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Assessment of the spawning habitat, spatial distribution, and Lagrangian dispersion of the European anchovy (*Engraulis encrasicolus*) early stages in the Gulf of Cadiz during an apparent anomalous episode in 2016

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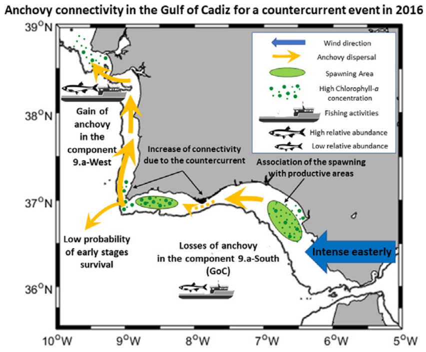
HIGHLIGHTS

- The European anchovy spawning areas linked to chlorophyll-*a* with a lag of 3 days.
- Countercurrents (CC) increase larval connectivity between Spanish-Portuguese shelfs.
- Westward displacement of spawning contributes to increasing that connectivity.
- A small number of early life stages are also exported offshore by CC.

GRAPHICAL ABSTRACT



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ABSTRACT

Modelling the environmental factors influencing the spatial variation of fish early life stages density and their drift history can identify the key biological and physical processes for the recruitment variability. Distance-based linear multivariate techniques were used to characterize the spawning areas of the European anchovy *Engraulis encrasicolus* in the Gulf of Cadiz (GoC). Chlorophyll is the environmental variable that best characterized its spawning areas with a time-lag of three days. The use of Lagrangian models to simulate the dispersal of small pelagic species more dependent on advection such as the European anchovy early life stages (early larvae and eggs) in the GoC could provide the degree of connectivity between spawning and nursery areas and identify the physical drivers of the recruitment variability. The larval final destination is critical for the survival of a marine species which is coastal-dependent during its early life stages. Simulations with a Lagrangian transport model in the Southwest Iberian Peninsula were performed during the most intense spawning peak of 2016, when a strong and persistent countercurrent event developed. Most of the simulated early life stages were transported to the western Portuguese coast and, to a lesser extent, to the Atlantic oligotrophic waters, suggesting an increase in the connectivity between the subdivision 9a South and West components. Although different environmental processes occurring during ontogenetic stages, as well as overfishing, among others, can explain part of the

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variability observed in recruitment, events such as the development of coastal countercurrents during the spawning season could partly account for an increase of anchovy on the western Portuguese coast and a decrease in the Gulf of Cadiz one year later.

1. Introduction

Understanding how physical–biological interaction mechanisms affect marine life early stages is key to know the processes influencing recruitment success in fish stocks (Sundby and Kristiansen, 2015). Early life stages of most fish are dependent on circulation patterns for transport from the spawning grounds to the nursery areas, and thus variations in transport are an important parameter influencing recruitment variability in fish stocks (Stenevik et al., 2007). Recruitment of the European anchovy *Engraulis encrasicolus* (Linnaeus, 1758) in its first stages depends on the passive horizontal transport of eggs and larvae (Borja et al., 1998; Mullon et al., 2002) and on the diel vertical migration from spawning to nursery areas (Allain et al., 2001; Ospina-Alvarez et al., 2012). The passive transport in the Gulf of Cadiz (GoC) has been hardly studied, and the importance of this transport in short-lived species such as the small pelagic fish *Engraulis encrasicolus* (Linnaeus, 1758) could affect the recruitment success in this area.

The European anchovy is a small pelagic species (average length 13.5 cm), a fast growing specialist and short-lived (3 to 4 years) (ICES, 2010) that represents the most abundant species in the Gulf of Cadiz (Baldó et al., 2006). Its reproductive period begins in its first year of life, having a high fecundity, external, oviparous, and fractionated reproduction throughout the year (Millán, 1999). The spawning period is related to the sea surface waters warming season and the beginning of the water column stratification (Motos, 1996). In the GoC, the spawning period ranges from early spring (March–April) to early autumn (September–November), with two peaks, the most intense one between July and August (Baldó et al., 2006). Its spawning and nursery areas in the southwest Iberian Peninsula are associated with the rivers' mouths and estuaries (Caddy and Bakun, 1994), such as the Guadalquivir (Baldó and Drake, 2002; Baldó et al., 2006; González-Ortegón et al., 2015), the Guadiana (Chícharo et al., 2001; Faria et al., 2006; Morais, 2007; Morais et al., 2009), the Mira (Ré, 1996), the Alvor (Antunes et al., 1988) and the Tagus (Costa and Bruxelas, 1989). These areas are rich in river discharges that cause an injection of nutrients which stimulates primary and secondary production. The development of their early life stages, and thus the size, is strongly temperature-dependent; hence, if the ambient temperature is known, it is possible to estimate the growth rate and, therefore, the size and duration of each stage. Incubation experiments carried out with anchovy larvae showed a duration of the egg stage of about 36 h at 22 °C, with larvae typically hatching after this time (Bernal et al., 2012). This temperature corresponds to the average sea surface temperature in the GoC during summer (Vargas et al., 2003). In terms of anchovy eggs mortality, it is also temperature-driven, with temperatures above 26 °C or below 14 °C resulting in high egg mortality rates (Bernal et al., 2012). Anchovy larvae in this region start having some effective horizontal swimming capacity at a standard length of around 6 mm (~10 days after spawning), mainly depending on the ambient temperature (Morais et al., 2012; Huret et al., 2011). Additionally, the analysis of their vertical distribution indicates that larval drift in the GoC mainly occurs in the first few meters of the water column (0–10 m) before they develop the diel vertical migration capacity, i.e., before they reach a standard length of 10 mm (Morais et al., 2012). This suggests that, during the first 10 days after spawning, the horizontal dispersion of anchovy early stages in the GoC is mainly determined by the surface currents (Catalán et al., 2006). According to Roy et al. (1992), the environment also plays an important role in the dynamics of pelagic fish, even if fishing increases their natural instability. In this sense, unfavourable environmental conditions in the spawning area and during larval drift could determine larval feeding success, growth, and survival. In fact, although the population of the European anchovy could depend on recruits to persist in a specific region, in the GoC it could become more vulnerable to meteorological fluctuations, probably due to the vulnerability of its first stages (Ruiz et al., 2006, 2007). Namely, the passive transport of eggs and larvae between the spawning and the nursery area in the GoC could be key to understand the recruitment of anchovy, due to the high variability in the surface circulation. The abundance of anchovy in the GoC has decreased by 66% in the last decade, according to acoustic studies (Uriarte and General, 2018). Although a sustained period of time of intense fishing efforts could be the main reason for this decrease, the succession of low recruitments due to unfavourable environmental conditions could contribute significantly to this decline, which is a common feature of many fish stock collapses (Larkin, 1996). Furthermore, changes in the anchovy spawning zonation have been recently observed in the GoC (Baldó et al., 2006). More specifically, the highest egg densities have been found further west than normally (Fig. 2) during August 2016 (ICES, 2017). Interestingly, an increase in landings a year later was documented in the western Portuguese coast. This could indicate a change in the connectivity between the GoC and the western Portuguese region as a result of the observed change in the spawning location, as also reported in other regions (Huret et al., 2010).

In terms of management of the European anchovy, in the southwest Iberian Peninsula it is carried out by the International Council for the Exploration of the Sea (ICES), that area being specifically known as the subdivision 9a of the Spanish South-Atlantic region (Uriarte and General, 2018). This subdivision includes two components: the West component, which encompasses the southern Galicia (section N) and the Portuguese west coasts (section CN and CS), and the South component, which includes the Spanish and Portuguese coasts of the GoC (Fig. 1a). Within this division, the population is managed as belonging to a single stock, although in terms of abundance, the southern component (i.e., the GoC) is considerably more stable and productive than the western component, which is characterized by low abundance and great recruitment variability (Uriarte and General, 2018). Despite this general pattern, the abundance of anchovy in 2017 in the southern component of subdivision 9a was clearly lower compared to the western component, with a 30% reduction in catches (ICES, 2018).

