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Unravelling the drivers of variability in body condition and reproduction of the European sardine along the Atlantic-Mediterranean transition

M. Caballero-Huertas [a], M. Vargas-Yánez [b], X. Frigola-Tepe [a], J. Viñas [c], M. Muñoz [a,*]

[a] Institute of Aquatic Ecology (IEA), Department of Environmental Sciences. Universitat de Girona (UdG), Campus Montilivi, 17003, Girona, Spain
[b] Instituto Español de Oceanografía, IEO-CSIC, Puerto Pesquero de Fuengirola s/n, 29640, Fuengirola, Málaga, Spain
[c] Genetic Ichthyology Laboratory (LIG), Department of Biology, Universitat de Girona (UdG), Campus Montilivi, 17003, Girona, Spain

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ABSTRACT

Body condition and reproduction data are broadly used to assess the health status of fish because of its implications for recruitment and ecosystem structure. *Sardina pilchardus* is a small pelagic distributed throughout both Mediterranean and Eastern Atlantic. Seasonal trend analysis of energy storage and reproduction was carried out in sardines from two areas along the Atlantic-Mediterranean transition: Southern Portugal-Gulf of Cádiz (POR-GC) (Atlantic Ocean) and Alboran Sea (Alb) (Mediterranean Sea) from 2019 to 2021. Energetic condition was estimated using tissue and mesenteric fat content, hepatosomatic index (HSI), and the relative condition factor (Kn). Sex, reproductive developmental stage, and gonadosomatic index (GSI) were also obtained. In addition, the oceanographic and meteorological characteristics of the areas were analysed. Results showed that seasonal Kn, tissue and mesenteric fat content, and HSI values of POR-GC specimens exceeded Alb's with summer arrival, period in which sardine acquires reserves to allocate them to reproduction. These differences could be associated to greater productivity of the former area mainly due to rivers discharges and trade winds intensification during summer (from July to September). Furthermore, gonad maturation of POR-GC stock occurred before the Alb. However, no spawning capable individuals were identified until February in POR-GC. In contrast, in Alb it was observed a remarkable fraction of spawning capable and active spawner individuals in October. We hypothesized the migration of mature individuals from POR-GC to the spawning areas located in the Alb. Seasonal genetic population studies are required to untangle it and reliably evaluate the environmental effect on the stocks.

1. Introduction

The small pelagic clupeid European sardine (*Sardina pilchardus* (Walbaum, 1792)) is distributed along the Eastern Atlantic, from the North Sea to the Mauritania/Senegalese coasts, spanning from the Azores to the Mediterranean and the Black Seas, with the biggest populations and fisheries concentrated in the Atlantic coasts of north Africa and Europe (Stratoudakis et al., 2007). As forage species that feeds primarily on plankton, it plays an important ecological role in the ecosystem mainly due to its contribution to higher trophic levels at bottom-up scale (Cury et al., 2000). As one of the most commercialized species in areas such Southern Europe, lower values in both number of individuals and biomass have been pointed out, consequence of the high demand for sardines and consecutive downward trend in terms of stock abundance in the last years, added to other environmental pressures (Baptista et al., 2019; FAO, 2018; 2020). European sardine is a winter batch spawner with indeterminate fecundity, which accumulates lipids from spring to autumn to allocate them to somatic growth and reproduction, reproductive strategy that has been defined as capital breeding (Ganias, 2009; McBride et al., 2015). Thus, sardine's spawning mainly occurs during the coldest months of the year in both Atlantic and Mediterranean basins (Bandarra et al., 2018; Ganias, 2009; Stratoudakis et al., 2007). However, both batch fecundity and spawning frequency can vary considerably with areas, within the spawning season, between years, and with age and size, since sardine and other clupeoids display reproductive plasticity, being able to change their reproductive traits whenever the environmental conditions require or allow it (Ganias, 2009). Thus, variability in body condition and energy storage has important implications for recruitment (Albo-Puigserver et al., 2020), and morphometric indices and analysis of lipid content/bioenergetic index seem to be good complementary indicators for condition indices in sardine (Brosset et al., 2015a). Therefore, they result of great value for

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* Corresponding author.
E-mail address: marta.munyoz@udg.edu (M. Muñoz).

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the study or inference of the quality of spawning and recruitment (Van Der Lingen and Hutchings, 2005).

It is a fast-growing species with a relatively short life span and early maturation which, in addition to its significant interannual fluctuations in population recruitment and biomass, make sardine stocks especially difficult to manage (Blaxter and Hunter, 1982; Nunes et al., 2011) to ensure a sustainable fishery. Moreover, in recent decades, important changes in abundance, landings and biological features have been reported for this species, partially attributed to increases in fishing pressure and environmental fluctuations (i.e., variations in oceanographic parameters) (Albo-Puigserver et al., 2020; Van Beveren et al., 2014; Vargas-Yáñez et al., 2020). The impact of environmental variables such as temperature, salinity, and chlorophyll concentration on sardine habitat suitability has been notably reported in a significant number of studies (e.g., Jghab et al., 2019; Lloret-Lloret et al., 2022; Vargas-Yáñez et al., 2020). This is because environmental fluctuations can affect fish populations controlling food quantity and/or quality, directly influencing growth, condition and annual recruitment (Brosset et al., 2015b), being early life stages particularly sensitive (Fernández-Corredor et al., 2021). Moreover, as European sardine is close to the bottom of the pelagic food web and feed directly on phytoplankton and micro- and mesozooplankton prey, it is likely to be rapidly affected by spatial and temporal variability of the producers and first order consumers (Garrido et al., 2008b).

Thus, comparative studies between stocks at species level are very important since they elucidate the effect of habitat conditions on growth and recruitment of fishes (Basilone et al., 2017). Environmental complexity makes investigating the effects of climate variability along fish distribution particularly challenging (Tsikliras et al., 2019). Besides, genetic population structure and connectivity in the marine environment, especially, when it comes to pelagic species, make this task even more difficult (Caballero-Huertas et al., 2022).

The Southern Iberian coastal systems consist of two adjacent basins, the Southern Portugal-Gulf of Cádiz (POR-GC) and the Alboran Sea (Alb) (connected by the narrow Strait of Gibraltar), with different hydrographic, oceanographic and meteorological characteristics (Fig. 1). POR-GC is a warm basin during spring and summer (i.e., warm shelf waters mostly during summer, with an average temperature of 21.3 °C) (Huertas et al., 2005; Navarro and Ruiz, 2006; Prieto et al., 2009), especially in the coastal areas (García-Lafuente et al., 2006) where marshes and riverine influence is particularly high. The central area of the Gulf is highly oligotrophic with the presence of a quasi-permanent anticyclonic gyre (Vargas et al., 2003), whereas in specific coastal areas intermittent upwelling processes occur mainly due to wind forcing (Stevenson, 1977). On the other hand, the north-western (NW) Alb is strongly influenced by the circulation through the Strait of Gibraltar, as the incoming Atlantic Jet feeds and maintains the surface structures in the area (Viúdez and Haney, 1997) including a strong frontal area that divides a productive sector of intense upwelling in the coastal zone (García-Martínez et al., 2019; Vargas-Yáñez et al., 2017, 2019; Viúdez et al., 1996) and a more oligotrophic area far offshore. Thus, due to the different environmental characteristics potentially affecting sardine habitat shaping in both areas, we considered of interest the study of physiological parameters and indexes in European sardine under the oceanographic and atmospheric factors of both locations. In the case of the Alb Sea and along POR-GC, there are very few studies trying to establish and quantify the relationships between the abundance, distribution and condition of European sardine and other small pelagic fishes with environmental factors (Vargas-Yáñez et al., 2020), therefore, our study aims to contribute to improving knowledge in this regard.

The main objectives of this study were to seasonally characterise 1) the differences in the energetic body condition and health status, as well as in the reproductive cycle, between European sardines from two nearby areas, the Southern Portugal-Gulf of Cádiz (Atlantic Ocean) and the Alboran Sea (Mediterranean Sea) coasts, connected by the Strait of Gibraltar, and 2) the spatial patterns of environmental variables to identify those that may be influencing the condition and reproduction of sardine stocks in each area through a descriptive and qualitative analysis.

