Impact of individual early life traits in larval dispersal: a multispecies approach using backtracking models.

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Abstract

Dispersal is a key process shaping species population structure. In demersal marine fishes, which usually have sedentary adult phases, dispersion relies on drifting larval stages. However, the dynamics and seasonal variability of seawater masses can greatly determine the connectivity patterns of these species along the same geographic gradient. For this reason, detailed information on the release moment of larvae is needed to obtain accurate patterns of connectivity. In this study, we performed backtracking Lagrangian particle dispersion simulations, with individual-based early life traits data, obtained from otolith reading for 1,413 juveniles of nine fish species belonging to three families (Sparidae, Pomacentridae and Labridae). For each species, individuals had been sampled from four to seven localities in the western Mediterranean Sea between the Gulf of Lion to the Gibraltar Strait. These nine species reproduce in different seasons of the year and their pelagic larval duration (PLD) range from 7 to 43 days. We identified three hydrodynamic units separated by oceanographic discontinuities (Balearic Sea, West Algerian Basin and Alboran Sea) with low settler's exchange according to our simulations, independently of the PLD and reproductive season of the species. Hatching date and PLD showed significant effects on larval dispersal distance and orientation, both at the intraspecific and interspecific levels, highlighting the importance of these variables in determining the geographic origin of individuals. Our multispecies modelling approach adds a step forward for an accurate description of larval dispersion and recruitment, key to understand population resilience and define management strategies.

1 Introduction

In benthic and pelagic marine habitats hydrodynamic processes, e.g. temperature, productivity gradients and turbulent oceanographic features, interact with biological processes affecting species distribution and communities (Cowen, 2002). Physical processes are usually highly variable and their role in generating and maintaining patterns in community structure are essential in marine ecology studies (Shanks and Brink, 2005; White et al., 2019). There is a close relationship between temporal and spatial scales of this physical variability and the apparent high levels of asymmetry and stochasticity in biological processes (Ayata et al., 2010).

Most marine organisms, including most benthic fishes, have low-dispersive adult phases and high-dispersive pelagic larval stages. This dual life history makes early life processes especially pivotal to marine ecology, influencing not only dispersal but also settlement rates, with the resulting effects on community structure (Leis, 1991). In the plankton, the duration of the larval pelagic stage (PLD) determines the length of time that larvae are subject to movement by currents, winds or eddies, and other physical processes, influencing dispersal distances (Gaines et al., 2007; Kinlan et al., 2005; Shanks, 2009). PLD is a key biological factor for larval dispersion since longer PLDs potentially allow larvae to travel larger distances (Selkoe and Toonen, 2011; Shanks, 2009; Treml et al., 2012). PLD can also be influenced by the spawning periodicity or seasonality, potentially affecting dispersal and connectivity (Kough and Paris, 2015), suggesting that hatching time can also be important in dispersal patterns. The dispersive planktonic larval phase(s) is considered as a “black box” in part due to our limited understanding of the relationships between larvae and their environment (Cowen and Sponaugle, 2009; Paris and Cowen, 2004).

Numerous physical mechanisms, e.g. currents, eddies, waves, have been associated with the transport of larvae (Banks et al., 2007; Selkoe et al., 2010), emphasising the importance of their temporal and spatial variability on the larval transport and settlement dynamics (S. Sponaugle and

Cowen, 1996). On the other hand, the release of larvae in the plankton, e.g. hatching period, and their settlement time, show also a large temporal and spatial variability. The coupling of these physical and biological processes are difficult to identify, adding an element of stochasticity to these events (Sponaugle et al., 2005). Therefore, the difficulty to identify these fundamental physical-biological interactions, and how they change along space and time, remains scarcely studied, limiting a more complete knowledge of dispersal processes.

The displacements produced in the course of this pelagic period have been frequently modelled to describe the potential dispersal capabilities of species using Lagrangian-based larval dispersal modelling (Andrello et al., 2017; Calò et al., 2018; Rossi et al., 2014; Schunter et al., 2011a; Treml et al., 2012). Classic approaches use forward simulations, releasing particles from potential source areas and following the current fields to their settlement areas. This methodology has been used to study propagule dispersal and potential impact of climate change (Andrello et al., 2015) or spatial and temporal variability of larval dispersion (Barbut et al., 2019; Di Franco et al., 2012; Ospina-Alvarez et al., 2015). Nevertheless, when the study focuses on particular sampling areas, an alternative approach consists in backtracking the particles from the settlement areas by running the oceanographic model back in time in order to find their potential origin or source areas. Backtracking approximations have been used in larval dispersal modelling at population level to evaluate the effect of oceanographic structures in the area (Holliday et al., 2012), for potential hatch area identification (Calò et al., 2018; Christensen et al., 2007; Fraker et al., 2015), recruitment predictions for fisheries management (Allain et al., 2007) and to reconstruct the environmental history associated to larval growth rate (Payne et al., 2013; Ross et al., 2012).

