Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

Anomalous ocean currents and European anchovy dispersal in the Iberian ecosystem

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ABSTRACT: Unlike other upwelling areas where sardine and anchovy species dominate the pelagic ecosystems, the Western Iberian ecosystem has been consistently dominated by European sardine *Engraulis encrasicolus*, while anchovy had a residual presence from the start of acoustic surveys, in 1989, to 2014. Since 2015, the abundance of anchovy in the Western Iberian margins has sharply increased and continues to show an increasing trend as of 2023. It is unclear if this increase is a result of dispersal from nearby recruitment areas, higher survival rates of early life stages due to favorable environmental conditions, or both. We used a set of different models to simulate the dispersion and survival of anchovy early life stages in the Iberian region for the years preceding the increase in anchovy abundance. An ocean model simulation with the model CROCO provided the fields used as background for Lagrangian simulations coupled to an individual-based model of anchovy eggs and larvae. We simulated the years 2013—2015, and the results show that in 2014 and 2015, anomalous upper-ocean circulation patterns with strong and persistent eastward currents transported a large number of eggs and larvae from the Bay of Biscay (BoB) eastward along the Northern Iberian margin. The maximum transport occurred in June and July 2015, when 8 and 4 %, respectively, of the eggs spawned in the BoB potentially reached the Iberian west coast as larvae. This process might explain the increase in anchovy abundance in the Western Iberian ecosystem. The results of the study show that episodes of anomalous intense ocean currents, when coincident with high presence of eggs, can lead to the colonization of new areas, and connectivity between areas varies dramatically with time.

KEY WORDS: *Engraulis encrasicolus* · Larval dispersal · Oceanographic conditions · Iberia · Connectivity

1. INTRODUCTION

Small pelagic fish (SPF) species are subject to heavy exploitation, and their transformation products are increasingly being incorporated into the global food chain (FAO 2016). Managing these species is challenging due to significant inter-annual population variability in biomass, believed to be influenced by environmental changes impacting the survival of early life stages (Kaplan et al. 2016, Peck et al. 2021). The impact of environmental conditions in population dynamics is extremely important for SPF, whose stocks can potentially recover with 1 year of good recruitment (number of fish surviving to enter the fishery) or collapse with a short series of low-recruitment years (Katara 2014).

The European anchovy *Engraulis encrasicolus* is a small pelagic coastal marine fish, 20 cm total length

with a 3 yr life span, distributed from the North Sea to southeast Africa, including the Mediterranean basin. This species supports significant fisheries and economic activities in the countries bordering the Iberian Peninsula and Mediterranean Sea (Uriarte et al. 1996, Lleonart & Maynou 2003). Due to its market value, production, and widespread distribution across the East Atlantic and Mediterranean countries, anchovy is a major shared resource in the region.

Historically, the European anchovy has had 2 main distribution areas off Iberia: the Bay of Biscay (BoB) in the north and the Gulf of Cadiz (GoC) in the south, with limited presence along the western Iberian coast (Fig. 1). For management purposes, the anchovy inhabiting the north coast (BoB and Cantabrian Sea) is considered a different stock than that of the south, while the populations inhabiting western and southern Iberia are managed as a single stock. However, spatial distribution provided by acoustic surveys shows a persistent discontinuity between the western and southern anchovy for several life stages (eggs, juveniles, and adults), which is also reflected on landings, and for that reason, although it is considered a single stock, advice is provided separately for the western and southern components (ICES 2022).

Several studies conducted at, or in the vicinity of, Portuguese estuaries have shown a persistent presence of recruits in numerous estuaries, mainly in northwestern Iberia (Ribeiro et al. 1996, Pombo &

Rebelo 2002, Marques et al. 2003, Chicharo et al. 2006, Ramos et al. 2006, Cardoso et al. 2011, França et al. 2011, Chicharo et al. 2012, Nyitrai et al. 2012). However, before 2016, yearly spring acoustic surveys, validated by trawls, carried out in Atlantic Iberian waters showed a very low abundance off western Iberia, and for some years even absence, which agrees with the very low landings (ICES 2022).

The abundance of anchovy registered in acoustic surveys was low (<5000 t) for the large majority of the years before 2016. Only in 2011, the abundance was significantly higher (28 550 t), but it was not reflected in the following years when it dropped to very low numbers. In 2016, a large boost of anchovy biomass was registered in the area (38 507 t), and there has been an increasing trend since then, with >50 000 t registered in 2020, 2021, and 2022 (ICES 2022). It is unknown if these eruptions are the result of good environmental conditions favoring the residual populations inhabiting the estuaries or migration from nearby recruitment areas (GoC or BoB), where anchovy are ubiquitous.