Taking into account the sensitiveness of this species to the environmental conditions and ecosystem changes (Chícharo et al., 2001), assessing the relationship between the abundance of the anchovy early stages in the major spawning grounds and the environmental variables which best explain their spatial variation in that region is key to identify the drivers that determine their survival. This can be done through complex statistical techniques and by modelling the passive transport of these early life stages between the spawning and the nursery area in a region with a complex and varying surface circulation within the continental shelf, such as the GoC. The use of statistical techniques such as the Distant Based Linear Models is very common on community ecology studies to explore the relationship between biological traits or abundance and environmental factors. For example, they have been used to evaluate the influence of environmental variables on the spatial distribution of fish larvae such as anchovies (Inda-Díaz et al., 2014), or to assess the role of environmental variables or habitat descriptors on the fish assemblage structure (Cattani et al., 2016). Lagrangian transport models have been widely used to simulate the dispersion of planktonic organisms, including the eggs and larvae of the

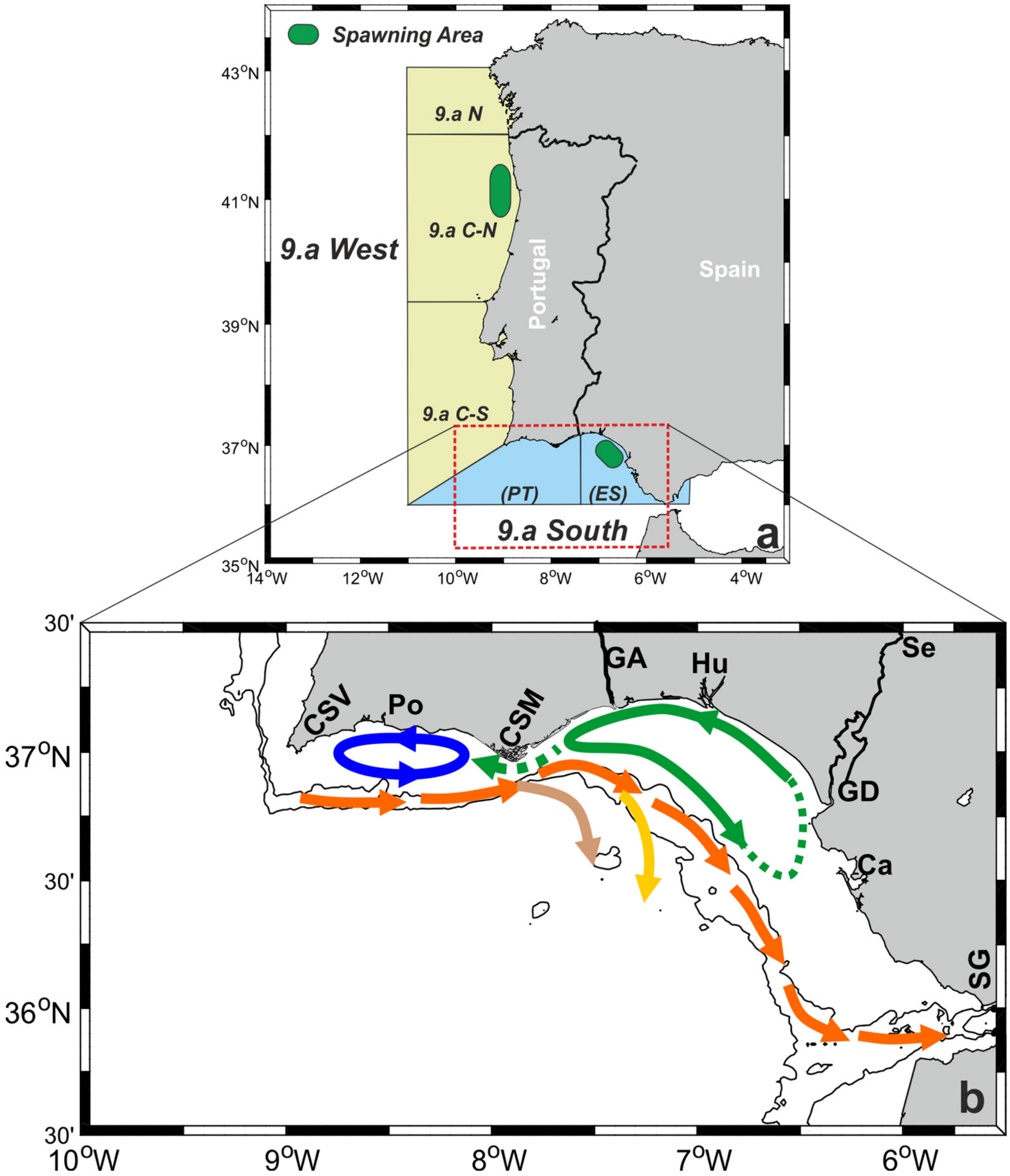

Fig. 1. Diagram of the general circulation patterns in the GoC slope and continental shelves (bottom panel, adapted from García-Lafuente et al., 2006 and from Peliz et al., 2009) and anchovy management areas in Division 9.a. ICES in the SW of the Iberian Peninsula (upper panel, adapted from ICES, 2018). The following circulation patterns are represented: eddy of San Vicente (blue arrows), Gulf of Cadiz Slope Current (orange arrows), including two alternative patterns (brown and yellow arrows), coastal countercurrent (green arrows). The following geographical features are shown: GA (Guadiana River estuary), GD (Guadalquivir River estuary), CSM (Cape Santa Maria), CSV (Cape San Vicente) and SG (Strait of Gibraltar).

European anchovy in regions of the Mediterranean Sea (Falcini et al., 2015; Palatella et al., 2014; Ospina-Alvarez et al., 2015), the Bay of Biscay (Allain et al., 2003; Huret et al., 2010) or the Guadiana estuary in the GoC (Morais et al., 2012). For instance, Lagrangian experiments comparing a purely passive two-dimensional (horizontal) drift with simulations that include vertical swimming have demonstrated that the latter produces differences in the dispersal patterns (Huret et al., 2010; Ospina-Alvarez et al., 2012; Parada et al., 2008). In addition, studies carried out in Chesapeake Bay with Lagrangian models indicated that the dispersal of the bay anchovy early life stages is related to the physical and biological conditions, as well as to the larval developmental stage (North and Houde, 2004). More specifically, the authors highlighted that the wind-induced circulation pattern is a key mechanism influencing the anchovy larvae transport, but that the diel vertical migration of both anchovy larvae and their prey (copepods) play an important role in their spatial distribution. These models have provided a better understanding of the stock dynamics of the anchovy fishery for each study area, which is highly unstable in connection with environmental processes (Bakun and Broad, 2003). Moreover, they could provide an insight on the degree of connectivity between spawning and nursery areas, as well as a better understanding of the species recruitment, and therefore a better management.

Following all the above, the hypothesis of our study is that the concurrence of anomalies in the spawning spatial distribution and a change in the meteorological and oceanographic conditions, such as an intense easterly event triggering a persistent coastal countercurrent at the time of spawning, could negatively impact the larval dispersal and contribute to reducing the anchovy recruitment in the GoC.

Therefore, the objectives of this work are: (a) To study the effects of multiple environmental factors on early life stages abundance and horizontal distribution to characterize the spawning areas of the European anchovy in the GoC, and (b) to assess the effect of a particular transport regime on the advection of anchovy early life stages. The first objective was addressed by performing a series of univariate and multivariate analysis using in situ measured anchovy eggs densities and different environmental variables. The second objective was covered by implementing a Lagrangian transport model coupled to 3D daily velocity fields obtained with the Regional Ocean Modeling System (ROMS) during August 2016, when a change in the anchovy eggs spatial distribution coincided with a strong and persistent coastal countercurrent.

2. Methods

2.1. Study area

The GoC (Fig. 1), located as a transition region between the Atlantic Ocean and the Mediterranean Sea, is delimited by Cape San Vicente (Portugal) at the northwest, the Strait of Gibraltar at the southeast and the Atlantic coast of Morocco at the south (García-Lafuente and Ruiz, 2007). Its continental shelf, defined by the 200 m bathymetry line, is divided by Cape Santa Maria into two areas, whose different geographic and oceanographic characteristics directly affect their primary and secondary productivity:

East of Cape Santa Maria there is a very productive area, with very smooth slope and an extensive shelf of around 50 km wide. This area, known as the eastern shelf, receives terrestrial contributions from the Guadiana and Guadalquivir Rivers and their adjacent saltmarshes, the most important rivers in terms of size, flow, transport of materials, and nursery areas (García-Lafuente et al., 2006; Cravo et al., 2006; González-Ortegón et al., 2018; Morais et al., 2009; Laiz et al., 2020). West of this cape, with a smaller extension, but with a steeper slope, is the western shelf, a less productive area, with a lower fluvial contribution, and frequented by valleys and submarine canyons (García-Lafuente et al., 2006).