Recently, these models have included some aspects related to larval behaviour. The natatory capacities are reduced at the initial pelagic phases, and consequently their transport is mainly passive and driven by the ocean currents in the area (Leis, 2007). However, larvae experience an ontogenetic improvement of swimming capabilities and can modify their trajectories at later pelagic phases through vertical migrations (Leis, 2007; Paris and Cowen, 2004) and horizontal orientated swimming (Faillettaz et al., 2018; Staaterman et al., 2012). The mechanisms allowing larval orientation in open waters are badly known, although they could have a notable impact on their final destination, and some authors have suggested the use of odour, sun, or magnetic fields (Bottesch et al., 2016; Faillettaz et al., 2015; Leis et al., 2014; Mouritsen et al., 2013; O'Connor and Muheim, 2017; Paris et al., 2013).

In fish larval dispersal studies, the high temporal and spatial variability of the oceanographic currents makes the accurate estimation of the dates and duration of the larval periods especially important. Otolith (ear bone) microstructure analysis provides a useful tool to obtain this information at individual level. Otoliths of most temperate fishes show daily growth rings and lay a clear settlement band when the individuals change from the pelagic to the benthic stage (Raventos and Macpherson, 2005, 2001; Wilson and McCormick, 1999). Using otolith reading, we can obtain the early life history of each settler, including the day of hatching and settlement, and the PLD. Therefore, the combination of otolith-inferred accurate early-life traits and high-resolution models of oceanographic currents represents an interesting strategy to analyse the dispersal patterns of individual fish larvae.

The Western Mediterranean Sea provides a good system to evaluate the effect of oceanographic processes on larval dispersal (Figure 1). It is connected with the Atlantic Ocean through the Strait of Gibraltar, where there is an inflow of surface Atlantic water and outflow of deeper Mediterranean water (Millot, 1999; Millot and Taupier-Letage, 2005). The circulation pattern and topography along the southern and eastern coasts of the Iberian Peninsula originate three main oceanographic discontinuities in the study area (Figure 1): the Almeria-Oran Front (AOF), the Ibiza Channel (IC) and the Balearic Front (BF). The AOF is a large scale density front located 400 km east of the Gibraltar Strait (GS) and formed by the convergence of the main jet of incoming Atlantic water and waters having recirculated in the Mediterranean Sea (Tintoré et al., 1988). The strength of the AOF varies with the changes affecting the Eastern Alboran Gyre (Renault et al., 2012). East of the AOF, the main current carries Atlantic water eastward along the African coast. Part of this water continues towards the eastern basin through the Sicily Channel, while the other part flows through the Tyrrhenian Sea (Astraldi et al., 1999; Millot and Taupier-Letage, 2005). The circulation in the Western basin is mainly cyclonic, with the Northern Current flowing south-westward along the French and Spanish coasts and bifurcating when reaching the south of the Balearic Sea (Garcia Lafuente et al., 1995; Salat, 1996). The IC, 80 km wide and 800 m depth, corresponding to the passage intersecting the Balearic topographic ridge between Ibiza and the Iberian Peninsula at Cape La Nao, is a key choke point with important exchanges between waters of recent Atlantic origin in the south and saltier waters of Mediterranean characteristics in the northern side (Heslop et al., 2012; Pinot et al., 2002). Finally, the part of the flow directed north-eastward along the northern Balearic shelf edge forms a well-defined density front, the BF, present in the upper 200 m (Figure 1). The dynamic behaviour of these oceanographic discontinuities generate significant intra- and inter-annual variability (Tintoré et al., 2019) that can affect larval dispersal patterns (Su Sponaugle and Cowen, 1996).

