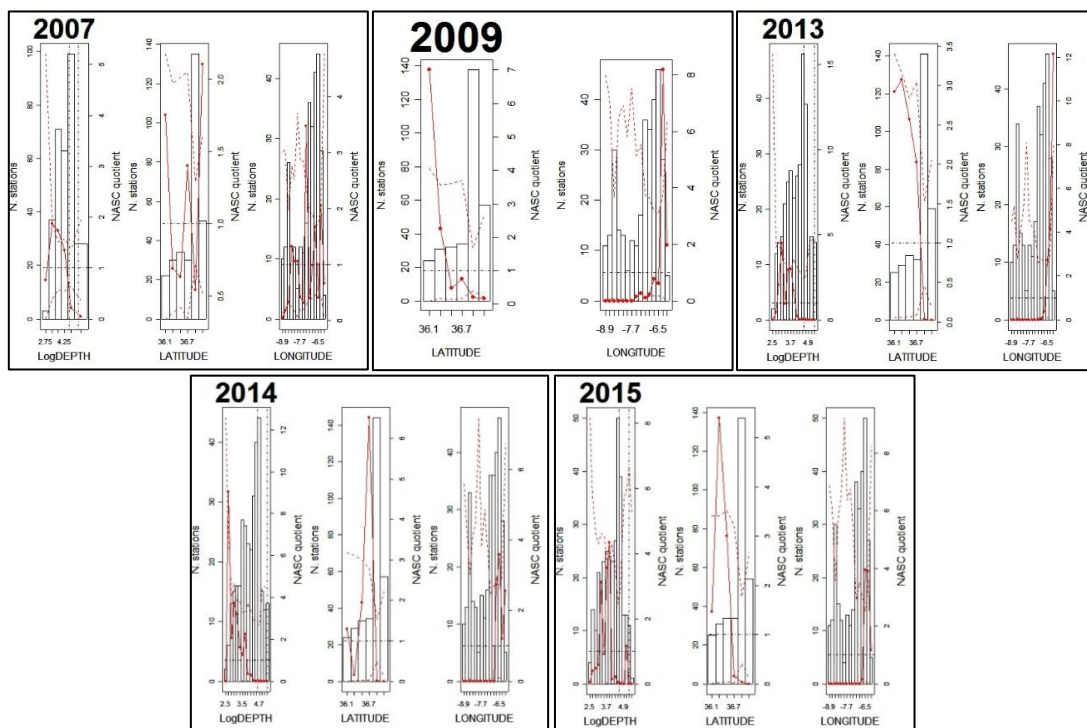


Figure 12S: *Trachurus mediterraneus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Quotient analyses representing the spatial variables depth, latitude and longitude by year when the data were available. The red lines represent the relative NASC value (nautical area scattering coefficient, i.e. the acoustic energy attributed to species, in $m^2 mn^{-2}$) over each spatial variable. Note that in 2009, the variable depth was not available.