Numerous studies using in situ and remote sensing data suggested that the upper slope circulation in the GoC is a continuation of the western Iberian upwelling system (see García-Lafuente and Ruiz (2007) for a review). Upwelling-favourable winds, that intensify in summer, generate a southward flowing geostrophic current along the western Portuguese coast (Fiúza et al., 1982). After reaching Cape San Vicente, this coastal jet normally flows eastward along the GoC upper slope (Relvas and Barton, 2002; Criado-Aldeanueva, 2004) until Cape Santa Maria, where it can follow three different anticyclonic patterns (García-Lafuente and Ruiz, 2007): it can be deflected offshore towards the centre of the GoC (brown arrow, Fig. 1b), it can continue flowing along the continental slope as the Gulf of Cadiz Slope Current (orange arrows, Fig. 1b) (GCC, Peliz et al., 2007), or it can be deflected southeastward along an intermediate path (yellow arrow, Fig. 1b). A numerical study by Peliz et al. (2009) suggested that this Gulf of Cadiz Slope Current is also linked to the exchange with the Mediterranean Sea through the Strait of Gibraltar. Off Cape San Vicente there is a quasi-permanent upwelling region linked to the cyclonic cell located between Cape San Vicente and Cape Santa Maria, known as the eddy of San Vicente (blue cell, Fig. 1b), that is intensified during summer by the western Portuguese southward flowing current (Relvas and Barton, 2002; Criado-Aldeanueva, 2004).

An intermittent coastal upwelling is observed during summer along the GoC western shelf, as a result of the enhanced westerly winds (García-Lafuente and Ruiz, 2007). Under these conditions, the surface currents flow eastward along the shelf.

The eastern shelf surface circulation presents a higher complexity. García-Lafuente et al. (2006) proposed the existence of a cyclonic circulation cell during summer, that would extend between the Guadalquivir River mouth and Cape Santa Maria (green cell, Fig. 1b). The northern part of this cyclonic cell would correspond to the so-called warm coastal countercurrent, a westward flowing current whose origin has been attributed to different forcing mechanisms (Mauritzen et al., 2001; Relvas and Barton, 2002; Sánchez et al., 2006; García-Lafuente et al., 2006; Teles-Machado et al., 2007; Garel et al., 2016). According to Criado-Aldeanueva et al. (2009), this coastal countercurrent disappears during autumn and winter when it is replaced by an eastward flowing coastal current. However, more recent studies have observed alternating eastward or westward flowing currents occurring through the year (Garel et al., 2016). Coastal countercurrents transport surface waters westward along the eastern shelf (Criado-Aldeanueva, 2004) and, under certain wind conditions, can continue beyond Cape Santa Maria (dotted green arrow, Fig. 1b), invading the western shelf and displacing southward the cold upwelled waters off Cape San Vicente (Fiúza, 1983; Folkard et al., 1997; Relvas and Barton, 2002). In some extreme cases, this coastal countercurrent has been observed to extend beyond Cape San Vicente and propagate northwards along the Portuguese western coast (Relvas and Barton, 2002). Recent studies have noted that this coastal countercurrent may continue flowing until upwelling-favourable winds have been blowing for some time (Garel et al., 2016). A similar time lag has also been observed along the Californian coast from sea surface temperature images (Melton et al., 2009).

The GoC physical characteristics have a notable effect on the anchovy population. In this sense, the greatest abundances of eggs, larvae and juveniles in the GoC are generally found on the eastern shelf, within the Guadalquivir estuary (Baldó et al., 2006; González-Ortegón et al., 2015). This is due to its high productivity, which is related to the pool of chlorophyll-rich water that recurrently appears around the Guadalquivir River and the neighbouring Cadiz embayment as a result of tidal forcing (Navarro and Ruiz, 2006). Furthermore, this permanent tidal fertilization can be sporadically enhanced under large river discharges (González-Ortegón et al., 2018; Prieto et al., 2009) or due to the Ekman pumping produced by westerly winds (Navarro and Ruiz, 2006) and increase the primary production if the light conditions are not limiting (Ruiz et al., 2006). Eastward flowing currents along the eastern shelf, which are usually linked to westerly winds, concentrate this pool of chlorophyll-rich waters near the Guadalquivir mouth, thus providing favourable environmental conditions for the development of anchovy eggs and larvae (Baldó et al., 2006). In fact, higher concentrations of fish larvae have been reported in this region under eastward currents, and near Cape Santa Maria under a coastal countercurrent scenario (Catalán et al., 2006). On the contrary, easterlies lead to oligotrophic conditions along the shelf (Navarro and Ruiz, 2006). If a coastal countercurrent is developed but veers southward at Cape Santa Maria to form the above mentioned cyclonic cell over the eastern shelf (García-Lafuente et al., 2006), it will concentrate the eggs and larvae near the nutrient-rich Guadalquivir River mouth, hence benefiting the anchovy recruitment (Baldó et al., 2006). Under strong or persistent easterly winds, the coastal countercurrent may surpass Cape Santa Maria and invade the western shelf, hence biologically connecting both basins in an East-West direction (García-Lafuente and Ruiz, 2007) by causing the westward transport of plankton away from the eastern shelf, which can adversely affect the recruitment (Catalán et al., 2006). Probably, this transport of planktonic particles can cause, directly, a decrease of anchovy early life stages in the region and, indirectly, a food-limited condition and thus, starvation problems to the anchovy early life stages that remain in the nekton. In fact, low anchovy catches in the GoC have been mainly correlated with periods of noticeable easterly winds intensity followed by persistent coastal countercurrents (Ruiz et al., 2006).

2.2. Data

2.2.1. Sampling

Anchovy eggs were collected in the GoC during the ECOCADIZ 2016 campaign between July 31 and August 11, 2016 from the R/V Miguel Oliver. The execution of this campaign and the abundance estimation followed the methodology adopted by the ICES (ICES, 1998). During the daytime acoustic assessment, a CUFES (Continuous Underway Fish Egg Sampler) system was used to collect the anchovy eggs, providing their abundance per cubic meter. Samples were collected with an average flow of 600 l min^{-1}, a 335 mesh size, and a depth of 5 m. Besides, a

Sea-bird Electronics ™ SBE 21 SEACAT thermosalinograph was employed to continuously monitor the sea surface salinity (S).

The sampling grid consisted of 21 transects with a total of 136 stations (Fig. 2).

2.2.2. Remote sensing and wind data

Daily averages of chlorophyll-*a* (Chl-*a*) in mg m^{-3} were downloaded for the study area, for August 2016 from the Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu/). The product is generated using a multi-sensor and multi-algorithm approach and is provided at level L4 with a 4 km spatial resolution (product ID: OCEANCOLOUR_ATL_CHL_L4_REP_OBSERVATIONS_009_098). The maps produced were used to complete the chlorophyll data from the ECOCADIZ 2016 campaign matrix.

Daily means of sea surface temperature (SST) were also obtained for the same region and time period with a spatial resolution of about 2.2 km. Data were jointly provided by the Group for High Resolution SST and CMEMS as the result of a combination of several sensors (ATSR, AVHRR, AVHRR_GAC, SEVIRI, GOES_Imager, MODIS, TMI) with a L3 processing level (product ID: SST_EUR_L3S_NRT_OBSERVATIONS_010_009_-A). It must be noted that the high level of smoothing in the L4 SST product resulted in the disappearance of key features, such as the Cape San Vicente upwelling cold signature or the warm coastal countercurrent.

Daily means of wind data were obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim product (https://www.ecmwf.int/). The zonal (U) and meridional (V) wind components at 10 m were retrieved for August 2016 with a spatial resolution of 25 km.

2.2.3. Numerical model

Data from a set of coupled numerical models were used to study the transport of the first stages of anchovy within the GoC and its dispersion along the Iberian coast: A hydrodynamic model, an atmospheric model, and a Lagrangian transport model.