In the present work, and using a multispecies approach, we evaluated how differing hatching dates and pelagic larval durations interact with variable oceanographic features to influence larval dispersal patterns throughout the Western Mediterranean. We modelled individual-based potential larval movement of 1,413 settlers of nine common coastal fish species along the western Mediterranean Sea, reproducing in different seasons and with different PLD. We used individual-based information on early life traits (day of hatching and settlement, and PLD) from otoliths readings (Raventos et al., 2021). We backtracked each settler running Lagrangian trajectories back in time using currents from a high-resolution model of the Western Mediterranean Sea (Juza et al., 2016; Mourre et al., 2018), in order to find their potential origin and to evaluate the effect of the oceanographic variability. Our specific objectives were: a) to determine the effect of the currents and oceanographic structures and their seasonal variability on dispersal patterns and b) to assess the influence of interspecific and intraspecific variation of hatching date and PLD on dispersal potential of the nine species. We hypothesized that the dispersal patterns of fishes would be influenced by variations in hatching date and PLD, between species as well as within species, coupled with changes in oceanographic conditions, and thus should be considered for accurately modelling dispersal.

2 Materials and Methods

2.1 Species data

In the present work we modelled the dispersal capacity of nine coastal co-occurring fish species from three different families along the western Mediterranean Sea: (1) Sparidae, the common two-banded seabream *Diplodus vulgaris*, the white seabream *D. sargus*, the sharpsnout seabream *D. puntazzo*, the salema *Sarpa salpa* and the saddled seabream *Oblada melanura*; (2) Pomacentridae, the damselfish *Chromis chromis*; (3) Labridae, the Mediterranean rainbow wrasse *Coris julis*, the ocellated wrasse *Symphodus ocellatus*, and the East Atlantic peacock wrasse *S. tinca*.

We based our study on the individualized early life traits information of 1,413 settlers from these nine species (Table S1) obtained in the study of (Raventos et al., 2021): *Diplodus vulgaris* (n=174), *D. sargus* (n=175), *D. puntazzo* (n=206), *Sarpa salpa* (n=72), *Oblada melanura* (n=216), *Chromis chromis* (n=146), *Coris julis* (n=150), *Symphodus ocellatus* (n=177) and *S. tinca* (n=97). Settlers of all sizes were collected at the end of the settlement period of each species to ensure the representation of the entire hatching period. We mostly restricted our analyses to individuals born during the same reproductive period for a given species with the exception of S. *tinca* where the samples from Blanes were included despite being from a different year, to be able to model at least four locations for each species, and *S. ocellatus* where the samples from La Herradura were used (Table S1). For each individual, the age at sampling was determined by counting the total number of bands in their otoliths, from core to margin. Their individual PLD and settlement day was determined by counting the number of daily rings visible between the core and the settlement mark, and ages were used to calculate their day of birth. The settlers of these nine species were sampled at seven locations of the Western Mediterranean Sea, from Colera in the Gulf of Lion (42°40’N, 3°11’E) to La Herradura (36°44’N, 3°44’W) in the Alboran Sea (Figure 1, Table S1). Some species were not collected in all locations (e.g. *Sarpa salpa*, 4 locations) due to the lack of settlers’ availability during the sampling periods in those localities. The nine selected species have different pelagic larval duration (PLD) and reproduce in different seasons of the year, with no large differences found between localities within species (Figure 2, Table S1).