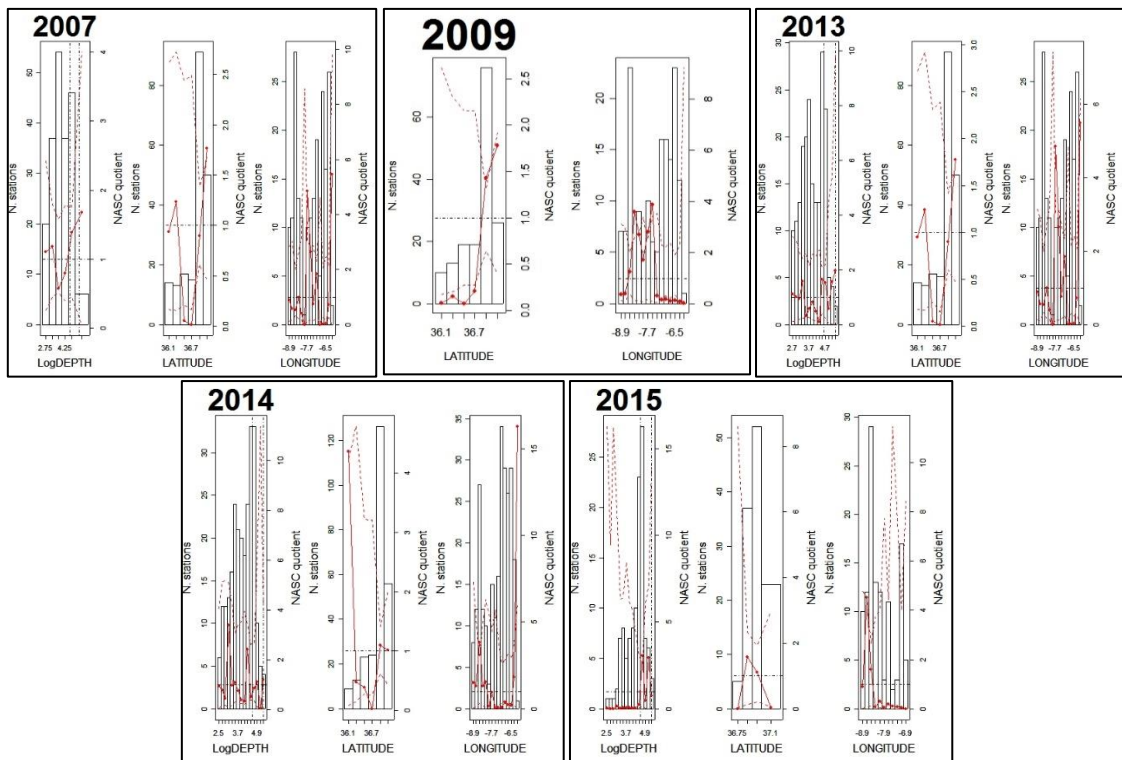


Figure 13S: *Trachurus picturatus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007–2015). Quotient analyses representing the spatial variables depth, latitude and longitude by year when the data were available. The red lines represent the relative NASC value (nautical area scattering coefficient, i.e. the acoustic energy attributed to species, in $m^2 mn^{-2}$) over each spatial variable. Note that in 2009, the variable depth was not available.

Scomber scombrus

Scomber colias

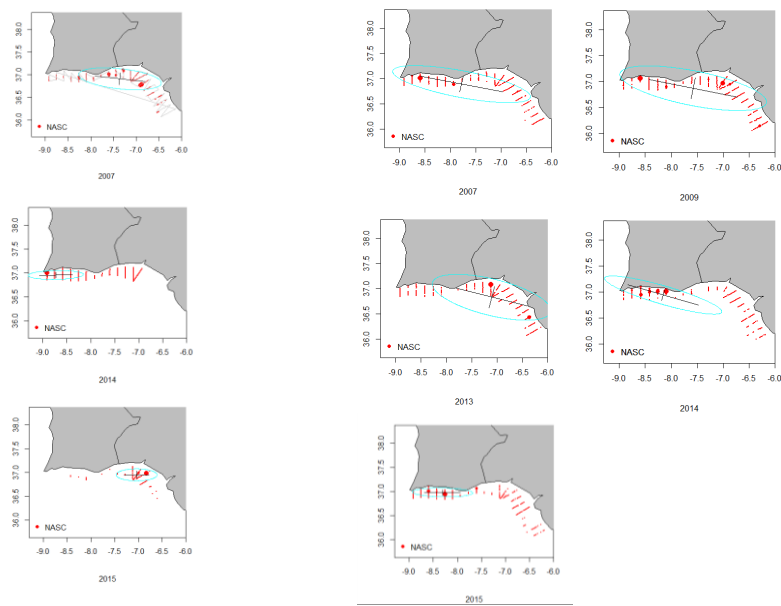


Figure 14S: *Scomber* spp. in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007–2015). *S. scombrus* (left) and *S. colias* (right) center of gravity, inertia and isotropy of the distribution of the acoustic energy attributed to the species (NASC, nautical area scattering coefficient, in $m^2 mn^{-2}$) in the years when the data were available for each species.