The currents data were obtained from the high resolution hydrodynamic model *Regional Ocean Modeling System* (ROMS), which had been implemented in the study area for 2016, coupled to the *Weather Research and Forecasting Model* (WRF) atmospheric model (Laiz et al., 2020). The model configuration (Peliz et al., 2013) used a grid with 32 sigma levels and ~2 km of spatial horizontal resolution, covering the GoC and the Alboran Sea (see Fig. 1 in Peliz et al., 2013). The temperature and salinity initial and open boundary conditions were retrieved from the WOA2005 (www.nodc.noaa.gov/OC5/WOA05) and the MEDATLAS (MEDAR Group 2002) databases, for the Atlantic and Mediterranean sides, respectively. The model results were validated by comparing the ROMS currents with in situ ADCP data at 20 m depth as well as with SST maps (more details in Laiz et al., 2020). Taking into account that tidal currents vanish a few tens of km west of the Strait of Gibraltar (García-Lafuente and Ruiz, 2007), the ROMS velocity fields were stored as daily means. The three-dimensional fields of daily velocity averages for August 2016 were used to force the *Lagrangian TRANSport model* (LTRANS, http://northweb.hpl.umces.edu/LTRANS.htm) for the same spatial domain, in order to study the advection of the first stages of anchovy in the GoC. LTRANS is a particle-tracking model that runs off-line with the stored predictions of ROMS. It was initially designed to simulate the three-dimensional transport of oyster larvae, but it can be adapted to simulate passive particles or other planktonic organisms (North et al., 2006, 2008, 2011). The model includes a 4th order Runge-Kutta scheme to perform the particles advection and a random displacement model to simulate the vertical turbulent motion of particles. As particles were assumed to be passive tracers, the LTRANS behaviour and settlement sub-models were not activated. Finally, the model's internal time step (i.e., for particle tracking) was set to 30 s and the default diffusion coefficient was used.

The positions where the particles were released correspond to the ECOCADIZ 2016 campaign sampling locations (Lat, Lon). This decision was taken following the results obtained with a backward simulation carried out with the LTRANS model to analyse the eggs spawning zonation (see Section 2.2 of the Supplementary material), which suggested that the eggs had been spawned approximately at the same location where they had been sampled (Fig. S2). The number of particles released (6867) was proportional to the egg densities found at each sampling point during that campaign. More specifically, since the lowest density found was 0.03 eggs m^{-3}, the densities were multiplied by 100 to release at least 3 particles per station. All the particles were released simultaneously at 5 m depth, which was the sampling depth during the ECOCADIZ 2016 campaign. The release time was chosen to be the day and time when the highest egg densities were sampled, which corresponds to 08/09/2016 at 12:00. The LTRANS model was run for 10 days and the outputs were stored every 12 h, including the position (latitude, longitude and depth) of each particle at each time step.

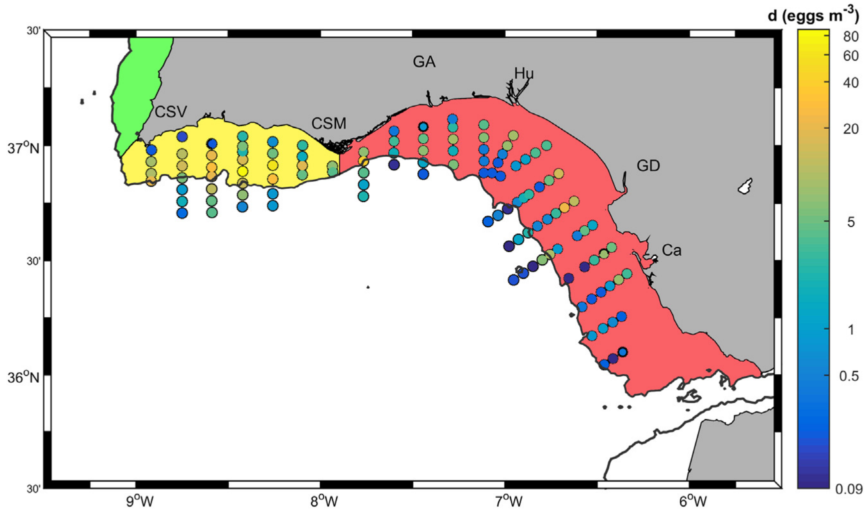

Fig. 2. Map of the areas defined to evaluate the results from the Lagrangian simulation. From east to west: red (GoC eastern shelf, GoC -E), yellow (GoC western shelf, GoC -W), green (western Portuguese shelf, PORT) and white (rest of the domain, OUT). Coloured dots correspond to the density of anchovy eggs sampled at each station. The geographical features that limit the areas are shown: CSM (Cape Santa María), CSV (Cape San Vicente). The continental shelf limit is shown by the 200 m depth bathymetric contour (thick dark line).

2.3. Data analysis

2.3.1. Statistical analysis

The univariate and non-parametric multivariate techniques of the distance-based linear modelling package (DistLM) contained in PRIMER 6.1 (Plymouth Routines in Multivariate Ecological Research, Anderson et al., 2008) were used to explore the anchovy eggs density in the GoC, and tested against environmental variables: salinity (S), chlorophyll-*a* concentration (Chla), sea surface temperature (SST), depth of the sampling station in meters (depth), latitude (Lat), longitude (Long), distance to the nearest coast (Dist), and the West-East (U) and North-South wind components (V). In addition, considering that egg spawning could be affected by the environmental conditions present during the previous days, a new set of those variables (SST, Chla, U, and V wind components) was created and included in the analysis. In this sense, five new values were used for each variable, corresponding to a time lag of 1 to 5 days before the eggs sampling date. These variables were obtained through the processing of satellite (SST, Chl-*a*) or reanalysis (wind components) daily-mean data; more specifically, each variable represents the average value within a radius of 4 km centred at each sampling station. More details on the statistical analysis are given in Section 1 of the Supplementary material.

DistLM was employed to verify relationships between the anchovy egg density across all sampling stations and the environmental variables. DistLM produces a marginal test, which assesses the variation each predictor (environmental variable) has on its own, and a sequential test, assessing the variation of all the environmental variables (McArdle and Anderson, 2001). The most parsimonious model was identified using the Akaike's information criterion (AIC) and a stepwise selection was used to determine the relative importance of predictors. Distance-based redundancy analyses (dbRDA) were used for visualizing the results as an ordination, constrained to linear combinations of the environmental variables. The DistLM was based on abundance and environmental data with 9999 permutations. The Euclidean distance of samples and the normalized Euclidean distance of variables were compared by the RELATE routine in PRIMER using the rank correlation by Spearman. This comparison provides a significance test with the matching coefficient of correlation (Spearman's r_S), which is equivalent to the Mantel's test (Clarke and Warwick, 2001).

2.3.2. Dispersion patterns

The region of study was divided into four different subregions with the aim of analysing the particles dispersion patterns obtained with the LTRANS simulation (Fig. 2). The division was made taking into account the West and South components of the Spanish South-Atlantic region subdivision 9a, as well as the oceanographic boundary imposed by Cape Santa Maria. In this sense, the GoC eastern continental shelf (GoC-E in Fig. 2) is bounded by Cape Santa Maria and the Strait of Gibraltar, the GoC western shelf (GoC-W) is located between Cape San Vicente and Cape Santa Maria, the western Portuguese shelf (PORT) corresponds to the coastal region north of Cape San Vicente, and the rest of the domain (OUT) is the region beyond the continental shelf. Finally, while both the eastern and western GoC continental shelves belong to the subdivision 9a South component, the western Portuguese shelf belongs to the West component (Fig. 1a).

In order to obtain an estimate of the percentage of the anchovy first stages that could be retained in each of the predefined shelf areas (GoC-E, GoC-W, PORT), only the particles found in each of these areas on day 10 of the simulation were counted. The counting was carried out automatically with the MATLAB R2020a program.

Bearing in mind that the objective of this work was to assess the effect of a persistent coastal countercurrent event on the advection of anchovy early life stages, only the egg phase and the pre-flexion and flexion stages were considered in this study, given that anchovy larvae become able to control their position at the post-flexion stage, when they start performing diel rhythms of vertical migration (Ré, 1996). As mentioned before, these early life stages last approximately 10 days in the GoC, as suggested by previous works in the region (Morais et al., 2012). Therefore, during this period, the ocean circulation patterns will force the passive dispersion of the early life stages in our complex domain.