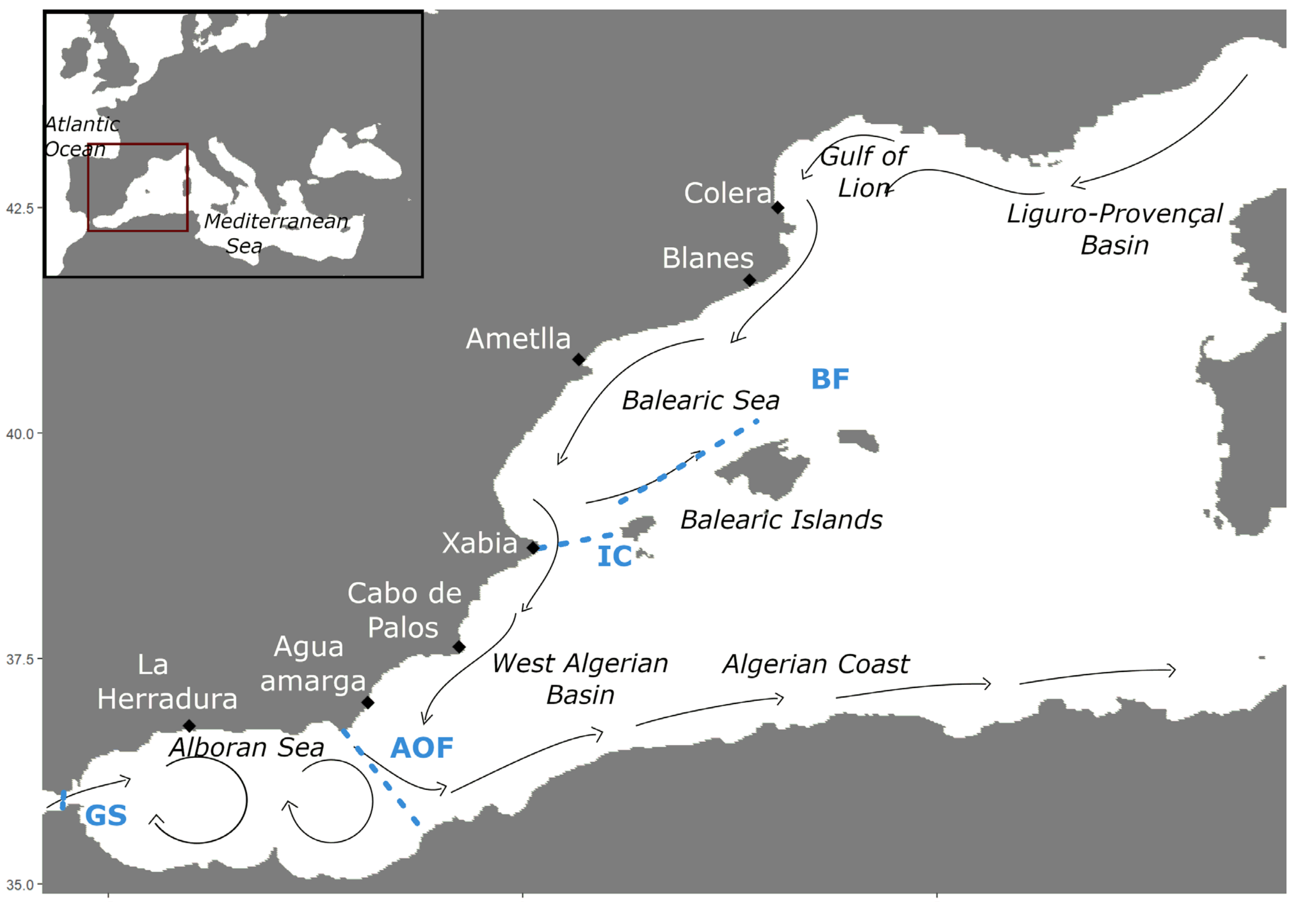

Figure 1. Map of the sampling locations and main schematic oceanographic currents in the Western Mediterranean Sea. The red square in the map of Europe correspond to the enlarged map of the analysed area. Diamonds: sampling localities; Dashed blue lines indicate oceanographic barriers; BF:

Balearic front; IC: Ibiza channel; AOF: Almeria-Oran front; GS: Gibraltar Strait. Currents are represented as thin black lines with arrows identifying its main direction (Millot, 1999).