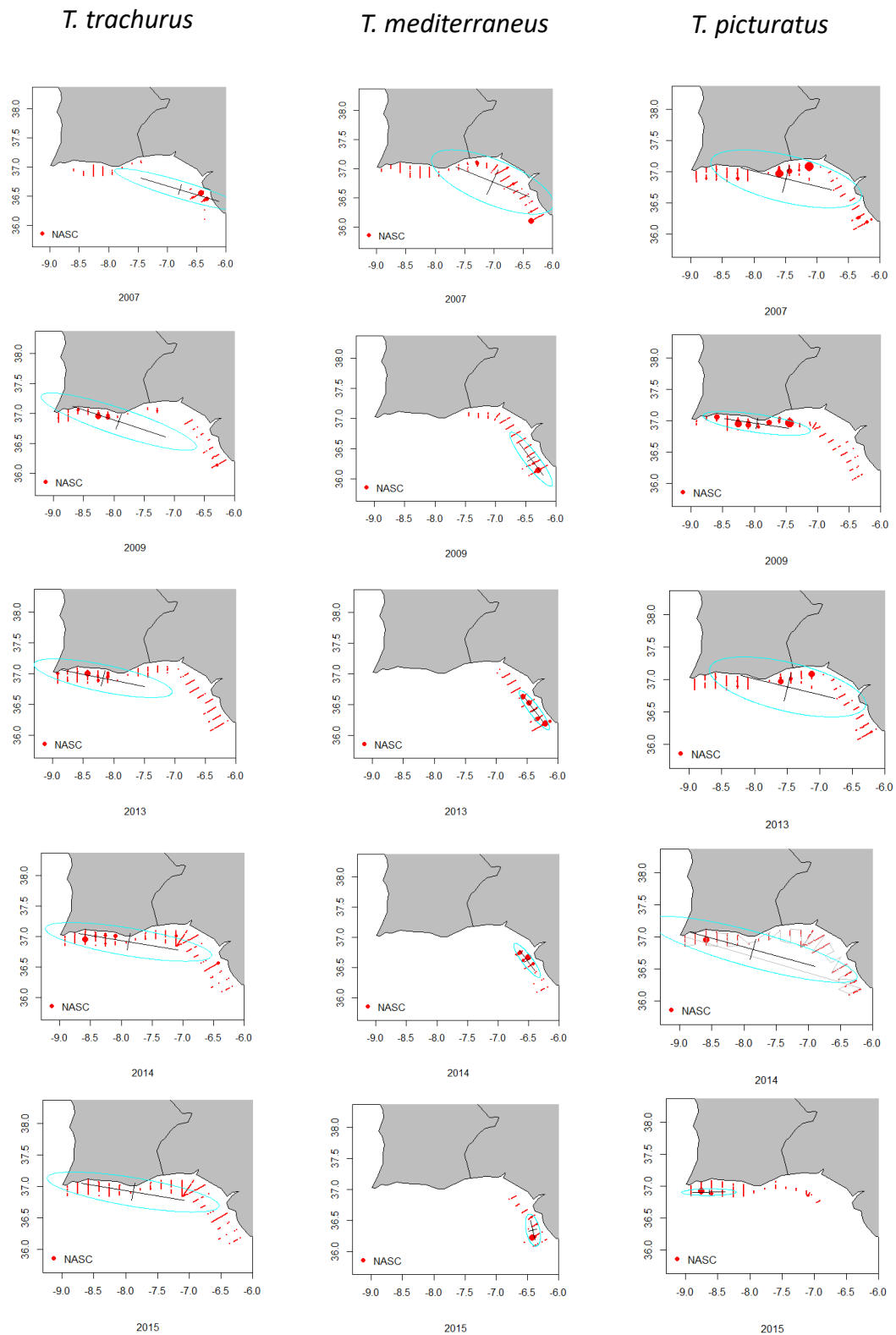


Figure 15S: *Trachurus* spp. in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). *T. trachurus* (left), *T. mediterraneus* (middle) and *T. picturatus* (right) center of gravity, inertia and isotropy of the distribution of the acoustic energy attributed to the species (NASC, nautical area scattering coefficient, in $\text{m}^2 \text{mn}^{-2}$) in the years when the data were available for each species.

Table 1S: *Scomber scombrus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Descriptive statistics of the size composition for the specimens sampled are represented by sex including mean length ML (SD, standard deviation), minimum (Min) and maximum (Max) length in cm. Length at first maturity (LFM) in cm is also shown for the total population. Parameters of length-weight relationships are estimated by sex including a (intercept), b (slope), R (coefficient of determination) and type of growth (i.e. positive allometry (A+), negative allometry (A-) and isometry (I)).