Several works have studied the connectivity of anchovy populations off Iberia. Morphometric studies found a differentiation between anchovy populations from northwestern Iberia and those from the BoB (Junquera & Pérez-Gándaras 1993), while a more recent study sampling fish in 2000 and 2001 found, by cluster analysis, a separation between anchovies from
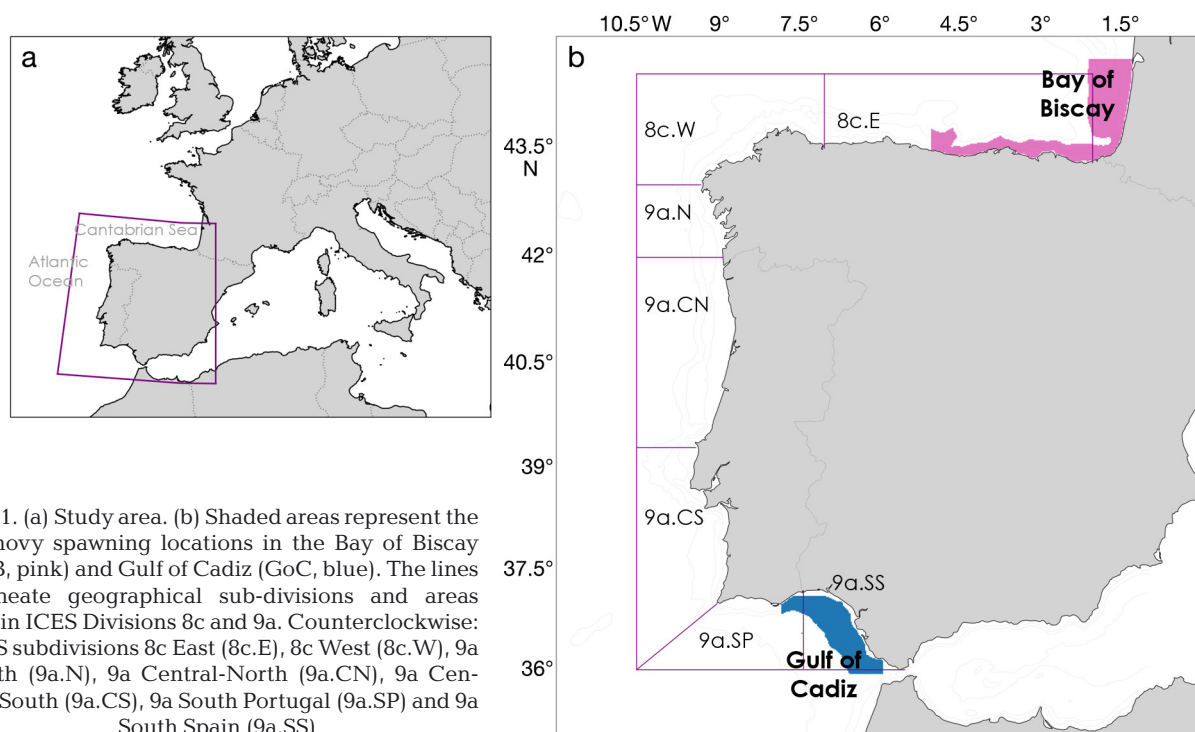

Fig. 1. (a) Study area. (b) Shaded areas represent the anchovy spawning locations in the Bay of Biscay (BoB, pink) and Gulf of Cadiz (GoC, blue). The lines delineate geographical sub-divisions and areas within ICES Divisions 8c and 9a. Counterclockwise: ICES subdivisions 8c East (8c.E), 8c West (8c.W), 9a North (9a.N), 9a Central-North (9a.CN), 9a Central-South (9a.CS), 9a South Portugal (9a.SP) and 9a South Spain (9a.SS)

the BoB and those from western and southern Iberia (Caneco et al. 2004). However, genetic studies have not provided conclusive evidence regarding the population structure of anchovy due to its complex evolutionary history. The species exhibits 2 ecotypes (oceanic and coastal), which display more differentiation between them than between distant locations such as the Atlantic Ocean and Mediterranean Sea (Le Moan et al. 2016, Catanese et al. 2017). This complex evolutionary history hinders the inference of population connectivity through molecular identification unless an intense sampling scheme at different latitudes and distances to the coast is achieved. Modeling larval dispersal can help understand the degree of connectivity of Iberian populations at the early life stages, and in particular investigate the potential of recruitment areas in north and south Iberia to be responsible for the recent surge in anchovy abundance in the western region.

The objective of this study was to develop a modeling approach to study the dispersion of anchovy eggs from the main spawning grounds in the BoB and in the GoC for the years preceding the observed increase in anchovy abundance along the west coast of Iberia, with the aim of identifying a potential source area.

2. MATERIALS AND METHODS

An individual-based model (IBM) for anchovy eggs and larvae was developed and coupled to a Lagrangian model to simulate the transport of anchovy eggs and larvae by ocean currents, from the spawning grounds in the GoC and BoB (Fig. 1). Each particle represents a population of anchovy eggs and larvae that experience similar environmental conditions and follow similar trajectories. In our IBM, the survival and evolution of the early life stages of anchovy depend on (1) the temperature they experience along the trajectories and (2) on a food availability index estimated from satellite-derived chlorophyll *a* (chl *a*) values. The ocean current velocity and the temperature fields were obtained from a regional ocean model simulation of Iberia (Section 2.1), and the chl *a* data are from a satellite product (GLOBCOLOUR, http://globcolour.info).

2.1. Regional ocean model

The ocean currents and temperature fields used are outputs from IBv2.0, a regional ocean model simulation for the Iberian region, performed with the Coastal and Regional Ocean Community model (CROCO). CROCO is a primitive equation, hydrostatic, sigma-coordinate, free-surface ocean model (Shchepetkin & McWilliams 2003, 2005).