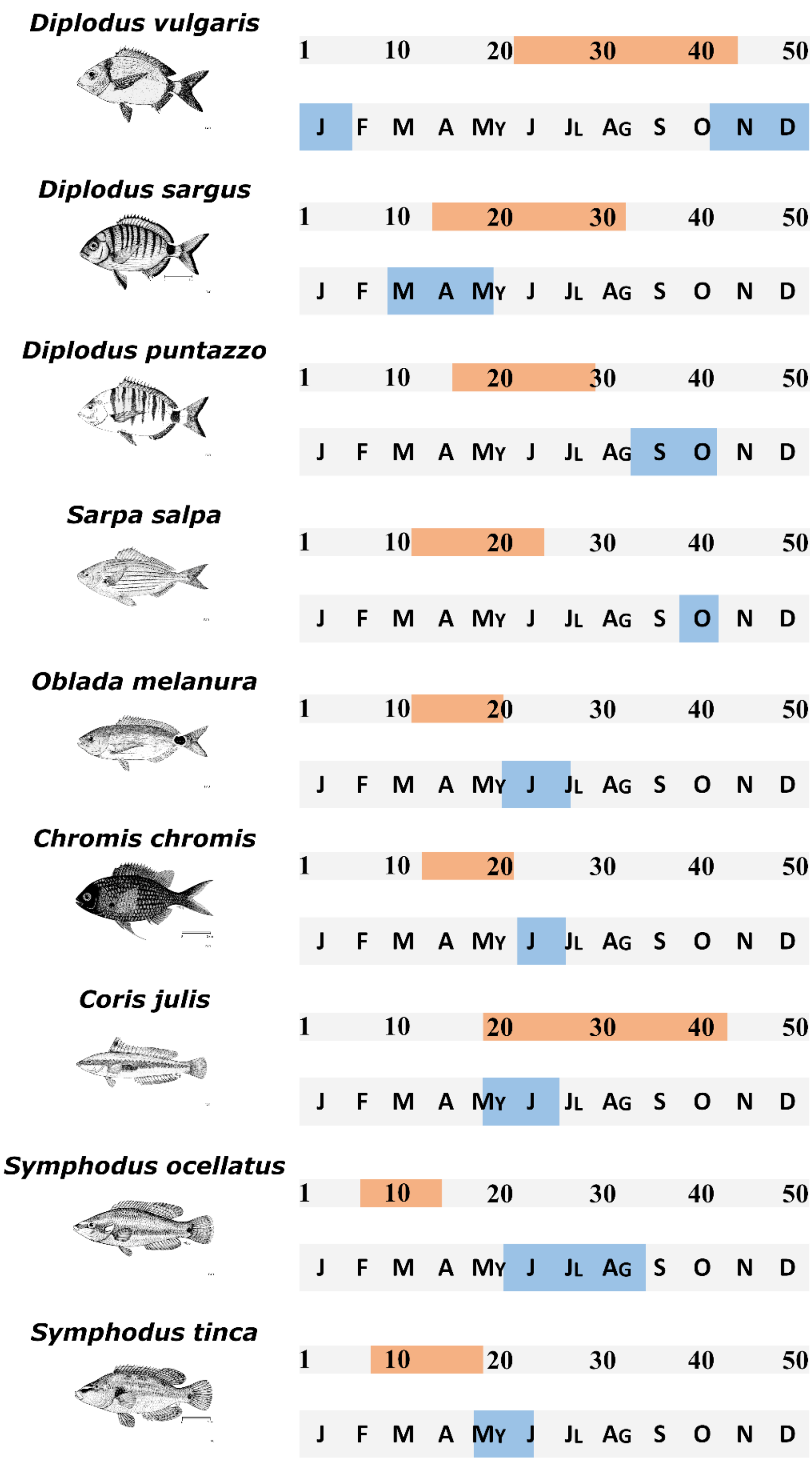

Figure 2. Ranges of Pelagic larval duration (PLD) in days (orange bar) and Hatching season in months (blue bar) for each species obtained from (Raventos et al., 2021). Species' images obtained from (Bauchot, 1987; Schneider, 1990).

2.2 Modelling

For our modelling analyses we used the ocean current fields provided by the Western Mediterranean OPerational forecasting system (WMOP) (Juza et al., 2016; Mourre et al., 2018), developed at the Balearic Islands Coastal Observing and Forecasting System (www.socib.es, Tintoré et al., 2013). WMOP uses 5km-resolution surface atmospheric forcing from the HIRLAM model of the Spanish Meteorological Agency AEMET, with a temporal resolution of 3h before March 2017 and 1h afterwards. In particular, WMOP near-surface currents include the effects of the winds blowing on the sea surface. The boundary conditions are provided by the outputs of the larger scale Mediterranean model from the Copernicus Marine Service (Clementi et al., 2017). WMOP has a spatial coverage from Gibraltar strait to Sardinia Channel (35°N-44.5°N, 6°W-9°E) and a horizontal resolution of around 2 km and 32 sigma-levels in the vertical dimension. Detailed assessments of the WMOP model from the basin to the coastal scales have demonstrated that the model was able to represent the mean large-scale surface circulation and the associated modes of variability with a satisfactory level of realism (Aguiar et al., 2020; Juza et al., 2016; Mourre et al., 2018). Comparisons with satellite altimetry have shown that the model was generating realistic statistics of large eddies and accurate magnitude and spatial variability of eddy kinetic energy. At the coastal scales and based on surface drifter data, the model was found to represent small scale processes such as topographically driven coastal eddies or localized sea breeze effects close to Mallorca Island. High-Frequency (HF) radar data have demonstrated that the model was able to properly represent the position of the Northern Current and the coastal flow intensification in the coastal region off Ebro delta. In the Ibiza Channel, while some overestimation of the northward surface flow was highlighted based on HF radar measurements, the seasonal and interannual variability of the Western Intermediate Water was positively evaluated in the model using underwater glider time series (Juza et al., 2019). Daily updated comparisons with satellite SST, altimetry, ARGO profiles, mooring time series, glider sections and coastal currents from HF radars in 3 different locations (Gibraltar strait, Ibiza Channel and Ebro Delta) are available at https://socib.es/?seccion=modelling&facility=wmedvalidation.