2. Materials and methods

2.1. Body condition and reproduction analyses

2.1.1. Biological sampling and processing

Specimens of *Sardina pilchardus* ($N = 1128$) were collected seasonally (monthly samples were averaged per season) from 2019 to 2021 along the Southern Portugal-Gulf of Cádiz coast (Northeast Atlantic Ocean, Portuguese Waters - East (FAO fishing area division 27.9.a)) and the coast of Málaga, bathed by the Alboran Sea (Mediterranean Sea, GFCM – GSA 1) by purse seiners (Fig. 1 and Table A.1.). Samples were immediately frozen at - 20 °C, which has been demonstrated to have no significant effect on the studied parameters (Brosset et al., 2015a). Each sardine was measured (total length, TL ± 0.1 cm) and weighed (total body weight, TW ± 0.01 g); eviscerated body weight, EW ± 0.01 g). Gonads (GW ± 0.0001 g) and liver (LW ± 0.0001 g) were also weighed. A proxy of body condition was obtained by the calculation of the relative condition index (Kn) (Le Cren, 1951) ($Kn = EW/\alpha TL^{\beta}$), where EW is eviscerated weight, TL is total length, and α (0.0045) and β (3.1793) are constants obtained by the regression line of the logarithms of length and mass from the samples. It is interpreted as a higher-than-average physical condition for an individual when Kn exceeds 1, and lower condition when it does not reach this figure. As a measure of energetic reserves and reproductive activity, the hepatosomatic ($HSI = 100 \cdot [LW/EW]$) and gonadosomatic ($GSI = 100 \cdot [GW/EW]$) indexes, respectively, were also calculated. The sex of each specimen was determined macroscopically, and gonads were classified according to the criteria of Brown-Peterson et al. (2011) for reproductive developmental stages (i.e., immature, developing, spawning capable, actively spawning, regressing, and regenerating, see Fig. 2A). Regarding the lipidic and energetic body condition, tissue fat content (i.e., muscle total lipids) was estimated by the average of both sides along the sardine lateral line using a fish fat meter (Distell Model FM 992 with SARDINE-2 calibration). This device allows the rapid measurement of water content and provides the relative tissue fat content (%) of each individual due to the inverse relationship between water and lipid content (Bayse et al., 2018; Brosset et al., 2015a). Also, a visual scale for sardine ranging from 1 to 7 was applied to quantify the fat mesenteric reserves (Van Der Lingen and Hutchings, 2005), where 1 = fat lines invisible or thin and indistinct; 2 = depth greater than width of one or more fat lines; 3 = pyloric fat line noticeably thicker than the other fat lines, and about one-third the thickness of the pyloric junction; 4 = depth greater than width for all fat lines but no fat lobes present; 5 = all fat lines slightly lobed, but no overlap between lobes; 6 = fat line lobes obvious and show some overlap; and 7 = fat line lobes large, lots of overlap, and fundulus well-covered with fat.

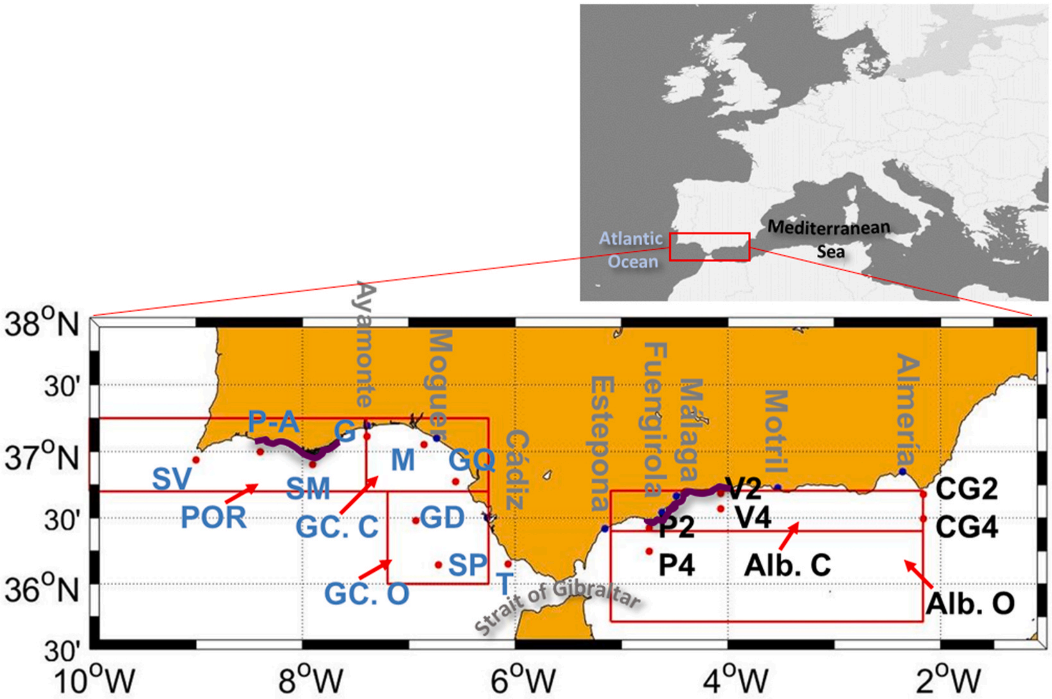

Fig. 1. Map of the two defined sample areas. Oceanographic information was obtained from the different stations (red dots) reflected (Southern Portugal-Gulf of Cádiz stations (blue letters) - SV: Cape San Vicente, P–A: Portimao-Albufeira, SM: Cape Santa María, G: Guadiana River mouth, M: Mouth of Rivers Tinto and Odiel, GQ: in front of the Guadalquivir River mouth, GD: Gualdalquivir River offshore, SP: Sancti Petri, T: Trafalgar; Alboran stations (black letters) - P2: Cabopino inshore, P4: Cabopino offshore, V2: Vélez inshore, V4: Vélez offshore, CG2: Cabo de Gata inshore, CG4: Cabo de Gata offshore). Stations were classified according to their location (red rectangles) as follows: POR (Southern Portugal): SV, P-A, SM; GC. C (Gulf of Cádiz, Coastal area): G, M, GQ, T; GC. O (Gulf of Cádiz, Open sea): GD, SP; Alb. C (Alborán Sea, Coastal area): P2, V2, V4, CG2, CG4; or Alb. O (Alborán Sea, Open Sea): P4. Wind intensity and direction data were collected from the following locations (blue dots): from west to east, Ayamonte, Moguer, Cádiz, Estepona, Fuengirola, Málaga, Motril, and Almería. The purple outline indicates the sardine sampling areas.

2.1.2. *Statistical analysis*

Using R software version 3.5.1. (R Development Core Team, 2018) to examine the differences among areas, seasons, and sex for all the indexes, Shapiro-Wilk test was applied to test the assumption of normality and Levene's test was executed to check the homogeneity of variances (Zar, 1996) in all parameters. When both assumptions were met, independent two-sample *t*-test (i.e., to compare morphogravimetric parameters between locations), one-way analysis of variance (ANOVA) (i.e., to compare mean values of the biological indexes between sexes in a concrete season or between consecutive seasons for the same sex in an area) or Multi-factor Analysis of Variance (i.e., to examine the effect of area, season, and reproductive stage on the parameters) tests were performed. Pearson's Chi-squared test was applied to compare among categories of qualitative variables (i.e., mesenteric fat by sex). Conversely, if both assumptions of normality and equality of variances were not met, the data were transformed to normality. When only homoscedasticity assumption was violated, data was analysed with Welch's *t*-test (i.e., GSI by gonadal developmental stage). For those parameters in which normal distribution was lacking but homoscedasticity was present, Kruskal-Wallis analysis of variance was applied (i.e., GSI, Kn, tissue fat content, and HSI by sex). When required, multiple comparison or post-hoc tests (Tukey's range test, Dunn's method with Bonferroni adjustment, or Games-Howell test, when corresponded) were applied to identify the different categories. Statistically significant differences were considered if $P < 0.05$*.

2.2. *Oceanographic and meteorological analysis*

2.2.1. *Data and methods*

A large data set of environmental variables was analysed to characterise those factors that may have some influence on the reproductive cycle and general health/condition of European sardines. We collected data with different spatial resolution and different geographical extension to have information on those meteorological and oceanographic patterns operating at a large scale and on the local one.

Sea Surface Temperature (SST; °C) data were obtained from the National Oceanographic and Atmospheric Agency (NOAA) "High-resolution Blended Analysis of Daily SST and Ice" (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html, Huang et al., 2021). These data have a daily frequency and spatial resolution of 0.25° × 0.25° and extend from 1981 to 2021 (inclusive). Time series were averaged to obtain monthly values for each pixel. Finally, they were spatially averaged to obtain SST (°C) time series corresponding to those red rectangles named in Fig. 1 as POR (Southern Portugal), GC. C (Gulf of Cádiz, Coastal area), GC. O (Gulf of Cádiz, Open Sea), Alb. C (Alboran Sea, Coastal area), and Alb. O (Alboran Sea, Open Sea). These areas were selected as representative of the environmental conditions affecting the sardine stocks sampled both in the Gulf of Cádiz and in the Alboran Sea. Because of the large mobility of this species, the regions where we collected environmental data represented both coastal and open sea environmental conditions.