This simulation had a horizontal resolution of about 1.6 to 1.9 km and 60 vertical levels. It ran in a 2-way nested grid configuration, where the smaller, higher-resolution grid extends from 35° N, 12° W to 45° N, 1° W. The atmospheric variables are obtained from ERA5 (Hersbach et al. 2020), and the heat and freshwater fluxes are computed internally using a bulk flux parameterization. The model was initialized with data from the global ocean reanalysis GLORYS12V1 (https://doi.org/10.48670/moi-00021) and continuously fed along the open boundaries with monthly fields of the same GLORYS12V1 reanalysis. The regional simulation used here is an updated version of the one described by Teles-Machado et al. (2016a).

2.2. Lagrangian model and IBM of anchovy eggs and larvae

To study the advection of the particles, which represent anchovy eggs and larvae, we used the Lagrangian model Parcels (10.5281/zenodo.8427125) (Delandmeter & van Sebille 2019, Kehl et al. 2023). Parcels is a group of Python functions and scripts that uses 3D outputs from ocean circulation models to perform particle tracking simulations. We chose Parcels due to its versatility, and because it is easily customizable to attribute characteristics, sensitivities, and behaviors to the tracked particles. Particles were advected using the Runge-Kutta4 advection scheme, already implemented in Parcels, and we included Smagorinski diffusion. We programmed the IBM as 3 different kernels inside Parcels, so that the Lagrangian model and the IBM are coupled and interact.

We used as inputs 3D horizontal velocity and temperature fields from CROCO, and 2D satellite chl *a* fields. The particles are advected by the ocean currents, and their evolution and survival are dependent on the average temperature and chl *a* values experienced along the trajectories. The impact of temperature and chl *a* depends on the ontogeny phase and is detailed below.

We developed an IBM for anchovy eggs and larvae that simulates 4 different stages of evolution as illustrated in Fig. 2:

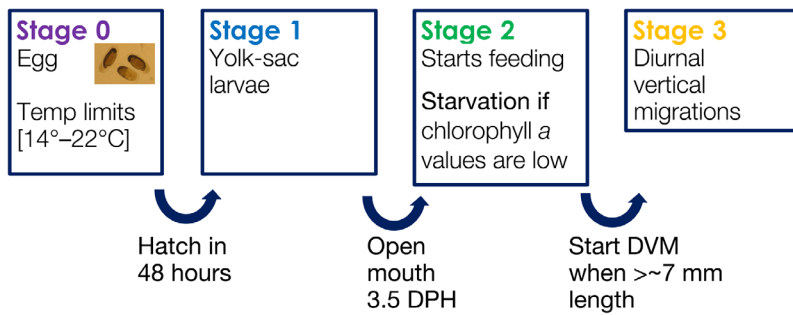Stage 0 is the egg phase. For eggs, we considered the optimal thermal interval of survival to be between

Fig. 2. Schematics of the anchovy individual-based model (IBM) representing the different early life stages considered. DPH: days post hatch; DVM: diurnal vertical migration. See Section 2.2 for more details

14 and 22°C (Shannon 1998). Eggs that experienced temperatures above or below this interval were eliminated. Each particle remained an egg for 48 h (Garrido et al. 2012)

Stage 1 represents the yolk-sac larva. The particle remains in this stage for 3.5 d post hatching (Aldanondo et al. 2008). After that, the larvae evolve to Stage 2, when they open their mouth and start feeding.

Stage 2 represents a larva that already feeds itself but still has no swimming capacity. During this stage, we considered that a larva can die of starvation if the chl a values it experiences along the way are too low (average value along the trajectory below 0.2 mg m−3, which is just a statistical threshold). Growth of the larvae was simulated depending on the temperature values they experience along their trajectories, using the equations obtained by Aldanondo et al. (2008): L = 2.88 + 0.15age, at 17.6°C; L = 2.21 + 0.26age, at 19.3°C; L = 2.4 + 0.33age, at 20.8°C, L = 2.69 + 0.29age, at 22.3°C (L is larval length, and age is in days); at each time step, we used the equation for the temperature closest to the mean temperature experienced by the larvae along their trajectories, which was recomputed at each time step. Larvae evolve to Stage 3 when they reach 7 mm in length, the moment when the first schooling behavior begins, that coincides with the notochord flex and onset of vertical migrations (Somarakis & Nikolioudakis 2010).

Stage 3 represents larvae that can already control their buoyancy and begin diurnal vertical migrations. We considered that they oscillate between the surface and 25 m depth (Coombs et al. 2003).

The particles were passively advected by the ocean currents and the only active movement included were the diurnal vertical migrations that moved them up and down every day, subjecting them to different horizontal velocities whenever there is vertical shear in the horizontal velocity fields.

2.3. Description of the experiments

In our simulations, we deployed particles (eggs) at the 2 main spawning grounds of the region: the GoC and BoB (shaded areas in Fig. 1). The release was done during the period from March to August, which are the main months of the spawning season, for the years 2013, 2014, and 2015. We computed the trajectory of each particle for 40 d, i.e. the average duration of the larval phase. The number of particles deployed is proportional to the spawning area dimension; 930 and 1683 particles were deployed every day from the GoC and the BoB, respectively.