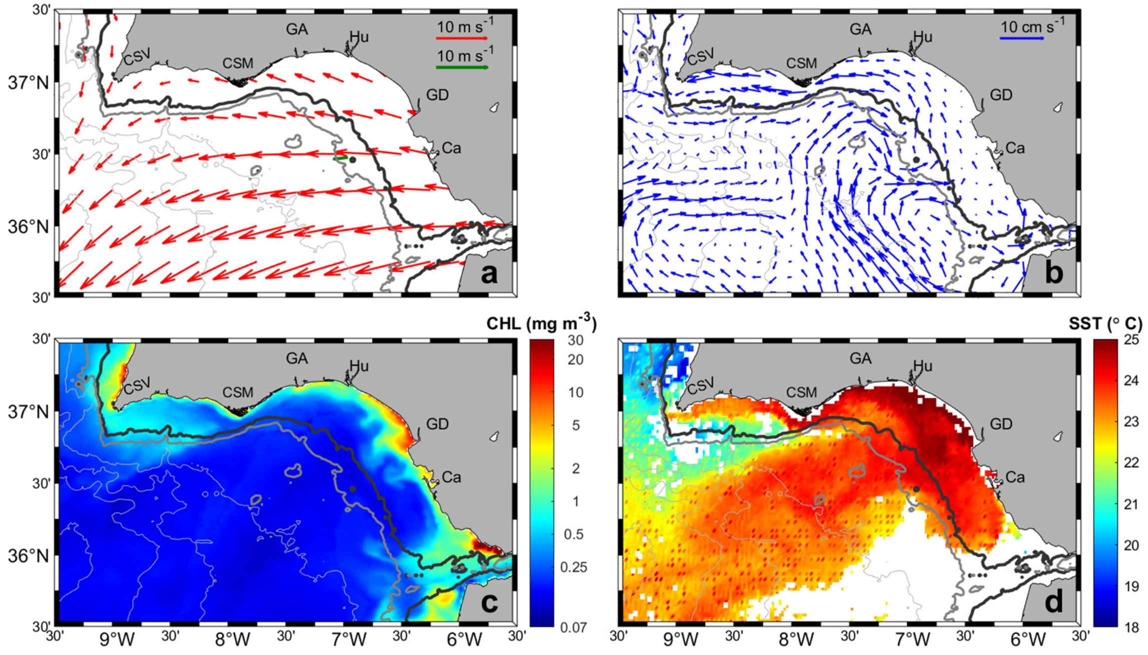

Fig. 3. Daily means of (a) wind, (b) surface currents, (c) chlorophyll-a concentrations and (d) sea surface temperature for August 9, 2016, which is the day when the highest egg densities were sampled. Bathymetric contours of 100, 200 (thick dark line), 500 (thick grey line), 1000, 2000, 3000 and 4000 m are shown.

3. Results

3.1. Relationships of anchovy egg abundance to environmental variables

The anchovy eggs density obtained during the ECOCADIZ 2016 campaign (31/7/2016–11/08/2016) ranged between 0.09 and 87.89 eggs m^{-3}, with the lowest values (<0.30 eggs m^{-3}) located at the most distant stations from coast and the largest ones (16.20–87.89 eggs m^{-3}) in the region delimited by Cape San Vicente and Cape Santa Maria, between the continental shelf and slope (Fig. 2). The eggs density spatial variability was compared with the environmental conditions existing during the sampling campaign (Fig. 3).

Higher chlorophyll-*a* values were observed in the coastal zone (Fig. 3c), especially in the areas associated with the Guadalquivir River (~5.0–16.9 mg m^{-3}) and Cape San Vicente (~0.6–2.5 mg m^{-3}). In the latter case, the highest concentrations of chlorophyll-*a* seem to be related to the upwelling-favourable local winds (Fig. 3a) that generate an offshore Ekman transport. Water transported offshore is then replaced by colder (Fig. 3d) and nutrient-rich deeper waters. This productivity seems to be exported to the GoC western shelf (Fig. 3c) following the same spatial variability as the egg densities. In fact, the highest egg densities (87.9–16.2 eggs m^{-3}) seem to concur with the largest chlorophyll-*a* values of the GoC western shelf (0.21 mg m^{-3}), showing a positive and significant correlation (Spearman's $r_S = 0.48$, $P < 0.001$).

SST (Fig. 3d) showed its highest values between the Guadiana (24.3–20.6 C°) and Guadalquivir Rivers (24.8–20.0 C°), possibly related to the fresh water discharge and its westward propagation by the coastal countercurrent. This is consistent with the above-mentioned chlorophyll-*a* distribution that presents its maximum values within the Guadalquivir River mouth and a westward-decreasing plume (Fig. 3c). The egg densities were also higher in the stations located along this coastal plume (Fig. 3a). That is, there is a negative correlation between eggs density and salinity (Spearman's $r_S = -0.31$, $P < 0.001$).

Correlation analyses between the two resemblance matrices, eggs density and environmental variables, were significant when the RELATE function (in PRIMER) was used for different time lags ($P \leq 0.05$) although the rank correlation showed a poor match (Spearman's r_S 0.15–0.19). The correlation analyses exhibited an increase of this match with the time lag, until 5 days before collecting, showing highly significant correlations ($P \leq 0.001$) at a time lag of 3 (Spearman's r_S 0.17) and 4 (Spearman's r_S 0.19) days.

The DistLM marginal analysis indicated that not all environmental variables were significant (Table 1) and that the significant various 'explanatory' variables are not independent of each other and need to be considered in combination to explain the variation in the abundance of anchovy eggs (Table 2). The variables that contributed considerably to the variation observed (marginal tests) were mainly (ordered from highest to lowest contribution) Chl-a (31.32% with a lag of 3 days and 23.67% for a lag of 4 days), Long (16.49%), Lat (14.11%), Dist (11.92%) and S (11.56%).

In order to ensure a more robust regression model, DistLM sequential tests with a step-wise procedure were run for anchovy eggs abundance and environmental variables for the GoC at different time lags (Table 2). The optimal models (lower AICc) with the studied environmental variables which explained a higher percentage of the anchovy eggs variation occurred at the time lag 3 (37.75%, Table 2 and Fig. S1) and without time lag (39.3%, Table 2). Overall, Chl-*a* and variables related to location such as latitude and longitude contributed to about 30% of the total variation (Table 2 and Fig. S1 dbRDA), while other

Table 1
Statistics for the Distance-based Linear Model (DistLM) analyses marginal tests based on a step-wise selection procedure. The Akaike's corrected information criterion (AICc) was applied to select the group of variables that accounted for the greatest proportion of anchovy eggs abundance at the 136 sampling stations in the GoC. Marginal tests show how much variation each variable explains when considered alone, ignoring other variables. Percentage of variance explained (Prop. (%)) represents the explained variation attributable to each variable. Significance (P) is indicated. In bold, the variable with the highest contribution. The variables names followed by an underscore symbol indicate the time lag in days between the eggs sampling and the variable date. For example, Chla_Lag1, indicates that the Chl-a value corresponds to one day before.

Variable	SS(trace)	Pseudo-F	P	Prop. (%)
Lat	21.4190	22.02	0.0001	14.114
Long	25.0380	26.4760	0.0001	16.499
Depth	4.2797	3.8885	0.0490	2.820
S	17.5440	17.5160	0.0002	11.561
Dist2	18.0910	18.1360	0.0001	11.921
Chla	23.8030	24.9270	0.0002	15.685
Chla_Lag1	18.5490	18.6590	0.0003	12.223
Chla_Lag2	19.0720	19.2610	0.0002	12.567
Chla_Lag3	47.5320	61.1100	0.0001	**31.321**
Chla_Lag4	35.9310	41.5690	0.0001	23.677
Chla_Lag5	7.8333	7.2932	0.0081	5.161
SST	11.7030	11.1970	0.0013	7.711
SST_Lag1	11.5560	11.0450	0.0011	7.615
SST_Lag2	11.4050	10.8880	0.0011	7.515
SST_Lag3	10.6590	10.1230	0.0016	7.024
SST_Lag4	9.8123	9.2631	0.0036	6.465
SST_Lag5	8.7168	8.1659	0.0061	5.743
U	2.7200	2.4455	0.1214	1.792
U_Lag1	2.7200	2.4455	0.1213	1.792
U_Lag2	12.9540	12.5060	0.0010	8.536
U_Lag3	7.7680	7.2290	0.0081	5.118
U_Lag4	0.3661	0.3240	0.5714	0.241
U_Lag5	8.5490	7.9993	0.0045	5.633
V	0.2093	0.1850	0.6698	0.137
V_Lag1	0.8366	0.7428	0.3892	0.551
V_Lag2	1.4727E-2	0.01300	0.9121	0.009
V_Lag3	2.0112	1.7998	0.1780	1.325
V_Lag4	11.8300	11.3290	0.0017	7.795
V_Lag5	18.1630	18.2180	0.0001	11.968

Table 2
Statistics for Distance-based Linear Model (DistLM) analyses sequential tests based on a step-wise selection procedure. The Akaike's corrected information criterion (AICc) was applied to select the group of variables that accounted for the greatest proportion of anchovy eggs abundance at the 136 sampling stations in the GoC. Sequential tests explain the cumulative variation attributed to each variable fitted to the model in the order specified, taking previous variables into account. Cumulative percentage of variance explained (Cum. (%)) represents explained variation attributable to each variable added to the model when fitted sequentially. Significance (P) is indicated. In bold, the optimal model with the lowest AICc value plotted in Fig. S1.