Surface chlorophyll concentrations (mg/m^3) were obtained from the NASA (National Aeronautics and Space Administration) Ocean Colour web site (https://oceandata.sci.gsfc.nasa.gov). These data have a monthly frequency, and a spatial resolution of 0.083° × 0.083°. The final data set used corresponds to the MODIS and SEAWIFS sensors and the final time series extend from 1997 to 2021 (both included). Monthly time series were spatially averaged to obtain surface chlorophyll concentration time series (Chl; mg/m^3) at the same areas (red rectangles) used for SST.

To infer possible spatial differences within the regions determined by the red rectangles, monthly time series of SST and Chl were also obtained at single positions marked as red dots in Fig. 1 (see also the nomenclature used to name these positions in Fig. 1). These positions were selected in such a way that they could reflect any west-east gradient and also reflect the influence of river runoff and the differences between coastal and open-sea regions.

To have information about the atmospheric conditions, we downloaded reanalysis monthly time series of west-east (Ux hereafter) and south-north (Uy) components of the wind (km/h), and precipitation rates (P) from the National Centre for Environmental Prediction/National Centre for Atmospheric Research (NCEP/NCAR, https://psl.noaa.gov/data/gridded/data_ncep.reanalysis.derived.surface.html/, Kalnay et al., 1996). These time series extend from 1948 to 2021 (both included) and have a spatial resolution of 2.5° × 2.5°. Time series were averaged by regions (POR, GC. C, GC. O, Alb. C, and Alb. O) (red rectangles in Fig. 1).

Local meteorological conditions were obtained from the Agencia Estatal de Meteorología (AEMET, Spanish meteorological agency). Hourly time series of wind intensity and direction (km/h) were obtained from eight meteorological stations distributed along the Gulf of Cádiz and Alboran Sea coasts: from west to east, Ayamonte, Moguer, Cádiz, Estepona, Fuengirola, Málaga, Motril, and Almería (see blue dots in Fig. 1). These time series extend from 1990 to 2020 (both included) when available (some stations started operating at a later date). Daily precipitation data (P) were obtained at the same stations from the web site (https://datosclima.es), also from AEMET. These time series extend from 1990 to 2021 (inclusive).

2.2.2. *Data processing*

SST, Chl, Ux, Uy and P are scalar time series. In the case of daily time series, they were averaged for obtaining monthly values. Then, data corresponding to the same calendar month was grouped. For instance, in the case of a time series extending from 1990 to 2021, we have 32 data corresponding to January, 32 data for February, etc. These data were averaged, and the standard deviation was calculated. Considering a t-student distribution, a 95% confidence interval was estimated for each mean value. The set of twelve mean values, corresponding to the twelve months of the year, represent the climatological or average seasonal cycle of the variable considered.

In the case of wind time series from AEMET stations, hourly values of wind intensity and direction (km/h) were available. Besides the calculation of monthly time series of both cartesian components (Ux and Uy), wind intensity and angle of provenance referred to the north were calculated for daily wind vectors.

3. Results

3.1. *Reproductive period analysis: signs of a more advanced maturation in the Southern Portugal-Gulf of Cádiz*

Based on visual inspection and GSI values, a high proportion of immature individuals from the Alboran (Alb) were detected in June (78.57%), while in Southern Portugal-Gulf of Cadiz (POR-GC) only one immature individual was reported throughout the entire sampling

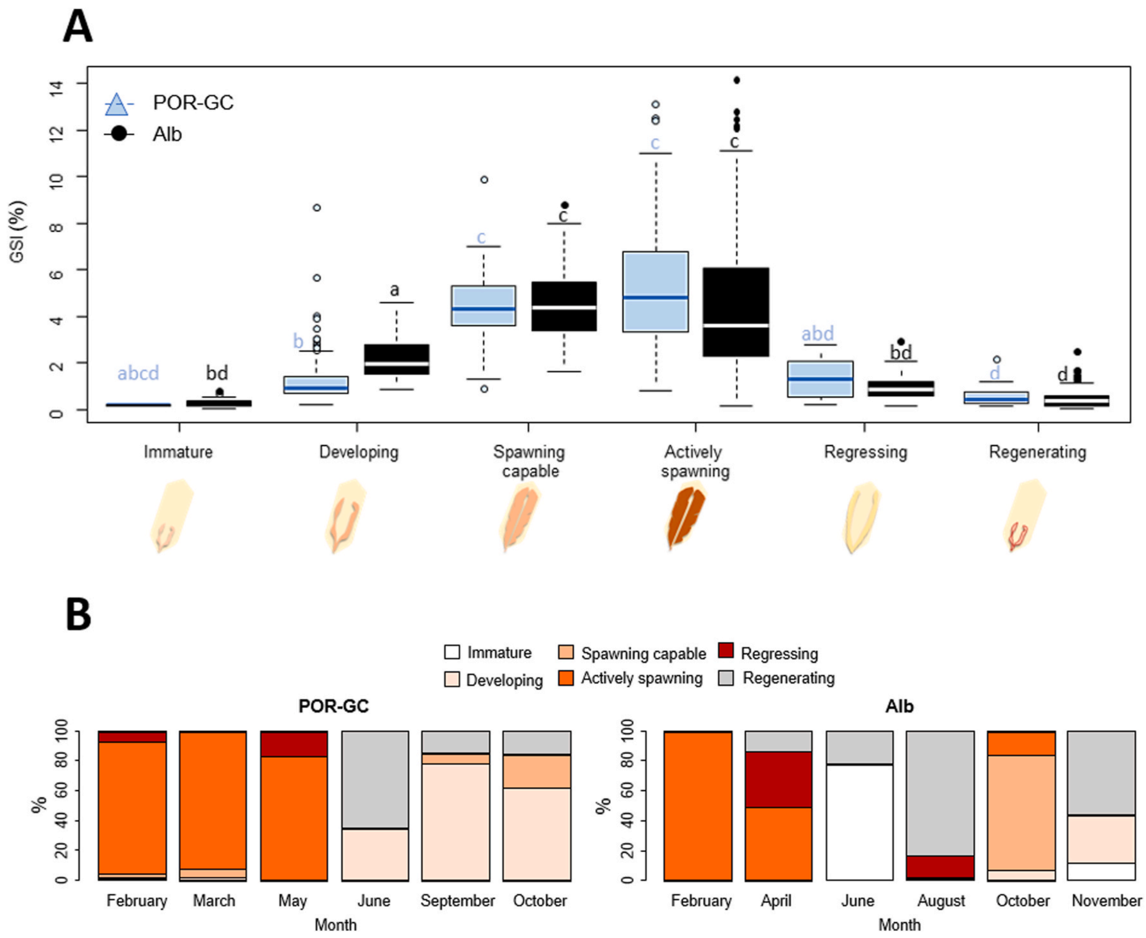

Fig. 2. Reproductive analysis of European sardine (*Sardina pilchardus*) along the Southern Portugal-Gulf of Cádiz (POR-GC) (Atlantic Ocean) and the Coast of Málaga, Alboran Sea (Alb) (Mediterranean Sea). A) Box plot of the gonadosomatic index (GSI; %) by reproductive developmental stage according to the classification of Brown-Peterson et al. (2011) in the study areas. Different letters on the graph indicate significant differences among stages and/or locations. The minimum, the maximum, the sample median (line in the boxes), the first and third quartiles, and the outliers (○) are showed. **B)** Individuals (%) at each reproductive developmental stage by month per location.

(Fig. 2B). While individuals in Alb were starting the gonad maturation (developing stage) during October (values of 7% in this month), in POR-GC this process was found earlier, during June (35.24%). As no significant differences in GSI were observed among sexes for none of the locations (Kruskal-Wallis χ^2, POR-GC: 0.166, P = NS; Kruskal-Wallis χ^2, Alb: 0.608, P = NS) (see also Table A.1.), and the sample size per gonadal stage by sex was not sufficient to establish a robust comparison, analyses were performed grouping males and females in both cases. Results indicated significant differences among gonad developmental stages in GSI by area (Welch F-test, POR-GC: $F_{7,591} = 122.300$, $P < 0.0001$***; Welch F-test, Alb: $F_{7,424} = 81.930$, $P < 0.0001$***), and a significant interaction between area and gonad developmental phase (Welch F-test, developmental stage*area: $F_{11,1019} = 135.200$, $P < 0.0001$***) (Fig. 2A). Significant lower GSI values were therefore quantified in developing individuals in POR-GC compared to those of the Alb, reaching similar values once fish were able to spawn. Nevertheless, a higher percentage of spawning capable fish were observed in October in the case of Alb than in POR-GC, finding also actively spawning individuals in the former (16%). However, in November we did not detect individuals at any of these two reproductive statuses in Alb. In February, it was shown a high rate of active spawners in both areas. Nevertheless, some individuals started the regression period in POR-GC (8.79%) in this month, which did not occur in Alb until April.