3. RESULTS

3.1. Dispersion patterns from GoC and BoB spawning grounds

The annual percentage of eggs that reaches each of the areas of Fig. 1 (equivalent to ICES sub-divisions 8c East [8c.E], 8c West [8c.W], 9a North [9a.N], 9a Central-North [9a.CN], 9a Central-South [9a.CS], 9a South Portugal [9a.SP], and 9a South Spain [9a.SS]) is represented in Fig. 3. The number of particles that were released and that arrived in each of the areas were weighted by the average spawning curves of both BoB and GoC to take into consideration the fact that the average number of particles deployed in each month is different. For the BoB, we used the shape of the gonadosomatic index mean seasonal cycle calculated for the period 1987−2015 (Erauskin-Extramiana et al. 2019). For the GoC, we computed the average seasonal cycle of the gonadosomatic index from the seasonal cycles of the years 1989 to 1992 obtained from Millán (1999).

Nearly half of the eggs/larvae deployed in the spawning area of the GoC ended up in area 9a.SS (49, 44, and 58% in 2013, 2014, and 2015, respectively) (Fig. 3). Around 10% reached area 9a.SP (10, 11, and 11%, in 2013, 2014, and 2015, respectively), while 1% reached the southwest coast, more specifically, area 9a.CS, recurrently in the 3 years. The remaining eggs died, were lost offshore, or were transported into the Mediterranean Sea (Fig. 4).

At least half of the eggs/larvae deployed in the BoB remained in area 8c.E (51, 65, and 52%, respectively, in 2013, 2014, and 2015). Some larvae followed west-
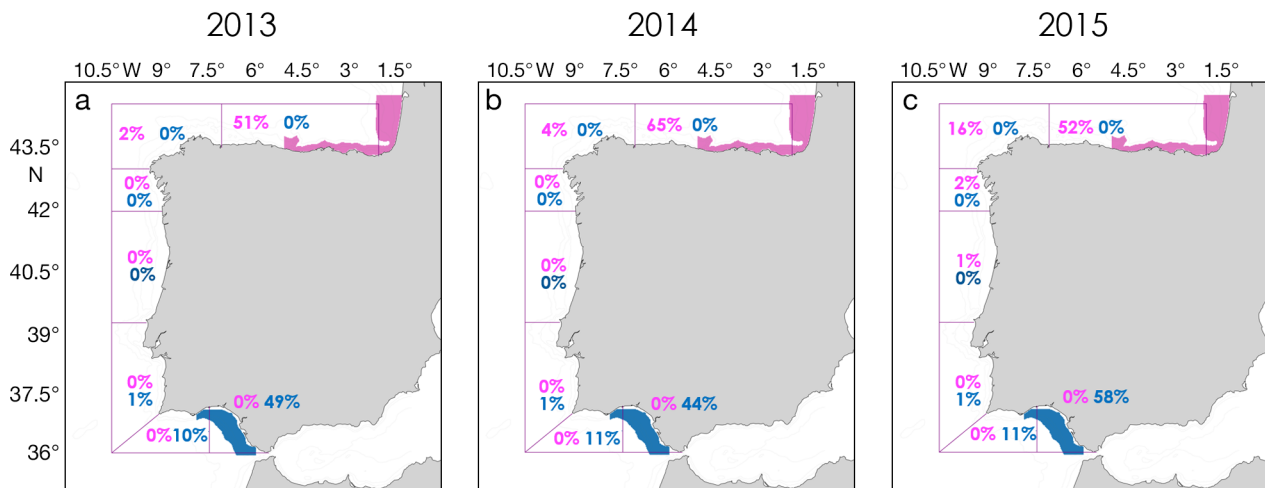
Fig. 3. Percentage of eggs deployed from the Bay of Biscay (BoB; numbers in pink) and the Gulf of Cadiz (GoC; numbers in blue) in 2013, 2014, and 2015, that survived and arrived in each of the areas. The spawning areas are represented in pink (BoB) and blue (GoC), as in Fig. 1
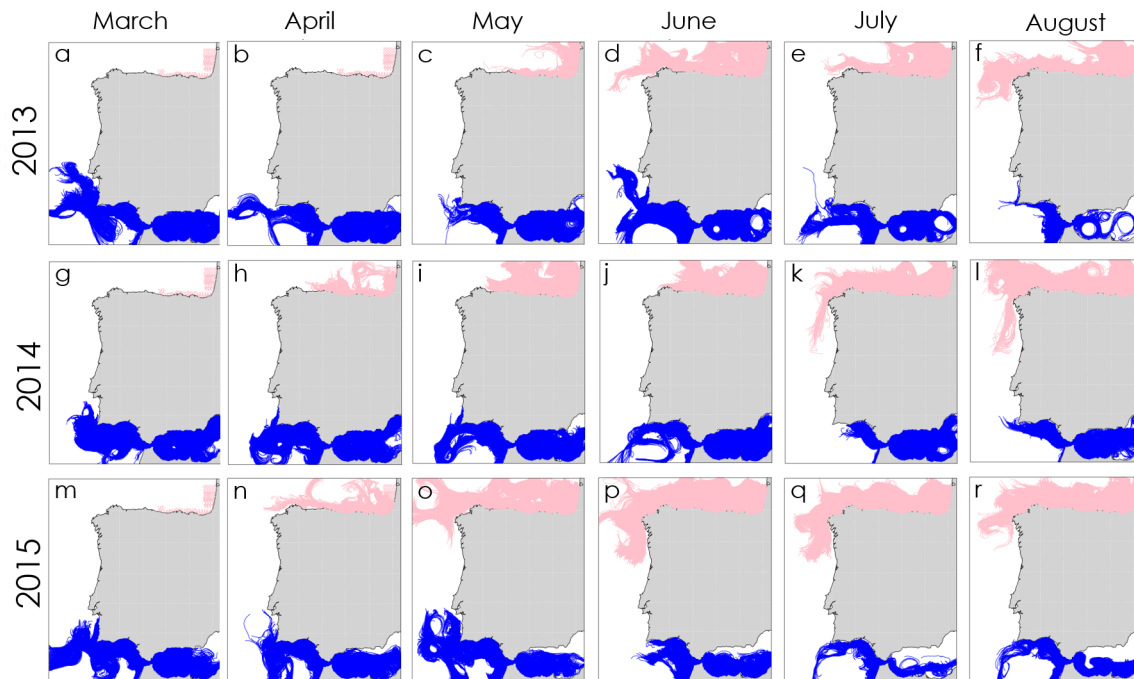