Year	Size composition and LFM							Length-weight relationships											
	Males		Females		Total			Males				Females				Total			
	ML (SD)	Min-Max	ML (SD)	Min-Max	ML (SD)	Min-Max	LFM	a	b	R	Type	a	b	R	Type	a	b	R	Type
2007	26.5(4.36)	16.8-39.4	26.2(3.60)	20.5-39.4	25.1(3.56)	16.8-39.4	25.6	0.006	3.06	0.95	A+	0.003	3.28	0.95	A+	0.003	3.22	0.94	A+
2008	26.4(2.65)	21.2-37.3	26.3(2.33)	23.4-38.2	26.2(2.41)	21.2-38.2	26.6	0.001	3.56	0.94	A+	0.001	3.71	0.95	A+	0.008	3.64	0.95	A+
2009	28.8(2.61)	25.3-34.3	28.4(2.85)	19.2-38.2	28.4(2.82)	19.2-38.2	29.0	0.002	3.49	0.91	A+	0.001	3.51	0.93	A+	0.011	3.55	0.92	A+
2011	24.6(4.03)	16.9-35.9	24.3(4.31)	12.6-36.1	24.5(4.16)	12.6-36.1	26.1	0.003	3.22	0.96	A+	0.006	3.05	0.91	A+	0.005	3.13	0.93	A+
2013	27.8(2.40)	17.7-33.0	28.6(2.89)	19.2-37.9	28.2(2.63)	17.7-37.9	29.9	0.003	3.25	0.93	A+	0.002	3.46	0.94	A+	0.002	3.35	0.94	A+
2014	28.0(3.34)	18.4-36.2	28.0(2.81)	18.1-32.8	27.8(3.25)	18.1-36.2	27.7	0.004	3.17	0.93	A+	0.010	2.92	0.83	A-	0.006	3.07	0.90	A+
2015	29.9(2.66)	25.0-37.1	30.0(2.83)	23.6-38.0	30.0(2.74)	23.6-38.0	30.0	0.001	3.63	0.96	A+	0.001	3.50	0.97	A+	0.001	3.54	0.96	A+

Table 2S: *Scomber colias* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Descriptive statistics of the size composition for the specimens sampled are represented by sex including mean length ML (SD, standard deviation), minimum (Min) and maximum (Max) length in cm. Length at first maturity (LFM) in cm is also shown for the total population. Parameters of length-weight relationships are estimated by sex including a (intercept), b (slope), R (coefficient of determination) and type of growth (i.e. positive allometry (A+), negative allometry (A-) and isometry (I)).

Year	Size composition and LFM							Length-weight relationships											
	Males		Females		Total			Males				Females				Total			
	ML (SD)	Min-Max	ML (SD)	Min-Max	ML (SD)	Min-Max	LFM	a	b	R	Type	a	b	R	Type	a	b	R	Type
2007	22.1(3.05)	14.8-31.2	23.3(3.03)	16.2-32.5	21.8(3.34)	13.0-32.5	22.9	0.006	3.12	0.97	A+	0.008	3.00	0.89	I	0.004	3.22	0.95	A+
2008	23.7(2.50)	16.7-32.2	24.0(2.00)	17.6-32.7	23.7(2.22)	14.3-32.7	23.9	0.005	3.11	0.96	A+	0.006	3.06	0.96	A+	0.005	3.10	0.96	A+
2009	22.6(2.58)	16.0-28.6	22.5(2.18)	16.0-30.4	22.4(2.32)	15.7-34.6	22.0	0.003	3.29	0.98	A+	0.004	3.19	0.96	A+	0.004	3.24	0.97	A+
2011	20.3(3.49)	13.9-30.0	20.1(3.44)	13.7-30.0	20.0(3.46)	13.7-30.0	24.2	0.003	3.36	0.98	A+	0.002	3.38	0.98	A+	0.002	3.37	0.98	A+
2013	23.7(2.24)	19.4-33.2	23.9(2.25)	19.4-30.9	23.8(2.24)	19.4-33.2	23.0	0.004	3.19	0.96	A+	0.005	3.17	0.97	A+	0.005	3.18	0.97	A+
2014	22.5(2.67)	18.2-30.0	23.3(2.82)	18.0-29.5	22.6(2.76)	16.7-30.0	24.6	0.006	3.10	0.95	A+	0.006	3.11	0.95	A+	0.006	3.10	0.95	A+
2015	22.5(2.64)	17.8-31.5	24.3(1.74)	18.5-29.7	23.2(2.51)	17.8-31.5	24.1	0.004	3.17	0.93	A+	0.010	2.92	0.83	A-	0.004	3.24	0.96	A+

Table 3S: *Trachurus trachurus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Descriptive statistics of the size composition for the specimens sampled are represented by sex including mean length ML (SD, standard deviation), minimum (Min) and maximum (Max) length in cm. Length at first maturity (LFM) in cm is also shown for the total population. Parameters of length-weight relationships are estimated by sex including a (intercept), b (slope), R (coefficient of determination) and type of growth (i.e. positive allometry (A+), negative allometry (A-) and isometry (I)).