3.2. *Relative condition and energy storage: larger lipid reserves throughout the year in the Southern Portugal-Gulf of Cádiz area*

The total body length (TL) of the sardine specimens in POR-GC was 17.73 ± 1.30 cm (mean ± SD) (from 13.5 to 22 cm), while in the Alb it was 15.97 ± 3.14 cm (from 9.1 to 23 cm). Total body weight (TW) was 49.26 ± 13.14 g and 38.59 ± 21.59 g for POR-GC and Alb, respectively. Thus, POR-GC sardines presented larger values for both measurements ($t = -12.027$, $P < 0.0001$***; $t = -9.867$, $P < 0.0001$***, for both length and weight, respectively).

For Kn, as no significant differences were observed among sexes for any of the locations (Kruskal-Wallis χ^2, POR-GC = 0.040, P = NS; Kruskal-Wallis χ^2, Alb = 0.318, P = NS), males and females were analysed together (Table A.1.). The relative condition index of the specimens was minimal during the winter and began to recover during the spring similarly in the two areas (Fig. 3). However, the marked increase in Kn that occurred in summer was significantly more pronounced in POR-GC specimens than in those from Alb. These differences between areas remained significant during the beginning of the decline in condition in autumn. Moreover, average Kn in POR-GC was maintained from summer to autumn, when in Alb, the decline from summer towards autumn was significant.

General differences between sexes were detected for tissue fat content (Kruskal-Wallis χ^2, POR-GC = 4.003, $P < 0.05$*), mesenteric fat (χ^2, POR-GC = 14.919, $P < 0.05$*), and HSI (Kruskal-Wallis χ^2, POR-GC = 30.815, $P < 0.0001$***) for POR-GC individuals (analysis by season in Table A.1.), while sex differences were only observed for HSI in Alb samples in autumn (Fig. 3 and Table A.1.). Tissue and mesenteric fat content values were the lowest during winter for both locations, while in spring they were significantly higher in the specimens from the Atlantic (POR-GC). This coincided with the detection of differences between sexes for both parameters in this area, higher in females. In the case of mesenteric fat, it reached similar values among locations during summer. Regarding HSI, lower values were also observed during winter for both areas, and similarly to fat indexes, differences appeared in spring with POR-GC showing higher values. During this season, females of this area presented the highest figures. In the Alb, similarities regarding sex were established until autumn, when females mean value was significantly above the one of males.

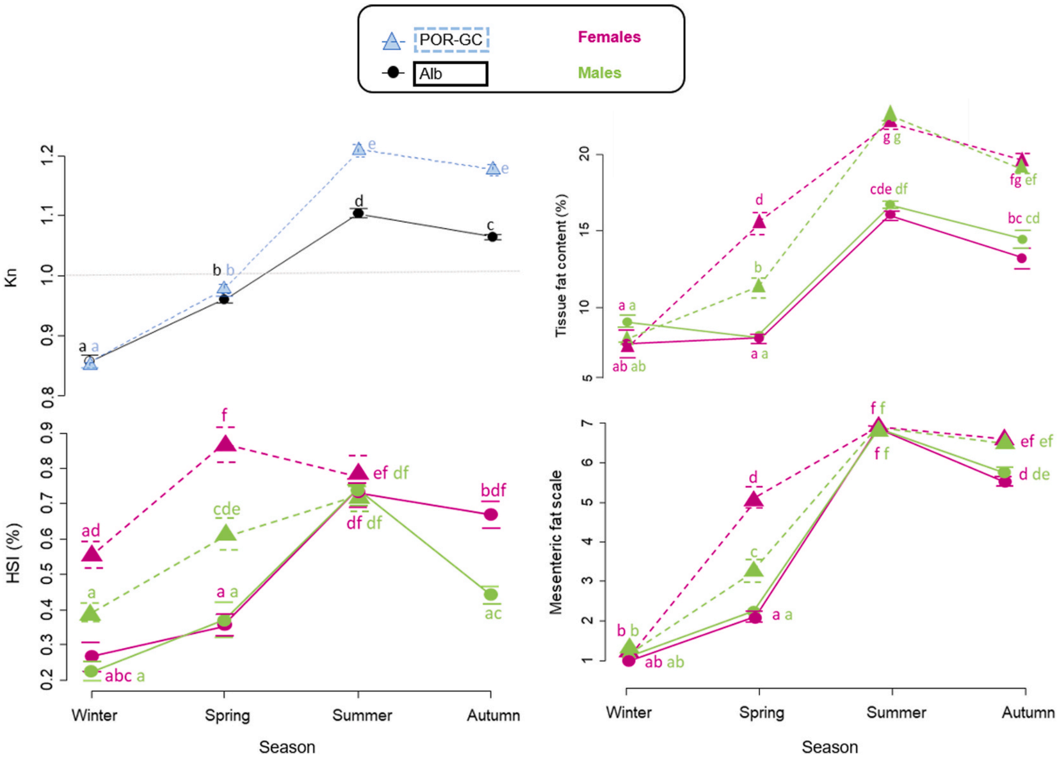

Fig. 3. Energetic condition indexes of European sardine (*Sardina pilchardus*) along the Southern Portugal-Gulf of Cádiz (POR-GC) (Atlantic Ocean) and the Coast of Málaga, Alboran Sea (Alb) (Mediterranean Sea). Average ± standard error (SE) of the relative condition factor (Kn), tissue fat content (%), mesenteric fat, and hepatosomatic index (HSI; %) by season, area and sex are shown. Different letters on the graphs indicate significant differences among season, sex and/or locations. Sexes were represented separately when significant differences ($P < 0.05$*) were found within the same locality for the corresponding parameter.

3.3. Oceanographic and meteorological characterisation

3.3.1. SST and surface chlorophyll

Fig. 4 shows the average SST (°C) and Chl (mg/m^3) concentrations for four months of the year (January, April, July and October), each representing one season (i.e., winter, spring, summer and autumn, respectively). Surface temperature was lower in the northern Alb coast than in the coast of POR-GC area for most of the seasonal cycle. The only exception occurred during the summer season, when warmer surface waters occupied both regions. Surface temperatures in the area surrounding Cape San Vicente (SV) were higher than those in the coastal waters of the GC and the northern Alb Sea during winter months, and cooler for the rest of the year. It cannot be established a correspondence between the spatial pattern of the SST seasonal cycle, and that of the chlorophyll concentrations, at least from this large-scale description. Regardless of the time of the year and the values of the water temperature, the coastal waters of the GC seemed to be the most productive ones. The highest chlorophyll concentrations in the Alb Sea were observed in coastal waters to the northeast of Gibraltar and to a lesser extent in the Málaga Bay. Notice that the shape of the Atlantic Current, surrounding the anticyclonic gyre in the western Alb Sea, can be perceived from the chlorophyll concentration distribution in April, July, and October. In the Portuguese waters, the most productive areas were found around SV during summer months. The highest chlorophyll values were observed between SV and Cape Santa María (SM) for the rest of the year.

Fig. 5 shows the climatological seasonal cycles of SST and Chl for the five areas presented in Fig. 1 (POR, GC. C, GC. O, Alb. C, Alb. O). SST cycles showed a clear longitudinal gradient with the coldest waters in the POR sector (west), increasing towards the east. The Chl seasonal cycles also showed clearly that the most productive waters correspond to the coastal waters of the GC (GC. C - G, GQ, and M in Fig. 5). This figure also evidences an important difference in the seasonal Chl cycle between the waters of the GC and Alb Sea, and those of POR. In the former cases, the maximum values were reached during the end of winter or beginning of spring, and then they started to decrease to minimum values in summer. Then, the productivity of surface waters increases again during autumn months. In the case of POR waters, there was a secondary maximum during summer months (see Fig. 5E and F).