Fig. 4. Trajectories of anchovy larvae deployed from the spawning grounds in the Bay of Biscay (BoB, pink) and Gulf of Cadiz (GoC, blue) in the main months of the spawning season (March to August) from 2013 to 2015

ward trajectories along the Iberian northern coast, reaching area 8c.W (2, 4, and 16%, respectively, in 2013, 2014, and 2015) (Figs. 3 & 4). In 2015, 3% of the larvae reached the Iberian west coast: 2% area 9a.N and 1% area 9a.CN (Fig. 3).

Transport between areas was estimated for each month of the spawning season (Fig. 5). Larvae arriving in area 9a.CS in 2014 (Fig. 5) were mainly those that evolved from eggs spawned in the GoC, mostly during March and May. In 2015, larvae resulted from eggs deployed in the GoC also in March and May. In 2013, most larvae resulted from eggs deployed in the GoC in June, followed by March.

In 2015, 5% of the eggs deployed in June and 3% of the eggs deployed in July arrived in area 9a.N as larvae (Fig. 5). In June and July of the same year, 3 and 1% of the eggs, respectively, reached area 9a.CN (Fig. 5).
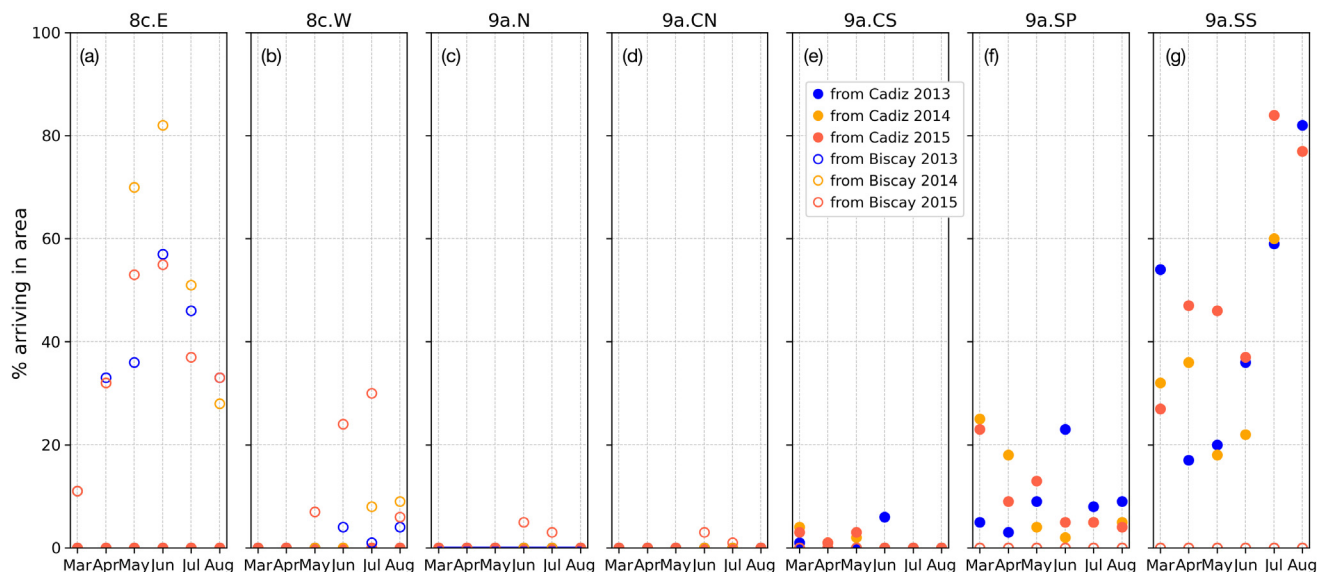
Fig. 5. Percentages of particles deployed from the Gulf of Cadiz (GoC, closed circles) and Bay of Biscay (BoB, open circles), in each month of the spawning season (*x*-axis), in 2013 (blue), 2014 (yellow), and 2015 (red), that arrived in the different ICES areas shown in Fig. 1. Each plot represents a different destination area

3.2. Interannual variability of the alongshore currents in northern Iberia

In order to verify if this was an anomalous or recurrent event in terms of ocean circulation, we computed the average surface zonal (east—west) velocity along the northern Iberian Coast (Fig. 6). Each bar in Fig. 6 represents the monthly average, and we represent the months of April to July, the main months of the anchovy spawning season. The years 2014, 2015, and 2016 stand out as 3 consecutive years of strong west-

ward velocities, especially in July 2014, June and July 2015, and July 2016. The year 2015 was particularly anomalous due to the consecutive months of westward intense surface velocities.