	Variable	AICc	SS (trace)	Pseudo-F	P	Prop. (%)	Cum. (%)	res. df
No Lag	+Long	−5.52	25.03	26.47	0.0001	16.49	16.49	134
	+Chla	−25.50	18.98	23.43	0.0002	12.50	29.00	133
	+Depth	−32.57	7.04	9.23	0.0033	4.64	33.65	132
	+V	−36.39	4.32	5.87	0.0148	2.85	36.50	131
	+U	−37.42	2.25	3.11	0.0785	1.48	37.98	130
	+S	**−38.12**	2.00	2.80	0.1001	1.32	**39.30**	129
Lag 1	+Long	−5.52	25.03	26.47	0.0001	16.49	16.49	134
	+Chla_Lag1	−21.30	15.60	18.68	0.0001	10.28	26.78	133
	+Depth	−29.37	8.02	10.26	0.0016	5.28	32.06	132
	+SST_Lag1	−29.70	1.86	2.41	0.1255	1.23	33.30	131
	+S	−30.25	2.01	2.64	0.1056	1.33	34.62	130
Lag 2	+Long	−5.52	25.03	26.47	0.0001	16.49	16.49	134
	+Depth	−19.14	13.82	16.28	0.0003	9.11	25.60	133
	+Chla_Lag2	−25.99	7.21	9.01	0.0036	4.75	30.36	132
	+S	−26.68	2.18	2.76	0.0956	1.44	31.80	131
	+SST_Lag2	−27.10	1.96	2.52	0.1122	1.29	33.09	130
Lag 3	**+Chla_Lag3**	−32.09	47.53	61.11	0.0001	31.32	31.32	134
	+Lat	−36.65	4.97	6.66	0.0118	3.27	34.59	133
	+Depth	−37.12	1.87	2.54	0.1117	1.23	35.83	132
	+S	**−39.11**	2.92	4.05	0.0445	1.92	**37.75**	131
Lag 4	+Chla_Lag4	−17.74	35.93	41.56	0.0001	23.67	23.67	134
	+Lat	−22.52	5.70	6.88	0.0079	3.75	27.43	133
	+S	−24.91	3.59	4.45	0.0364	2.37	29.80	132
	+Depth	−29.00	4.78	6.15	0.0152	3.15	32.95	131
Lag 5	+Long	−5.52	25.03	26.47	0.0001	16.49	16.49	134
	+Depth	−19.14	13.82	16.28	0.0002	9.11	25.60	133
	+S	−22.86	4.75	5.80	0.0181	3.13	28.74	132
	+SST_Lag5	−23.31	2.04	2.52	0.1104	1.34	30.09	131

environmental variables such as the wind components hardly added on average 5% to the overall variation, with the remaining 60% unexplained.

3.2. Maps of particles trajectories

Fig. 4 shows the positions of the Lagrangian particles at the time of release (Fig. 4a) and after 5 (Fig. 4b) and 10 (Fig. 4c) days of simulation. Results indicated that most particles (>99%) were transported westward, following the coastal countercurrent. In this sense, while approximately 48% of the particles surpassed Cape San Vicente and continued northward along the Portuguese continental shelf (first behaviour) after ten days of simulation (Fig. 4c), about 30% of them remained within the GoC (second behaviour), the larger percentage being located within the eastern shelf (22%). The remaining particles (22%) were transported outside the continental shelfs, with less than 0.5% having landed in the Mediterranean Sea or in the Strait of Gibraltar.

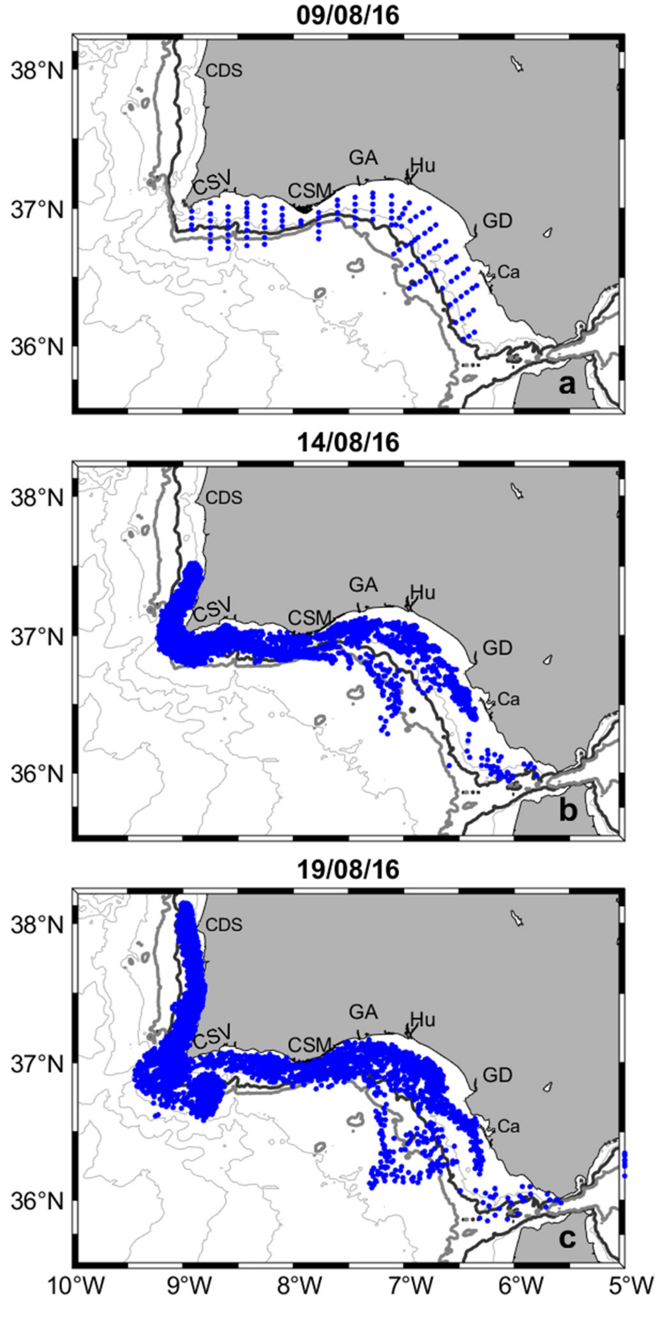

Fig. 4. Maps of the distribution of particles released in the GoC for the dates indicated in each figure: day 0 (a), day 5 (b), and day 10 (c). The following geographic features are shown: GA (Guadiana River estuary), GD (Guadalquivir River estuary), Ca (Bay of Cádiz), Hu (city of Huelva), CDS (Cabo de Sines) Se (Setúbal district), CDR (Cape Roca). Bathymetric contours of 100, 200 (thick dark line), 500 (thick grey line), 1000, 2000, 3000 and 4000 m are shown.

3.3. Particle density per area

The distributions and densities of Lagrangian particles were obtained after 10 days of simulation at each of the areas defined (Fig. 5), including those that were transported off the shelf (area called OUT in Fig. 2). Results are separated according to the initial position of each particle with respect to Cape Santa Maria in order to compare the contribution of each side of the GoC continental shelf to the predefined areas. In this sense, GoC-E and GoC-W stand for the eastern and western sides of Cape Santa Maria, respectively, in Figs. 2 and 5.