Nevertheless, this spatial variability observed on a broad scale (red rectangles in Fig. 1) can mask some small-scale features of great importance. Fig. 5 (A, B) shows the SST and Chl seasonal cycles for three positions within the POR area (see Fig. 1): SV (Cape San Vicente), P-A (Portimao-Albufeira) and SM (Cape Santa María). As already mentioned, the P-A region (located between SV and SM) showed the highest chlorophyll concentrations all the year round, with maximum values during winter. The SM cycle was quite similar to that depicted for the GC and Alb Sea, while that for SV was completely different, with maximum values during the summer season. This latter area also exhibited the lowest temperatures. Monthly variations for GC and Alb areas are also presented in Fig. 5. The highest chlorophyll concentrations were observed at G (close to the Guadiana River mouth), M (close to the mouth of rivers Tinto and Odiel), and GQ (in front of the Guadalquivir River mouth). The concentrations at the offshore positions (SP, GD, which together make up GC. O, Fig. 5F) were much lower. Notice that the seasonal cycle at the coastal location T was different from the rest of

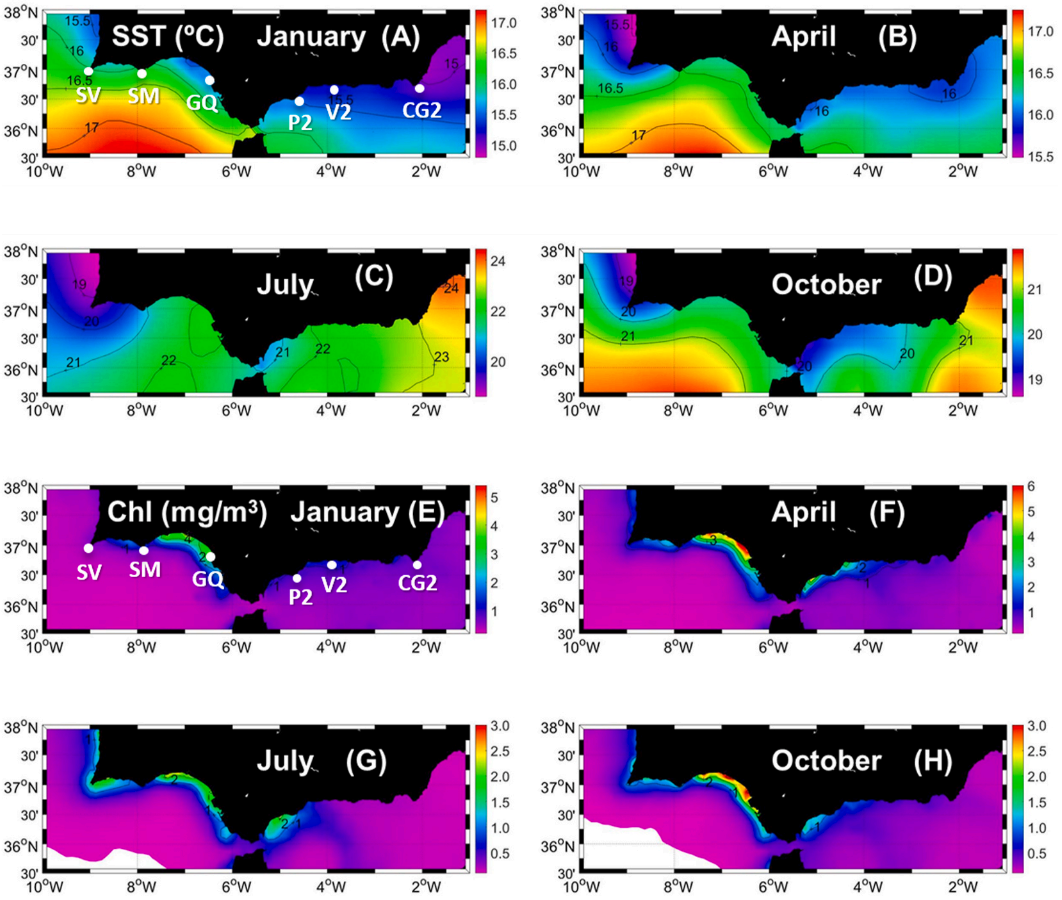

Fig. 4. Maps of the mean Sea Surface Temperature (SST; °C) (A, B, C, D) and mean chlorophyll concentrations (Chl; mg/m^3) (E, F, G, H) of one month per annual season along the Southern Iberian Peninsula. SST data was daily taken from 1981 to 2021 and Chl values had a monthly frequency, obtained from 1997 to 2021. Some stations have been added to make the map easier to understand: Southern Portugal-Gulf of Cádiz stations - SV: Cape San Vicente, SM: Cape Santa María, GQ: in front of the Guadalquivir River mouth; Alboran stations - P2: Cabopino inshore, V2: Vélez inshore, CG2: Cabo de Gata inshore.

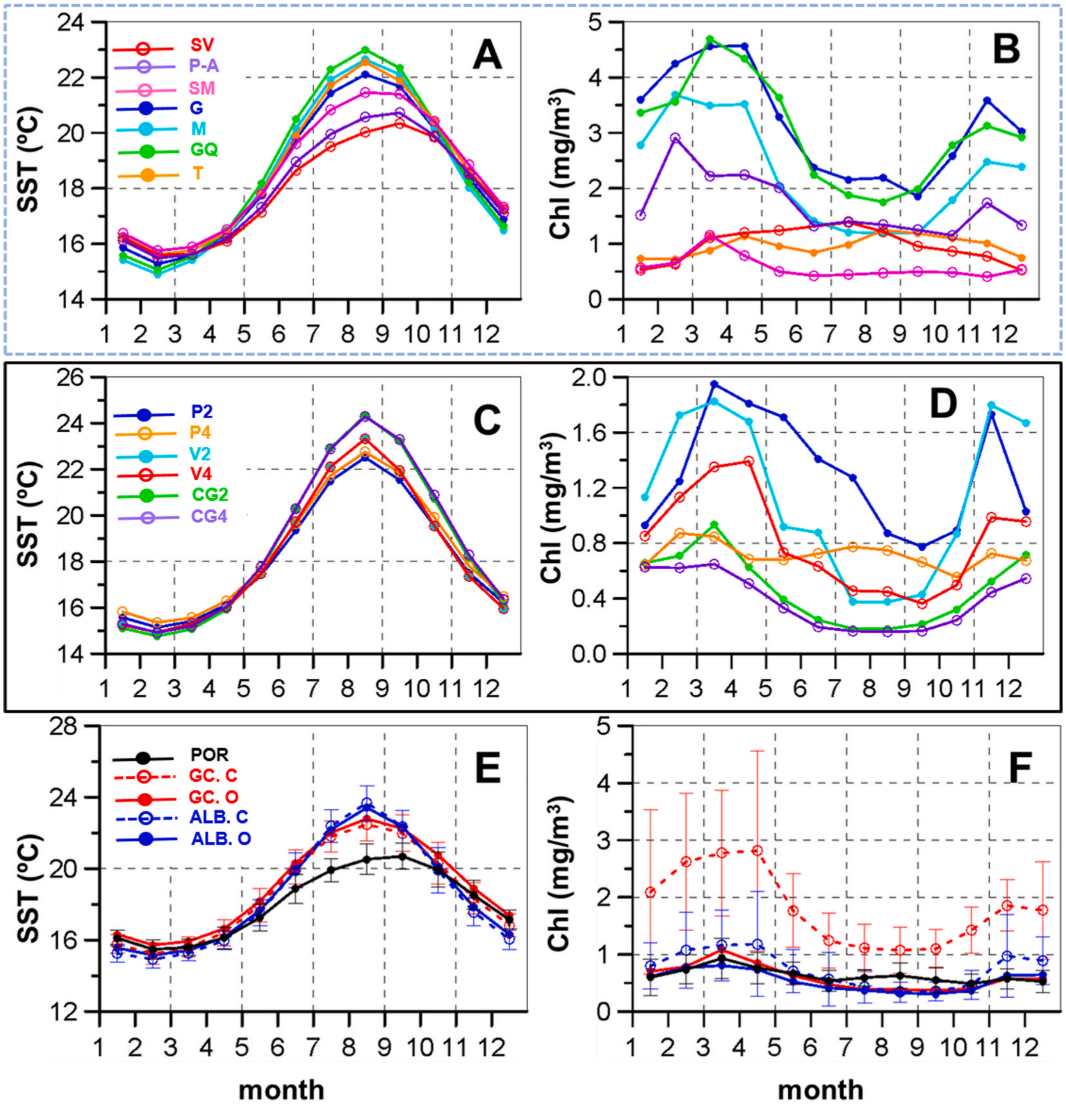

Fig. 5. Mean Sea Surface Temperature (SST; °C) and mean chlorophyll concentrations (Chl; mg/m^3) by month along the study areas. A, B) Mean SST and Chl values for Southern Portugal-Gulf of Cádiz (POR-GC) (Atlantic Ocean). **C, D)** Mean SST and Chl values for the Coast of Málaga, Alboran Sea (Alb) (Mediterranean Sea). **E, F)** Summarized comparison of mean ± SD SST and Chl values in the study areas (see Fig. 1 to identify the locations of the data extraction).
SST data was daily taken from 1981 to 2021 (inclusive) and Chl values had a monthly frequency, obtained from 1997 to 2021 (both included). Southern Portugal-Gulf of Cádiz stations - SV: Cape San Vicente, P-A: Portimao-Albufeira, SM: Cape Santa María, G: Guadiana River mouth, M: Mouth of Rivers Tinto and Odiel, GQ: in front of the Guadalquivir River mouth, T: Trafalgar; Alboran stations - P2: Cabopino inshore, P4: Cabopino offshore, V2: Vélez inshore, V4: Vélez offshore, CG2: Cabo de Gata inshore, CG4: Cabo de Gata offshore.