Year	Size composition and LFM								Length-weight relationships											
	Males		Females		Total			LFM	Males				Females				Total			
	ML (SD)	Min-Max	ML (SD)	Min-Max	ML (SD)	Min-Max	a		b	R	Type	a	b	R	Type	a	b	R	Type	
2007	19.6(2.60)	17.2-29.7	18.6(1.20)	16.7-22.2	18.7(1.49)	16.1-27.9	18.5	0.013	2.85	0.96	A-	0.018	2.76	0.87	A-	0.042	2.45	0.92	A-	
2008	20.2(3.01)	15.9-31.1	19.0(1.89)	15.7-25.9	19.5(2.59)	15.3-31.1	20.5	0.017	2.76	0.97	A-	0.018	2.74	0.94	A-	0.017	2.74	0.96	A-	
2009	22.1(3.85)	15.7-33.0	21.5(3.16)	15.7-33.2	21.1(3.80)	10.9-33.2	22	0.012	2.89	0.98	A-	0.010	2.95	0.96	A-	0.010	2.93	0.98	A-	
2011	20.2(2.58)	13.6-22.6	21.1(1.49)	15.9-23.1	19.4(3.12)	12.4-23.1	20.7	0.009	2.97	0.98	A-	0.006	3.12	0.93	A+	0.007	3.03	0.98	I	
2013	17.0(1.06)	14.2-22.5	17.2(1.24)	15.0-23.8	17.1(1.21)	11.0-23.8	17.7	0.015	2.81	0.77	A-	0.007	3.05	0.89	A+	0.008	3.00	0.87	I	
2014	20.7(2.24)	12.9-29.4	20.8(1.66)	11.9-25.8	18.1(4.58)	9.5-29.4	20.3	0.075	2.27	0.77	A-	0.501	1.64	0.49	A-	0.010	2.93	0.95	A-	
2015	21.7(2.13)	15.7-26.8	21.8(2.07)	15.9-25.1	15.3(5.42)	9.2-26.8	21.8	0.007	3.07	0.97	A+	0.006	3.10	0.97	A+	0.006	3.10	0.97	A+	

Table 4S: *Trachurus mediterraneus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Descriptive statistics of the size composition for the specimens sampled are represented by sex including mean length ML (SD, standard deviation), minimum (Min) and maximum (Max) length in cm. Length at first maturity (LFM) in cm is also shown for the total population. Parameters of length-weight relationships are estimated by sex including a (intercept), b (slope), R (coefficient of determination) and type of growth (i.e. positive allometry (A+), negative allometry (A-) and isometry (I)).

Year	Size composition and LFM								Length-weight relationships											
	Males		Females		Total			LFM	Males				Females				Total			
	ML (SD)	Min-Max	ML (SD)	Min-Max	ML (SD)	Min-Max	a		b	R	Type	a	b	R	Type	a	b	R	Type	
2007	22.4(4.18)	16.2-38.2	20.8 (3.14)	15.6-36.1	21.5(3.74)	15.6-38.2	22.2	0.021	2.71	0.98	A-	0.019	2.74	0.96	A-	0.020	2.71	0.97	A-	
2008	23.1(3.19)	17.6-34.3	22.5 (3.05)	18.3-30.8	22.9(3.15)	17.6-34.3	22.6	0.030	2.58	0.96	A-	0.027	2.61	0.97	A-	0.028	2.59	0.96	A-	
2009	23.1(2.29)	19.2-32.9	22.5 (1.68)	19.2-26.4	22.9(2.22)	12.3-32.9	22.6	0.056	2.40	0.94	A-	0.028	2.62	0.9	A-	0.036	2.53	0.94	A-	
2011	28.7(3.28)	24.4-40.0	27.7 (2.13)	25.5-36.8	28.4(2.96)	24.4-40.0	28.1	0.021	2.71	0.96	A-	0.020	2.72	0.94	A-	0.019	2.73	0.96	A-	
2013	28.2(3.52)	16.7-36.9	27.0(3.58)	15.8-31.4	27.3(4.01)	15.8-36.9	27.0	0.014	2.82	0.98	A-	0.016	2.76	0.98	A-	0.014	2.80	0.98	A-	
2014	24.5(3.26)	22.0-36.4	24.2(3.10)	12.4-36.7	24.3(3.13)	12.4-36.4	22.8	0.045	2.48	0.95	A-	0.158	0.63	0.36	A-	0.320	1.12	0.48	A-	
2015	26.6(2.41)	26.0-39.8	28.3(1.62)	25.3-32.0	28.9(2.12)	25.3-39.8	28.6	0.020	2.71	0.84	A-	0.046	2.47	0.78	A-	0.026	2.63	0.83	A-	