4. DISCUSSION

This study investigated the sudden increase in anchovy abundance off the western Iberian coast that occurred in 2016 after decades of very low abun-
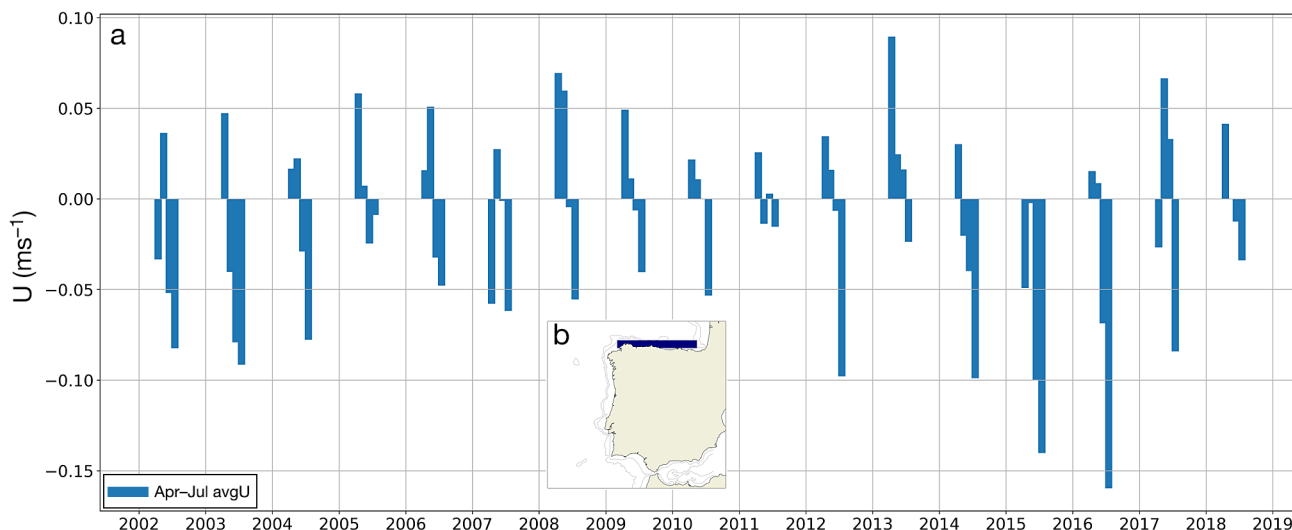

Fig. 6. (a) Time series of monthly averages of zonal (E—W) velocity, spatially averaged (avgU) in an area that covers the Iberian northern coast. The area is represented as a blue box in inset panel (b). Only the months corresponding to anchovy peak spawning season are represented (April to July)

dance. Our approach involved the use of a Lagrangian model coupled to an IBM specifically developed for the European anchovy to study the dispersion and survival of anchovy eggs and larvae, deployed from the 2 main spawning grounds in Iberia, situated in the BoB and in the GoC, with the aim of identifying anomalous oceanographic events that might explain this surge on the Iberian west coast. We modeled the 3 years that preceded the increase, i.e. 2013, 2014, and 2015, to compare the oceanographic conditions during consecutive years when anchovy abundance in the spawning areas off the Iberia was high but only one resulted in a proliferation off western Iberia.

Our results show that during 2013 and 2014, no larvae were transported from the spawning grounds in the BoB to the west coast, and few were transported to the Cantabrian Sea. In contrast, in 2015, 3% of the eggs deployed in the BoB survived the egg and larvae stages and reached the west coast (Fig. 3). The larger transport of potentially surviving larvae occurred during June and July 2015, when 8 and 4%, respectively, of the eggs deployed in the BoB survived and reached the west Iberian coast (Fig. 5, area 9a.N + area 9a.CN). Analysis of the interannual variability of the zonal currents in northern Iberia showed that 2014, 2015, and 2016 were characterized by the presence of anomalous intense and persistent westward surface currents (Fig. 6). The stronger currents occurred during July 2014, June and July 2015, and July 2016. These anomalous events were observed by coastal radar and acoustic Doppler current profiler moorings located in the BoB (von Schuckmann et al. 2019) that identified anomalous intense summer westward currents in 2014, 2015, and 2016. The 2015 event was observed by the coastal radar, and occurred in June and July 2015 (von Schuckmann et al. 2019, their Fig. 2.2.2). These events also have a clear signal in salinity, as they transport fresher waters from the BoB along the northern Iberian Coast (data not shown). These results suggest that the sudden increase in the anchovy abundance in 2016 could be explained by the increased transport of larvae from the spawning grounds in the BoB, more specifically in June and July 2015.