positions and had much lower values than those observed at G, M, and GQ (Fig. 5B). In the case of the Alb Sea, the highest chlorophyll concentrations were observed at P2 (Fig. 5D), coinciding with the lowest temperatures. Note that the lowest SST of both areas (GC and Alb) was observed in the coastal point P2, in the north-western Alb Sea (Fig. 5C). Nevertheless, these values in chlorophyll were lower than those observed in the GC (notice the different scales in the y-axes). Relatively high Chl concentrations were found at V2 and V4, whereas these values considerably decreased at the offshore point P4, and at the eastern boundary of the Alb Sea (CG2 and CG4).

3.3.2. Wind and precipitation rates

Fig. 6 shows the wind intensity (km/h) (black lines), Ux component (km/h) (red lines) and Uy component (km/h) (blue lines) of the wind in the areas named as POR (6A), GC (6B) and Alb (6C). Ux wind component is positive when directed towards the east (westerly winds) and Uy component is positive when directed towards the north (southerly winds). Precipitation rates (mm) are represented by green lines.

Precipitation rates showed a longitudinal gradient with higher annually accumulated precipitation values in POR (500 mm/year) and GC (561 mm/yr), and lower ones in the Alb Sea (390 mm/yr). Besides this difference in the annually accumulated precipitations, the seasonal cycles of the three areas had a similar form, with precipitations rates increasing from October, and maximum values at November/December. Monthly precipitation values still remained at relatively high values until April, whereas very low values were observed from May to September.

The seasonal wind cycles also showed spatial variations, with mainly the Alb Sea differing from the other two areas. The first difference was observed in the wind intensity (black lines and left y-axis in Fig. 6). Maximum intensities were observed during summer months (May to September) at POR and GC. On the contrary, the lowest intensity was observed from May to October in Alb. It is worth noting that the highest values corresponded to the POR area. The second difference concerns the south-north component of the wind (Uy, blue lines). This component was negative during the whole year, indicating the prevalence of

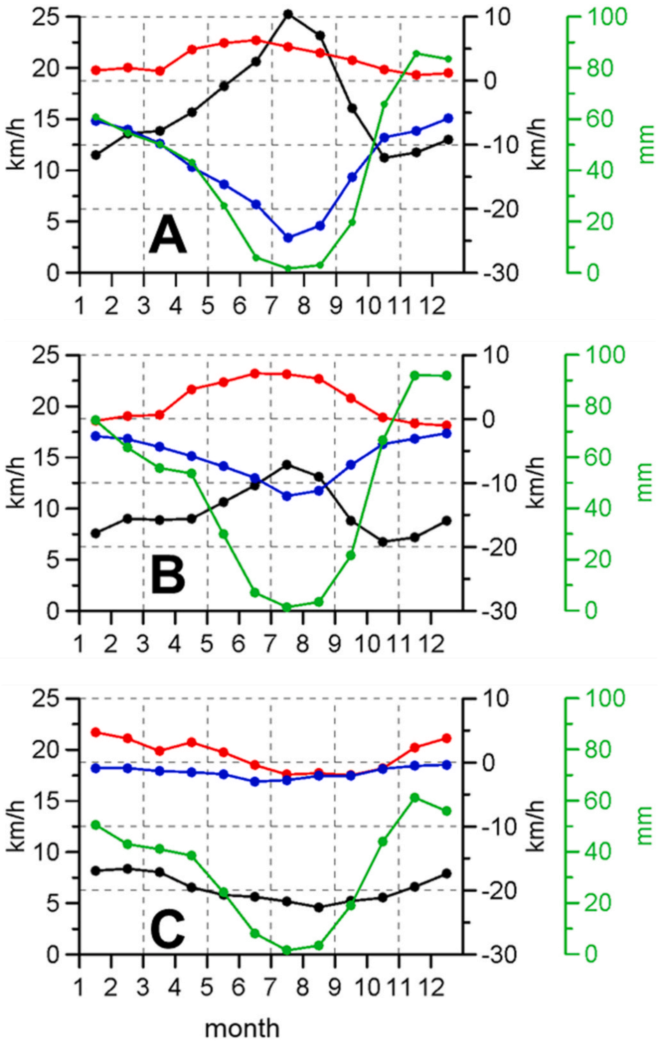

Fig. 6. Monthly time series of the wind intensity, west-east (Ux) and south-north (Uy) components of the wind, and precipitation rates (P) in the Portuguese Coast (POR) (A), Gulf of Cádiz (GC) (B), and Alboran Coast (Alb) (C). Wind intensity in km/h (black lines and left y-axis); west-east component in km/h (Ux, red lines and right y-axis); south-north component in km/h (Uy, blue lines and right y-axis); precipitation rates in mm (green lines and green y-axis).

northerly winds. Nevertheless, the amplitude of this cycle was larger at GC and mainly in the POR sector, where strong northerly winds prevailed from May to September as a result of the summer intensification of trade winds. The behaviour of the west-east component of the wind was also clearly different in both sides of Gibraltar. Whereas westerly winds prevailed throughout the year at POR and GC, with an intensification of this component from May to October, the opposite behaviour was observed in Alb. Wind blew from the west from November to May, but there was a reversal to easterly winds from June to October (red lines in Fig. 6). The characterisation of the local meteorological variables from the local meteorological stations (AEMET) showed a clear trend in the cycle of the wind direction and intensity and in the precipitation rates. Although these local cycles are similar to those inferred for the larger geographical areas, obtained from reanalysis data, there are some local effects (e.g., differences appeared between Ayamonte and Cádiz stations). These local differences made it more difficult to extract conclusions about the general meteorological conditions in the Gulf of Cádiz and in the Alboran Sea. The biological data analysed in this work corresponded to years 2019–2021. The length of these time series does not allow us to perform any kind of multivariate analysis in order to relate the variability of the sardine condition at the different regions with the variability of the environmental variables described above. This is the reason why we have focussed on the average seasonal cycle that should highly influence the seasonal cycle of sardine growth and reproduction. Nevertheless, for the completeness of the work, Figures A.1, A.2 and A.3 as supplementary material show the values of SST (°C) and Chl concentration (mg/m^3) (A.1), wind intensity (km/h) and components Ux (km/h) and Uy (km/h) of the wind (A.2), and the precipitation rates (mm) (A.3), from one year before the starting of the biological sampling (2018) until the beginning of 2022. The climatological seasonal cycles are superimposed on the 2018–2021 time series for comparison.

4. Discussion and conclusions

4.1. *Environmental patterns and annual energetic condition and health status*

European sardine presented seasonal variability in the relative body condition index (Kn) at local level, as well as differences when comparing samples from the two studied locations at certain times of the year. We can observe that the highest values of all the studied indexes mainly corresponded to summer, when sardine is in better condition prior to its investment in reproduction during the autumn-winter months (Basilone et al., 2021; Ganias et al., 2014; Mustać and Sinovčić, 2009). This pattern of energy distribution throughout the year is common in sardines in the Mediterranean, being reported in previous studies (Albo-Puigserver et al., 2017; Pethybridge et al., 2014). The peak in condition during the summer is related to its recovery, matching with the abundance of spring food resources and prior to its investment (Fig. 5B, D, F). In fact, phytoplankton are particularly important during spring and summer for sardines living in upwelling regions off the Iberian west coast (Garrido et al., 2008a).