Table 5S: *Trachurus picturatus* in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Descriptive statistics of the size composition for the specimens sampled are represented by sex including mean length ML (SD, standard deviation), minimum (Min) and maximum (Max) length in cm. Length at first maturity (LFM) in cm is also shown for the total population. Parameters of length-weight relationships are estimated by sex including a (intercept), b (slope), R (coefficient of determination) and type of growth (i.e. positive allometry (A+), negative allometry (A-) and isometry (I)).

Year	Size composition and LFM							Length-weight relationships											
	Males		Females		Total			LFM	Males				Females				Total		
	ML (SD)	Min-Max	ML (SD)	Min-Max	ML (SD)	Min-Max			a	b	R	Type	a	b	R	Type	a	b	R
2007	17.9(0.94)	16.3-19.2	18.1(1.83)	16.8-19.4	17.3(1.35)	13.6-22.3	17.3	0.037	2.49	0.95	A-	0.030	2.54	1.00	A-	0.053	3.17	0.94	A+
2008	19.1(1.18)	16.5-24.7	19.3(1.22)	16.5-23.9	19.2(1.32)	13.2-24.7	18.9	0.014	2.83	0.90	A-	0.018	2.76	0.91	A-	0.011	2.91	0.92	A-
2009	20.9(1.73)	14.6-23.9	21.4(1.72)	13.8-26.3	17.4(3.42)	11.4-26.3	20.7	0.009	2.99	0.94	A-	0.010	2.96	0.94	A-	0.005	3.20	0.98	A+
2013	18.9(0.98)	14.8-22.2	19.1(1.03)	16.8-21.9	18.6(1.17)	14.5-22.2	*	0.010	2.94	0.92	A-	0.019	2.72	0.94	A-	0.010	2.94	0.95	A-
2014	18.8(2.10)	11.8-21.3	20.1(2.05)	15.0-22.2	16.8(2.50)	11.8-22.2	*	0.411	1.68	0.46	A-	0.005	3.16	0.97	A+	0.014	2.80	0.89	A-
2015	18.5(1.74)	13.7-24.8	20.2(1.89)	16.3-23.9	18.6(1.88)	15.0-24.8	*	0.004	3.23	0.96	A-	0.020	2.71	0.97	A-	0.007	3.06	0.95	A-

Table 6S: MSFS in the Gulf of Cadiz shelf waters (20 – 200 m depth) under summer conditions (years 2007-2015). Non-seasonal Von Bertalanffy Growth Function (VBGF) parameters estimated from the two methods used in this study, NORMSEP-based Modal Progression Analysis (MPA) and ELEFAN 1: K (growth rate), L_{∞} (length at which growth is zero) and the age groups obtained. Note that age groups correspond to putative age groups. Rn means goodness of fit of the VBGF parameters.

Species	MPA			ELEFAN I			
	K	L_{∞}	Age groups	K	L_{∞}	Rn	Age groups
<i>S. scombrus</i>	0.51	38.2	0-10 years	0.24	44	0.21	1-8 years
<i>S. colias</i>	0.14	51.5	2-8 years	0.40	39	0.30	1-5 years
<i>T. trachurus</i>	-	-	-	0.23	42	0.20	1-6 years
<i>T. mediterraneus</i>	-	-	-	0.14	46	0.25	2-15 years
<i>T. picturatus</i>	-	-	-	0.66	29	0.26	0-3 years