Overall, the percentage of accumulated particles is higher in the eastern shelf (GoC-E). More specifically, while 56.3% of the particles released in the GoC eastern shelf remained in that area after ten days of simulation (Fig. 5a), only 5.1% of the particles released in the GoC western shelf were retained without being exported to other areas (Fig. 5b). In terms of particles transferred to other regions, 14.3% of the particles released in the GoC eastern shelf were exported to the GoC western shelf, 14.7% to the western Portuguese shelf, and 14.6% off the continental shelf (OUT). Similarly, the largest export of particles from the GoC western shelf occurred towards the western Portuguese shelf (68.6%), followed by the particles exported off the shelf (25.6%) and finally towards the GoC eastern shelf (0.7%).

Considering the joint contribution of both sides of the GoC continental shelf, the resulting accumulation of particles after ten days of simulation would be ordered from highest to lowest as: on the Portuguese western shelf (48.4%), on the GoC eastern shelf (21.5%), off the shelf (21.5%) and on the GoC western shelf (8.6%).

4. Discussion

The passive transport of eggs and larvae between the spawning and the nursery area is key to understand the recruitment of species such as anchovy, with a high commercial interest in the GoC, a region characterized by a high variability in the surface circulation. It is well known that juvenile anchovies feed and grow in shallow areas such as estuaries, mainly the Guadalquivir (González-Ortegón et al., 2015; Drake et al., 2007) and Guadiana in the GoC (Morais, 2007; Faria et al., 2006). Furthermore, a reproductive strategy for this species is to maintain the spawning area on the shelf near the estuaries. However, changes have been evidenced in the anchovy spawning area in the GoC, so, it is not always associated with the rivers' mouths (Baldó et al., 2006).

4.1. Effects of multiple environmental factors on early life stages abundance and horizontal distribution

In this study, the eggs densities sampled in the ECOCADIZ 2016 campaign, seemed to be somewhat higher west of Cape Santa Maria, in particular in front of Albufeira (Portugal), when larger densities are normally found in the vicinity of the Guadalquivir (ICES, 2016). Even so, the densities near the mouth of the Guadalquivir showed significant peaks that are not negligible, hence indicating a bimodal spatial pattern distribution in 2016 along the GoC. On the other hand, it is important to highlight that the egg densities found that year were relatively low compared to other years (ICES, 2016). In this way, any environmental variation can play an important role in the displacement of the egg density centre of mass; therefore, the centre of mass would not be an appropriate spatial indicator. Thus, the present work studied whether the environmental conditions east and west of Cape Santa Maria could determine this important variation in the spawning area during August 2016 with respect to previous years.

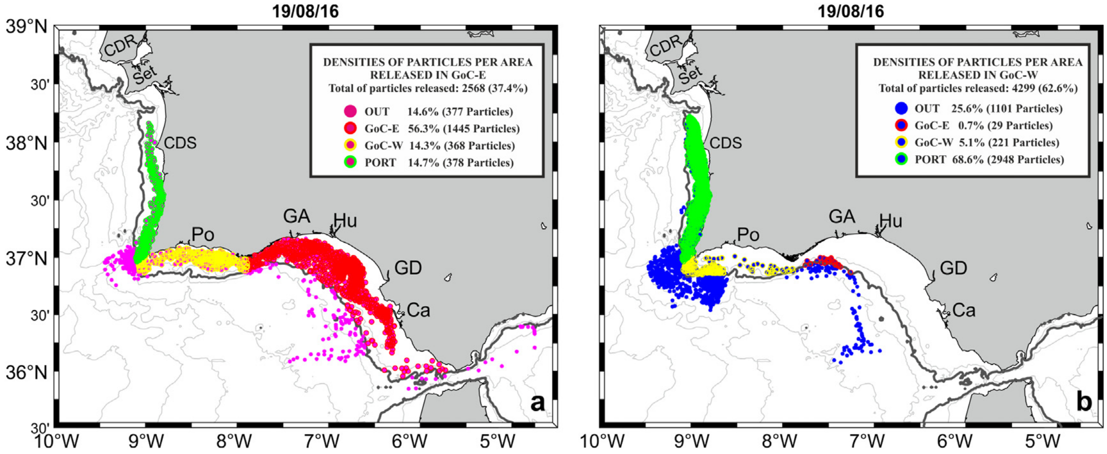

Fig. 5. Maps of particles distribution after 10 days of simulation according to the shelf where they were released: (a) GoC eastern shelf or GoC-E (magenta) and (b) GoC western shelf or GoC-W (blue). Depending on the final position of the particles, they were coloured differently according to the arrival area: red (GoC-E), yellow (GoC-W), green (western Portuguese shelf or PORT) and off-shelf or OUT (a, magenta and b, blue). The colours are presented in the legend to show the densities of particles per area. The following geographical features are shown: GA (Guadiana River estuary), GD (Guadalquivir River estuary), Ca (Bay of Cádiz), Hu (city of Huelva), Po (city of Portimão), CDS (Cabo de Sines), Se (Setúbal district), CDR (Cape Roca). Bathymetric contours of 100, 200 (thick dark line), 500 (thick grey line), 1000, 2000, 3000 and 4000 m are shown.

Overall, chlorophyll-*a* was the best predictor of the anchovy eggs density, explaining just above 30% of the variability. Chlorophyll-*a* is the best proxy of phytoplankton biomass for studies of primary productivity (Huot et al., 2007) and it can trigger an increase in food availability for anchovy larvae, hence favouring success for the first stages (García and Palomera, 1996). This is consistent with previous works identifying this variable as a key factor influencing spawning areas (Ganias, 2009). In the same way, the transport of organic matter from adjacent ecosystems such as saltmarshes could be clearly underestimated at the base of food webs for fish on coastal ecosystems (Melville and Connolly, 2005). In the GoC, organic matter of terrestrial origin, introduced into aquatic ecosystems mainly through the discharge of rivers and wetlands, is the major source of dissolved organic matter in the near shore waters (González-Ortegón et al., 2018; Amaral et al., 2020). Thus, the freshwater discharges on the GoC continental shelf between Cape Santa Maria (Portugal) and Cape Trafalgar (Spain), which are directly influenced by salt-marshes and three main estuarine systems (Guadiana, Tinto-Odiel and Guadalquivir), could explain the bimodal spatial pattern of eggs distribution found in the studied area. Although chlorophyll-*a* as a proxy of production would eventually integrate organic matter and support anchovy spawning, the inclusion of other factors related to other sources of organic matter could contribute directly to the unexplained variance of the selected model. In fact, variables related to the geographic position (longitude) contributed to the models, and could also explain the importance of some areas in the GoC as specific spawning grounds. In any case, the density of anchovy eggs correlated better with environmental variables at time lag 3 or 4 days, and the optimal models occurred at time lag 3 (Table 2). This could probably indicate that, before any spawning process occurs, anchovy adults require suitable environmental conditions such as high chlorophyll-a concentrations.

4.2. Effect of a particular transport regime on the advection of anchovy early life stages

During the studied period, the particle trajectories showed a preferential westward transport, consistent with the onset and intensification of the coastal countercurrent by easterly winds, causing a westward advection of warm surface water, as well as the Lagrangian particles. This is visible on the SST maps that show a displacement of the warm water tongue off the Guadalquivir, in synchrony with the coastal countercurrent (Fig. S3, Movie S2). Moreover, previous studies focused on the behaviour of river discharge plumes showed that when the discharge takes place within a current that flows parallel to the coast on the continental shelf in the direction of a Kelvin wave, all the water from the river discharge would be transported by this current in that direction (Fong and Geyer, 2002; Garvine, 1995; Nof and Pichevin, 2001). In the case of the GoC, this situation coincides with the existence of a coastal countercurrent that flows westward. On the other hand, the same authors demonstrated that if the ambient current flows in the opposite direction (in our case, towards the Strait of Gibraltar), the river discharge forms a small protuberance before being transported in the direction of the current. In our case, this protuberance can be observed in Fig. S3i (36° 45′N, 6° 30′W), when the coastal countercurrent had reversed over the eastern shelf (Fig. S3f). The weakened northerly winds blowing along the western Portuguese shelf (Fig. S3a, Movie S2a) favour the northward progression of this warm water beyond Cape San Vicente, in agreement with previous studies (Fiúza, 1983). Interestingly, this tongue of warm water continues flowing northward with the coastal countercurrent during some time after the northerly winds have increased their intensity (see for example, August 19 on Fig. S3c, f, I and on Movie S2a, b, d). Furthermore, it is quickly set up again a few days later as soon as the northerly winds decrease their intensity along the western Portuguese coast and easterly winds blow within the GoC (see for example, August 26 on Movie S2a, b, d). This is consistent with the onset of a coastal countercurrent due to a wind relaxation process as described by Garel et al. (2016) in the GoC or by Melton et al. (2009) in the California current system.