In autumn, the decrease of mean Kn until reaching the low winter values could be explained by reserves used for gonad growth and maturation, as well as the pressure on the digestive tract of fish, which can limit food consumption (Amenzoui et al., 2006). Notwithstanding, sardines continue to feed throughout the entire spawning season to maintain the required, although low, level of energy reserves in all tissues (Zorica et al., 2019). These trends were also reflected in the energy reserves indexes (especially, in the tissue fat content, but also, in the mesenteric fat) as well as in the liver size relative to eviscerated weight or HSI, except in females from the Southern Portugal-Gulf of Cádiz (POR-GC), which showed a marked increase in the HSI from the spring months (Fig. 3).

Kn mean value of individuals from POR-GC significantly exceeded Alboran's (Alb) index in summer and autumn. Furthermore, POR-GC sampled population presented in general larger values of tissue fat content, mesenteric fat scale and HSI than Alb individuals, except for winter for the three parameters, and summer for mesenteric fat and HSI, similar to the Alb. Although many uncertainties arise regarding sardine genetic population structure along the Iberian Peninsula, greater genetic similarity has been attributed between the Atlantic and Alboran stocks than between the latter and other areas of the Mediterranean (Caballero-Huertas et al., 2022). However, phenotypic plasticity could reflect either a difference in the total energy flux through a population under different environmental conditions or a genuine alteration in the proportion of energy allocated to each competing demand under different environmental conditions (McManus and Travis, 1998), as our results might reflect.

Thus, as differences in the measured biological variables could be influenced by the local and regional environmental conditions (Fernández-Corredor et al., 2021), we wanted to characterise the two study areas to obtain a global vision of the potential oceanographic and meteorological factors that may affect sardine condition and health status. The presence of cold waters close to coastal areas, or in the inner sector of cyclonic eddies, usually indicates the upwelling of nutrient-rich deep waters. This, in turn, enhances phytoplanktonic blooms, increasing the food availability for small pelagic species such as sardines (Somarakis et al., 2006). The results presented in this work showed these features, but they also indicated that the productivity of those waters in POR-GC and Alb are controlled by more factors than simply the wind induced or eddy induced upwelling of deep waters. In the westernmost area (POR), the seasonal cycle of chlorophyll concentration was similar to that observed in the other two areas (GC and Alb) when the whole POR region is considered, with maximum values during the end of winter. The only difference was a secondary maximum during summer (Fig. 4F). Our results suggest important differences produced by distinctive mechanisms. The maximum chlorophyll concentrations were observed in winter in the P-A area, to the east of Cape San Vicente, whereas the coldest waters (Fig. 5) and very likely the strongest upwelling occur at Cape San Vicente during the summer months (Fig. 6). These results point to the intensification of trade winds during summer as an important factor increasing primary production from May to September in the area surrounding SV, months in which European sardine begins to feed intensively (spring-summer) to storage lipid reservoirs. This may be reflected as a higher condition and lipid reserves in stocks of the POR-GC. Nevertheless, other factors operating during winter time at P-A are more important. It should be noticed that the river Arade is close to this location, and precipitations were more intense from October to May in this area (Fig. 6A), favouring large discharges. The influence of river discharges as a main factor modulating primary production in the GC is confirmed by the analysis of those locations extending from the river Guadiana (G) to Trafalgar (T, Fig. 5) and by comparison with the nearby Alboran Sea, which presented much lower chlorophyll concentrations even when the wind favours upwelling processes. In this sense, the importance of upwelling has been observed in terms of enhancing primary production, although it may have a secondary role compared to other factors such as riverine input and runoff (Bonanno et al., 2016). Moreover, in the GC, from G to T, the Ux component of the wind, which should induce upwelling, had minimum values during winter and autumn (Fig. 6B), but chlorophyll concentrations reached maximum values during these months. Based on this, we hypothesized that the main fertilizing factor in POR-GC is linked to the discharges of rivers Guadiana (G) and Guadalquivir (GQ), in the Spanish sector, and Arade, in the Portuguese one. Evidence of the influence of riverine inputs on the productivity of small pelagic fish has been provided in several studies, which support our conception (Bonanno et al., 2016; Feuilloley et al., 2020; Lloret et al., 2004; Vargas-Yáñez et al., 2020; Véron et al., 2020). This hypothesis is also supported by two other facts. First, the maximum chlorophyll concentrations were observed between autumn and the beginning of spring, when precipitations reached the highest values (Fig. 6), and second, such concentrations were much lower and had a different seasonal cycle in the nearby T location which is in the same area but it is not influenced by any river. Thus, direct food intake along the mentioned period (i.e., from autumn to spring) could be reflected in increased hepatic mass, which exerts a positive effect on individual ovarian mass and fecundity (Somarakis et al., 2006), and that may explain the differences in winter and, more pronounced and significant, in spring in HSI between POR-GC and Alb and, especially, in female at the Atlantic Ocean.

Coastal temperatures were colder in the Alb from autumn to spring, when the prevailing direction of the wind was from the west, favouring coastal upwelling (Fig. 6C). Besides this fertilizing mechanism, the area between Gibraltar and Fuengirola (see Fig. 1 for locations) exhibited high chlorophyll concentrations during the whole year, including the summer season when the winds shifted to easterlies in Alb, inhibiting the wind-induced upwelling. This is caused by two factors: the first one is the proximity of the Strait of Gibraltar where intense mixing occurs because of internal tides and the dynamics of the Atlantic Current flowing into the Mediterranean Sea (Echevarría et al., 2002; Huertas et al., 2012). The second one is the presence of a semi-permanent cyclonic eddy to the south of Estepona (see Fig. 1), producing the upwelling of sub-surface waters independently of the wind direction (García-Martínez et al., 2019; Vargas-Yáñez et al., 2017, 2019). These two factors have a limited spatial scope, and do not reach the area which extends from Málaga to the east. For this reason, the primary production in this latter area decreases during the summer months, when the wind shifts to easterly, which would be reflected as a lower lipid content in the muscle in summer in the Alb sardine compared to individuals from POR-GC (Pethybridge et al., 2014), despite the fact that mesenteric fat reached similar values.

Finally, it should be considered that the lowest chlorophyll concentrations corresponded to CG2 and 4 (Fig. 4. See also Fig. 1 for the location of these stations), simply indicating the west-east oligotrophic gradient in the Mediterranean Sea, and also to the location P4. This latter station is close to P2, where the highest chlorophyll concentrations of the Alb Sea were found. The reason seems to be, according to the existing literature (García-Martínez et al., 2019; Vargas-Yáñez et al., 2017, 2019; Viúdez et al., 1996,1997), that P4 is offshore and already under the influence of the oligotrophic waters in the inner part of the anticyclonic gyre that usually occupies the Western Alboran Sea.

4.2. Reproductive cycle along the Southern Iberian Coast: the migration hypothesis and its potential relationship with the energetic condition

Increases in sardine condition and fat reserves during the summer, when more food is available thus, higher feeding intensities, suggest that variations in reproductive traits may have been caused by environmentally driven changes in food availability (Silva et al., 2006). However, lipid storage may not be used directly to promote egg production or gonadal growth, but rather to provide energy needed for metabolism, permitting energy from food to be used for egg maturation (Somarakis et al., 2006). Thus, the analysis of curves showing the seasonal fat content could already be a first indication of potential differences in the reproductive cycle in sardines on both sides of the Strait of Gibraltar. In addition to the reserves destined for reproduction, there are other factors that seem to be associated with the spawning seasonality, as water temperature, since it has been assumed its preferences for spawning at 14–15 °C and avoidance for temperatures below 12 °C and above 16 °C (Ganias et al., 2007; Ganias, 2009; Stratoudakis et al., 2007).

Despite the fact that other works pointed out the similarities in the reproductive cycle of the two study areas (Stratoudakis et al., 2007), we reported hints of earlier maturation in sardines from POR-GC (Fig. 2B), which, as already mentioned, presented a higher tissue fat content at the intensive feeding season (i.e., summer). Moreover, it nearly coincided with the lowest temperatures recorded in the south of the Iberian Peninsula in the area SV-SM in July (Fig. 4C). However, individuals able to spawn were not observed until February in POR-GC, unlike in the case of individuals from Alb, which started the gonadal development earlier-along October, but also spawning capable and active spawners were found in this month, maybe linked to a drop in temperatures along this coast (Fig. 4D). Given these results, and although we lack data for some months (among other reasons, due to fishing closures), potential explanations could be provided. The first is that Atlantic (POR-GC) individuals entered in Mediterranean waters when they were able to spawn, reason why high percentages of spawning capable and active spawners were present in October in Alb whereas neither spawning capable nor developing individuals were found during August, the previous month when data were available. It seems to be difficult that both processes of developing and spawning capability occurred in the month of September (lacking data) until reaching the values observed in October for the local individuals in Alb. Thus, one of the reasons of this migration of spawning capable and active spawner individuals from POR-GC may be this drop in local temperature in October in the Alb area. Also, stable currents as the inflow of Atlantic water in the

Mediterranean Sea through the Strait of Gibraltar foster the exchange of species among adjacent basins (García-Lafuente et al., 2021), which would be promoting sardine mobility towards Alb in some way.