Understanding the variability of alongshore currents in the Cantabrian Sea is crucial, as these currents serve as the mechanism facilitating the transport of larvae between the BoB and the Iberian west coast. Seasonal variability is a well-documented aspect of this system, with winter exhibiting an eastward and more intense average circulation, while summer witnesses a predominantly westward and less intense flow (Charria et al. 2013). During winter, the

eastward currents are an extension of the Iberian Poleward Current (IPC), which characterizes the winter circulation on the west coast; it flows along the Iberian west coast and then turns eastward along the northern coast, transporting warmer and saltier waters from the south (Pingree & Le Cann, 1990, Peliz et al. 2005, Teles-Machado et al. 2016a). The IPC's intensity and progression along the northern coast are subject to interannual variability (e.g. Llope et al. 2006, Le Cann & Serpette 2009), particularly on the west coast, where it is largely influenced by wind intensity (Teles-Machado et al. 2015). In spring and summer, the average circulation along the Iberian northern coast is predominantly eastward, peaking from July to September (Charria et al. 2013). This season coincides with an increased number of upwelling events, also with significant interannual variability (Alvarez et al. 2010) that impacts the strength of westward currents. The pronounced interannual variability is evident in Fig. 6 for the months of April to July, where, although average velocities are westward, numerous months exhibit eastward velocities, even during the summer. Along the Iberian northern coast, alongshore currents are known to destabilize, giving rise to eddies that enhance transport between the shelf and offshore regions (Pingree & Le Cann 1992, Teles-Machado et al. 2016b). This variability, coupled with the presence or absence and positioning of mesoscale eddies, significantly influences larval transport, with greater persistence of currents resulting in larger larval transport. The mechanisms responsible for the occurrence of anomalous intense westward currents between 2014 and 2016 are not explored in this paper, but require further investigation in future studies. Understanding the drivers behind these events would offer valuable insights into the connectivity of anchovy and other species.

There were also larvae reaching the west coast that came from the south Iberia spawning grounds in the GoC. In this case, larvae were transported to the southernmost area of 9a.CS and the percentage was constant over the years, with 1% of the eggs deployed in GoC surviving and reaching the southwestern coast (9a.CS) in 2013, 2014, and 2015 (Fig. 3). Although the percentage was constant for the 3 years, the transport did not occur constantly in time, but in pulses occurring in March and May in 2014 and 2015, and in June in 2013 (Fig. 5, 9a.CS). These pulses are associated with events of the GoC counter-current that develops in the GoC under the influence of easterly winds, carrying warm waters westward in the GoC and northward along the western Iberian shelf (e.g. Relvas & Barton 2005, Teles-Machado et al.

2007). A strong counter-current event in 2016 transported early anchovy life stages to the western coast, increasing the connectivity between southern and western subdomains (Casaucao et al. 2021). As our results show, these events might be recurrent, as they occurred in all of the years that are part of this study (2013−2015), but the larvae never reached areas 9a.N nor 9a.CN. Acoustic surveys show that the large majority of anchovy off western Iberia concentrate on the northwestern Portuguese coast (mean 88%), followed by Galician waters (10%), while the proportion of fish on the southwestern Portuguese coast is significantly lower (mean 2%) (ICES 2022). This further suggests that migration to western Iberia is more likely to come from the northern BoB than from the southern GoC.

The year 2015 was also characterized by high abundance of eggs in the BoB when compared to previous years, as shown by data collected during the BIOMass of ANchovy (BIOMAN) survey in May 2015 (M. Santos et al. 2018). This year clearly stands out both in the higher number of eggs, and also in the larger spatial extent of their distribution (ICES 2016), expanding until 5° W along the Iberian northern coast (probably already as a response to the strong westward flow). The westernmost section of the BIOMAN survey in May 2015 detected the presence of anchovy eggs, suggesting that their presence could extend even further west. Thus, if in the simulation, eggs were deployed not from the main spawning area in the time series but specifically according to egg surveys, eggs would be deployed further west in the Cantabrian Sea during 2015, and this would have resulted in a higher percentage of larvae reaching the west Iberian coast areas at even lower latitudes. We used the same number and distribution of eggs for the 3 years because the objective was to focus on the differences in the environmental conditions. The fact that the anomalous connectivity identified in our results coincides with this maximum in the number and westward distribution of eggs in the BoB amplifies the impact of these results.

This study highlights the importance of studying potential dispersal during the larval phase to understand population dynamics. Although the larval phase is short compared to the average life spans of pelagic fish, its vulnerability to environmental conditions and weak or absent swimming capacities makes it significantly more susceptible to environmental changes and extremes, with larval survival and dispersion playing determinant roles in defining the spatial and temporal structure of the populations (e.g. Bonanno et al. 2013, A. M. P. Santos et al. 2018,

Somarakis et al. 2019). With recent advances in the quality of ocean numerical models, such as the one used in this study, and of modern techniques of genetic analysis, we are slowly learning about the connectivity of the different species and the way it is changing in time and in the actual context of global warming.

For several species, such as the European anchovy, different morphometric and genetic studies have been conducted regarding its population structure within the Atlantic Ocean. These studies reached inconclusive or contrasting results. Molecular analysis studies report the existence of 2 ecotypes, oceanic and coastal (Montes et al. 2016), and apparently more differentiation between these ecotypes than between populations of the Atlantic Ocean and Mediterranean Sea within the same ecotype (Le Moan et al. 2016). Additional analyses based on mitochondrial DNA have found 2 lineages in each area that are not related to the oceanic and coastal ecotypes (Magoulas et al. 2006, Silva et al. 2014). Some differentiation was also obtained between West Galicia and North of Portugal with the Gulf of Cadiz anchovies (Zarraonaindia et al. 2012, Silva et al. 2014). However, currently the results of traditional stock structure analyses are not yet helpful to understand the connectivity between the different anchovy populations, and a large sampling scheme covering the different latitudes and, within each area, different ecotypes and lineages is recommended to obtain useful results (ICES 2022).