Assuming that the anchovy eggs took two days to hatch, results from the 10-day Lagrangian simulation refer to larvae with 8 days of age (Morais et al., 2012; Huret et al., 2011). The Lagrangian model indicated an important displacement of these early life stages (48.4% of the total particles released) towards the south-western coast of Portugal, as the warm coastal countercurrent surpassed Cape San Vicente and continued flowing northward (see Movies S1 and S2). Bearing in mind that anchovy larvae start developing certain swimming capabilities after day 10, it is expected that part of the individuals that landed in that region may actively swim northwards along the Portuguese western shelf, where an overall high productivity is observed at least until the end of August 2016 (Movie S2c), thus ensuring the availability of food. This idea is in agreement with Teodósio et al. (2016), who proposed that temperate fish larvae, such as anchovies, are able to detect estuarine nursery areas and swim towards them by using a set of sensory cues, even when they are in offshore areas. More specifically, using either the earth's geomagnetic field or a sun compass will guide them back towards the coast, where post-flexion larvae are able to find an estuarine plume (infotaxis strategy) and swim in the correct direction by keeping bearing during navigation, thus avoiding displacement due to unfavourable longshore currents. In our case, this active swimming displacement would be favoured by the new northward flowing coastal countercurrent observed between August 25 and 30 along the western Portuguese shelf (Movie S2b). Hence, the simulation results suggest a potential gain of anchovy along the western coast of Portugal due to an increase in the connectivity between the South component and the West component of subdivision 9a. In fact, while an increase in landings was documented a year later in the West component (ICES, 2018), the abundance of anchovy in the South component was lower, with a 30% reduction in catches. More specifically, an increase of 10 tons was reported in the CS section (Uriarte and General, 2018), suggesting that this increase in catches could be related to an increased connectivity between both components during the 2016 spawning period.

A smaller percentage of particles (21.5% of the total particles released) were exported out of the continental shelf and, therefore, far from the area where the individual has the most suitable resources to ensure their survival (ICES, 2018). This may have negative implications when it comes to recruiting, probably explaining part of the reduction in anchovy catches in the South component during 2017. The results obtained in this study suggest that this decrease in catches could be due to the existence of periods of intense easterlies and a persistent coastal countercurrent at the time of spawning. In fact, the year 2016 presented a larger number of easterly winds, and more intense than previous years, between June and August (Fig. S4), which would in turn imply a larger number of days with coastal countercurrents in comparison with previous years. According to the Lagrangian simulation, this coastal countercurrent could lead to the transport of part of the anchovy eggs and larvae far from the optimal recruitment areas in the GoC. Although this phenomenon was previously suggested (Ruiz et al., 2006), the study area was limited to the eastern basin, evidencing the decline in this area but without considering the possible increase in connectivity between the GoC and the Portuguese west coast mentioned above. The repercussion that this offshore transport might have on the anchovy populations is an increase of mortality due to starvation, as described in the 'critical period' hypothesis (Hjort, 1914). In fact, offshore dispersal of fish larvae may lead to considerable losses in Eastern Boundary Upwelling Systems (Cury and Roy, 1989; Castro and Hernandez, 2000). For example, a study on the recruitment of south African anchovy in the Southern Benguela (Hutchings et al., 1998) stated that eggs spawned in the Agulhas Bank under strong south-easterly winds may be subject to large advective losses offshore, where food availability is lower, hence jeopardizing the recruitment success. They also reported that good feeding conditions tend to increase recruitment, although other factors such as changes in species dominance also play an important role. More recent studies, however, contradict the idea of an increased mortality as a result of offshore transport. For example, Irigoien et al. (2007) suggested that anchovy juveniles frequently observed off the shelf in the Bay of Biscay may be the result of a recruitment strategy, rather than advective losses. According to the authors, although in that region the food availability offshore is approximately half that on the shelf, the predatory risk is also lower; thus, larvae advected off the shelf will be able to survive and return to the shelf as older juveniles, when they are less susceptible to predation. Furthermore, the infotaxis strategy developed by anchovy larvae allows them to detect estuarine nursery areas and actively swim towards them, as mentioned above (Teodósio et al., 2016). This different behaviour could be due to the fact that upwelling systems, such as the Southern Benguela region, are characterized by strong advective transport and very oligotrophic waters outside the upwelling region, unlike bay-like systems such as the Bay of Biscay or the Gulf of Cadiz, where currents are slower and most of the food is provided through river discharges (Irigoien et al., 2007).

In terms of the retention capacity of each of the continental shelves, results from the Lagrangian simulation indicated that the western shelf had a considerably lower retention capacity (5.1%) than the eastern shelf (56.3%) during the study period. This could be related not only to the narrower with of the western shelf, but also to the intensity and persistence of the coastal countercurrent within that shelf (see Fig. S3d–f and Movie S2b). In fact, while an intense countercurrent was observed along the western shelf and continental slope until the eighth day of the simulation (Movie S2b), the surface circulation was highly variable over the eastern shelf, where a less intense coastal countercurrent occupying the shelf and continental slope alternated every few days with an anticyclonic circulation cell that presented an eastward flowing current over the inner shelf and a westward current over the outer shelf and slope. This anticyclonic cell would help retaining particles within the eastern shelf.

Keeping these results in mind, we could suggest that, a change in the spatial distribution of the anchovy eggs spawning, resulting in a higher density of eggs west of Cape Santa Maria under an intense and long lasting coastal countercurrent, would lead to an increase in the connectivity between the southern and western components of subdivision 9a during the studied period. Although the Lagrangian model used has helped to identify and understand the combined effect of a westward displacement in the spawning area under a coastal countercurrent regime, it must be taken into account that it only focused on the passive transport of early life stages (i.e., larvae aged up to 8 days) under a three-dimensional current field, i.e., particles were horizontally advected by currents and randomly displaced vertically by turbulence. Extending the period of time for the simulations to include larval behaviour, such as diel vertical migrations or active swimming, or even the effects of predation and competition with other pelagic species, such as sardine, would produce more robust quantitative results in terms of effective recruitment to nursery grounds and of population fluctuations.

5. Conclusions

The environmental variable that best characterized the spawning areas was chlorophyll-*a* with a lag of 3 days, suggesting that the density of this particulate organic matter, and probably organic matter of terrestrial origin, induces the laying of the European anchovy eggs. In this work, evidence is provided that, under intense countercurrents, the early life stages of the European anchovy *Engraulis encrasicolus* spawned in the GoC, can be transported to the Portuguese western coast and, to a lesser extent, offshore to the Atlantic oligotrophic waters. This transport not only increases the connectivity between the GoC eastern and western shelfs, in accordance with previous studies (García-Lafuente and Ruiz, 2007), but can also augment the connectivity between the southern component (GoC) and the western component (from Cape San Vicente to the west coast of Galicia) of subdivision 9a, if the coastal countercurrent is prolonged over time. Furthermore, if the anchovy eggs spawning region is mainly located over the GoC western shelf, a long-lasting coastal countercurrent can increase the connectivity more notably, as observed in August 2016. The dispersion pattern could explain why a year later there was a gain in anchovy on the Portuguese west coast and losses in the GoC. In order to get a better understanding of how spawning, hatching or survival are being affected by changes in oceanographic conditions, it is necessary to study more years. This would help decision-makers to plan a sustainable exploitation of resources under a climate change scenario that would guarantee the preservation of this species.

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CRediT authorship contribution statement

A. Casaucao: Conceptualization, Data curation, Formal analysis, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing.

E. González-Ortegón: Conceptualization, Data curation, Investigation, Methodology, Software, Visualization, Supervision, Writing – original draft, Writing – review & editing.

M.P. Jiménez: Project administration, Resources, Investigation, discussion of the final draft.

S. Plecha: Data curation, Formal analysis, Investigation, Software, Writing – review & editing.

A. Teles-Machado: Data curation, Formal analysis, Investigation, Software, Visualization, Writing – review & editing.

A. Peliz: Data curation, Formal analysis, Methodology, Software, Writing – review & editing.

I. Laiz: Conceptualization, Data curation, Investigation, Methodology, Software, Visualization, Supervision, Writing – original draft, Writing – review & editing.

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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