However, and additionally, studies pointed out the existence of a featured spawning area located in Alb. Important sardine nursery grounds along the northern coast of the Alb Sea, Málaga and Almería Bay (Quintanilla et al., 2020; Rubín, 1997; Würtz, 2010) provide shelter from the large-scale westerly wind flow (Würtz, 2010) that occurs in the area during the beginning of the reproductive season. Besides, the presence of the Alb gyre could be causing larvae retention (Naciri et al., 1999) and hindering dispersal and migration (Bacha et al., 2014) of the juveniles, potential reason to explain why we found a high percentage of immature individuals during June in this area while they were absent in POR-GC in the spring months. Bernal et al. (2007) characterised zones of significant spawning preference in the POR-GC region from 1985 to 1995. It has been shown that winters with strong southward winds and weak but consistent upwelling events along the Portuguese coast led to poor recruitment of sardines in the following months due to a large offshore transport of eggs and larvae when their spawning season takes place (Horta e Costa et al., 2014; Santos et al., 2001). However, our results reflected a prevalence of westerlies along the year in this area. Thereby, the coupling between spawning and circulation is particularly beneficial under westerly winds, when productivity in the eastern shelf is likely enhanced and the plankton is confined within the cyclonic cell (Lafuente and Ruiz, 2007). Nevertheless, it has to be taken into account that changes in the circulation patterns could affect the physical mechanisms of concentration and retention for a particular area (Mercado et al., 2007), which has been described and modelled in POR-GC, with a bimodal pattern of anticyclonic circulation in spring-summer that changes at a certain time in winter (sardine reproductive period) to cyclonic (Lafuente and Ruiz, 2007). Thus, it could be probable that potential migrations from POR-GC towards Alb were caused due to the greater success in spawning and recruitment in this area, which would be directly related to the behaviour of capital breeders, which spawn and feed in separate areas during different seasons (McBride et al., 2015).

The existence of a common spawning ground in fish for different subpopulations has been supported by various hypotheses, among which we can find the patchy population hypothesis, with the absence of a ‘source population’, or the metapopulation hypothesis, which considers that subpopulations can have autonomous (and eventually divergent) lives. Each subpopulation is mostly linked to a particular spawning area, but a small, albeit significant, quantity of adults may move from one spawning area to another (Gerlotto et al., 2012; Kritzer and Sale, 2004; Ovaskainen and Hanski, 2004). Contrary to the patchy population, the existence of a source population is one key characteristic of the metapopulation (Gerlotto et al., 2012). In the context of a metapopulation, it has also been suggested a migrant hypothesis for the clupeid Atlantic herring, in which the progeny of a given local population do not necessarily recruit to their natal population, but may become migrants, contributing to an adopted population having the same or a different reproductive season. Population affinity is established at the time or first maturation and is fixed for all subsequent spawning by adhering to an annual maturation cycle (McQuinn, 1997). Moreover, similar scenarios to the one proposed have been reported for the fully recruited E. sardine population in the central Mediterranean Sea during autumn and winter, with migratory behaviour for spawning purposes (Basilone et al., 2021). Also, and as an example, in the Adriatic Sea (Mužinić, 1973; Škrivanić and Zavodnik, 1973) authors suggested that spawning grounds are located in the areas with optimal biological conditions, where the hydrographical equilibrium is established between two types of sea water, the Mediterranean and the Alpic (Škrivanić and Zavodnik, 1973). Sardine migration to these locations is triggered by temperature and then, the return of fish schools to feeding areas takes place, resulting in limited mixing of sardine stocks inhabiting various regions of the Adriatic Sea (Škrivanić and Zavodnik, 1973). This would explain why a certain percentage of fish that have already spawned (regressing stage) was recorded in POR-GC in February, and then, registered again in May, due to differential spawning between individuals and the later return to their area of origin. Thereby, under any of these models, the genetic similarities (Antoniou et al., in press; Caballero-Huertas et al., 2022) between sardines in the study locations could be explained. The oceanographic processes occurring off the Strait of Gibraltar have been demonstrated to act as barriers to gene flow for many fishes, although studies suggest that for some species (among them, another clupeid as the European anchovy) there are not genetically isolated stocks on both sides of it (Bacha et al., 2014; Jemaa et al., 2015), which could also be occurring in sardine due to the reproductive patterns of migration suggested. However, and returning to the example of the anchovy, other investigations have proposed the Alboran stock as a population independent of the Gulf of Cádiz and the rest of the Mediterranean, being located between the barriers of the Strait of Gibraltar and the Almeria-Oran oceanographic front (Viñas et al., 2014). This lack of consensus is a common circumstance among pelagic fish taxa, since the study of their population structure is not only limited by the resolution of genetic markers but also by their wide dispersal capabilities in all the stages of the life cycle (Caballero-Huertas et al., 2022). Within the sardine scenario, the Almeria-Oran front has been proposed as a barrier to its dispersal that could be held responsible for founder effects, followed by genetic drift with selection acting on the local scale driving adaptations mostly related to minimum SST (Antoniou et al., in press). Nonetheless, the Strait of Gibraltar would not be an effective genetic barrier for this species, as proposed by our hypothesis and the previously mentioned genetic structure studies on the similarity between Atlantic and Alboran individuals.

POR-GC sardines reached their maximum condition in the months around the end of summer-the beginning of autumn (Fig. 3), reflected by Kn, tissue and mesenteric fat content, overlapping with an early gonadal maturation. The most advanced individuals in terms of gonad maturation stage may be those that migrate to Alb to spawn, so then in Alb we found worse condition (Kn) because those individuals that came from the Atlantic (and we may have identified as Alb individuals) spawned and, thus, a decrease of average Kn, tissue fat content and mesenteric fat is observed in this period in Alb. Meanwhile, those that remained in the Atlantic in autumn may have not yet started to spawn and, therefore, had better indicators, and similar to the ones registered in summer. In spring, it could be possible that Atlantic individuals kept coming back to POR-GC from the spawning areas in Alb, so it would be logical that Kn curve for POR-GC samples was close to Kn values of Alb individuals because general fish condition (as suggested by Albo-Puigserver et al. (2020), mostly focused on changes in protein content) had not recovered yet. Nevertheless, greater fat reserves were appreciated at this season due to the availability of feeding resources on this side of the Strait because of the environmental aspects previously mentioned. In this regard, it would be advisable to increase the sample size in future studies to be more accurate in these statements. In addition, we propose to carry out a monthly and balanced comparison in order to verify many of the hypotheses launched in this work.

Population connectivity plays a fundamental role in local and metapopulation dynamics, community structure, and the resiliency of populations to human exploitation, so detecting the connectivity in a managed area is essential (García-Lafuente et al., 2021; Muñoz et al., 2015). However, in order to confirm or discard the spawning migration hypothesis and set it within the framework of a patchy population or a metapopulation, a monthly/seasonal genetic sampling would be necessary to compare sardines from both sides of the Strait of Gibraltar over several years to check, also, if this potential migration is due to a punctual behaviour of few individuals or to a pattern that is repeated by a large percentage of the stock. In addition, this study shows that it is necessary to genetically identify the stocks in order to be able to draw the appropriate conclusions, given that there may be some confusion as to the origin of the differences (i.e., purely environmental or mix of individuals from different subpopulations) in certain parameters of condition and reproduction. These issues require special attention in terms of stock assessment and management.

CRediT author statement

Marta Caballero-Huertas: Conceptualization, Formal analysis, Investigation, Writing - Original Draft, Visualization **Manuel Vargas-Yánez:** Investigation, Formal analysis, Writing - Original Draft, Visualization **Xènia Frigola-Tepe:** Investigation **Jordi Viñas:** Conceptualization, Supervision, Project administration **Marta Muñoz:** Conceptualization, Supervision, Project administration.

Data availability statement

The data used for the oceanographic and atmospheric analyses and characterisation are openly accessible and their references are detailed in section 2.2.

Conflicts of interest

The authors declare no conflict of interest/competing interest.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105697.

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