The advances in the realism of regional ocean models makes them powerful tools to study larval dispersion and its variability in time, and infer the impact it can have on the explanation of population oscillations and connectivity. Due to the nonexistent or limited swimming capacities of eggs and early larvae, they are primarily transported by ocean currents. Therefore, an accurate representation of ocean currents and their spatiotemporal variability is crucial for capturing the patterns of connectivity during early life stages, which can be achieved using Lagrangian numerical tools that compute particle trajectories in the ocean.

The coastal ocean is characterized by the presence of intense alongshore currents, river plumes, fronts, eddies, and filaments (Peliz et al. 2005, Teles-Machado 2016b, Cordeiro 2015) that significantly influence larval dispersal. These phenomena can only be accurately reproduced through high-resolution ocean model simulations that incorporate the region's most relevant oceanographic processes. The simulation employed in this study includes realistic atmospheric forcing, the discharge of the main rivers

in the region, realistic ocean conditions along the model open boundaries, and it solves the exchange of Atlantic and Mediterranean waters through the Strait of Gibraltar. This simulation has evolved over the years (e.g. Peliz et al. 2007, 2013, Teles-Machado et al. 2016a).

By coupling Lagrangian models with IBMs that simulate biological behaviors observed in laboratory experiments and field data, these numerical tools become more realistic and powerful for studying not only larval dispersion but also the growth and survival of early life stages (e.g. Peck et al. 2018). In the present study, the model incorporates temperature-associated mortality during the egg phase, as well as temperature-dependent growth rates and durations in certain larval stages. The IBM also considers mortality due to starvation, employing a simple condition where larvae in environments with low chl a values are eliminated. However, further research on the trophic ecology of anchovy larvae is necessary (Garrido & van der Lingen 2014), particularly with regard to starvation and the influence of food availability on growth, development, and survival.

Other factors not included in the individual model can impact larval survival and can therefore be considered in future modeling exercises. Food availability for spawning females strongly influences the amount of fat accumulated by sardines prior to the spawning season (Garrido et al. 2007, 2008), with implications for changes in egg quality and consequently larval survival (Garrido et al. 2015b). However, there is still no sufficient knowledge of the differential survival of larvae with respect to female condition, and for that reason, this information was not included in the model. Female age impacts batch fecundity and also the extent of the spawning season, and therefore, the variability in age composition can also be considered in future studies.

In the past, there were single years when anchovy abundance increased, but this did not persist in time, and in following years, the abundance was again low. The increase in abundance off western Iberia occurring in 2016 has persisted until present day. Several top-down and bottom-up mechanisms can explain this. Off western Iberia, the European sardine has been persistently the most abundant coastal pelagic fish species (ICES 2022). The fact that the increase in the anchovy populations coincided with the minimum historical abundance of sardine may be related to the fact that both species have high trophic overlap and may compete for food (Garrido et al. 2015a, Fonseca et al. 2022), at least during the juvenile and adult stages, and because juvenile and adult sardines

are important predators of anchovy eggs in the studied area, impacting egg survival. However, other factors to explain the dynamics of both species must be explored, particularly in light of recent literature showing that it is unlikely that the dynamics of sardine and anchovy species around the world are compensatory enough to cause relevant changes in their abundance (Siple et al. 2020). Other species can also impact anchovy abundance such as the Atlantic chub mackerel, which also has high trophic overlap with anchovy and also includes pelagic fish eggs in the diet (Garrido et al. 2015a, Fonseca et al. 2022). The opposite fluctuation observed for both species in recent years may also be the result of different physical or biological factors impacting their dynamics. It is known that environmental variability significantly impacts sardine recruitment, with high recruitments being generally associated with higher productivity and low temperature during the spawning season (Garrido et al. 2017, Ferreira et al. 2023). Further studies are needed to understand the interannual variability in the connectivity patterns for anchovy to ascertain if the BoB can be a source area for western Iberia recurrently, and to understand the impacts of the local environmental and biological conditions on the survival of the larvae into juvenile and adult stages.

5. CONCLUSIONS

In this study, we investigated the dispersion and survival of European anchovy eggs and larvae in Iberian waters, with a focus on understanding the potential factors contributing to the recent increase in anchovy abundance along the Iberian west coast. By utilizing a combination of oceanic and Lagrangian models coupled with an IBM of anchovy early life stages, we simulated the transport and evolution of anchovy eggs and larvae from the main spawning grounds in the BoB and the GoC for the years preceding the observed increase in anchovy recruitment.

Our findings revealed that anomalous upper-ocean circulation patterns, characterized by strong and persistent eastward currents, played a crucial role in transporting a substantial number of eggs and larvae from the BoB eastward along the Northern Iberian margin. The peak of this transport occurred in June and July 2015, with approximately 8 and 4 %, respectively, of the eggs reaching the Iberian west coast (as larvae). These findings suggest that episodes of intense ocean currents, coinciding with high egg presence, can facilitate the col-

onization of new areas and potentially contribute to the increase in anchovy abundance in the Western Iberian upwelling ecosystem.

This study highlights the importance of considering oceanographic processes and larval dispersal dynamics in understanding the population dynamics of small pelagic fish species like the European anchovy. By integrating oceanic models, Lagrangian transport simulations, and an IBM, we were able to simulate the dispersion and survival of anchovy early life stages, shedding light on the mechanisms underlying the observed changes in anchovy abundance.

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