Backtracking individual-based Lagrangian particle dispersion simulations were performed with the WMOP data using the TRACMASS software (Döös and Jönsson, 2013), implemented through the TracPy interface (Thyng and Hetland, 2014). Each individual simulation considered the following data: release point (sampling locality), date (settlement date) and simulation duration (pelagic larval duration) based on each individual sample and otolith data. Simulations were then performed for different periods of the year in 2014, 2015 and 2017 according to individual data (Table S1, for full otolith data access, see Raventós et al., 2021). For each individual we simulated the release and movement of 10^3 particles from their settlement site to their potential source origin during their settlement and hatch dates. We added random velocity fluctuations to simulations in order to account for model uncertainties and unresolved processes. The magnitude of the random turbulent velocities was the result of the specific calibration experiments performed in the framework of the development of the TRACMASS algorithm (Döös et al., 2011; Döös and Engqvist, 2007), combined with our own experience with trajectory modelling using currents from the 2km resolution WMOP model when compared to real drifters (Mourre et al., 2018). The random coefficients were fixed so as to produce a standard deviation of random velocity fluctuations which reaches 0.8 times the standard deviation of the WMOP model velocities along the trajectories. During the last half of the larval period (first part of the backtracking simulation), we added a velocity vector towards the coastline, based on the larval Critical speed (Ucrit) of each species, representing larval swimming abilities. Ucrit values were obtained from laboratory studies, including the same or closely related species for each family, Sparidae and Pomacentridae (Faillettaz et al., 2018), and Labridae (Leis et al., 2011). We considered $\frac{1}{2}$ Ucrit as the mean velocity directed towards the coast when the particle was less than 5 km off the coastline. Therefore, we considered that within this distance larvae are capable of a good directional orientation due to the detection of more precise clues like odour or sound (Kingsford et al., 2002). For grid points more than 5km off the coastline, we assumed a velocity of $\frac{1}{4}$ Ucrit. Reducing velocities at further distances are the result of assuming a minor net displacement towards the coast due to reduced orientation capabilities and considering a bigger importance of individual stochasticity. Larvae of most of the studied species are usually concentrated in the upper 10 m of the water column, with very limited or negligible diel vertical migration (Sabatés and Olivar, 1996). Thus, particles representing fish larvae were simulated at fixed depths for the full advection period (Table S1) following observed mean larval depth (Olivar et al., 2010; Sabatés and Olivar, 1996).

In order to get insights into the impact of the oceanographic variability and evaluate the extent to which the year of study represents a typical current field, we have analysed the transport across the two oceanographic discontinuities (IC and AOF) separating the three hydrodynamic units present in the area (see results) from 2014 to 2018. The transports were computed at AOF (from -2.13E/36.75N to -0.79E/35.77N) and IC (from -0.15E/39N to 1.31E/39N) from model surface to bottom, separating northward and southward flows and integrating the product of model cross-section velocities by the surface of 2km-long cells.

2.3 **Data analyses**

We generated a total of 1000 backtracking particle trajectories for each of the 1,413 sampled individuals of the nine species. Since the studied species do not live nor reproduce in open sea, we only kept for posterior analyses those particles originating in coastal waters (less than 2 km to the nearest land point) in the backtracking simulations, using nn2 function in the R package ‘RANN’ 2.6.1 (Arya et al., 2019). We plotted potential origin maps of settlers for each species in R 3.4.4 (R Core Team, 2018) using the following packages: ‘ncdf4’ 1.16 (Pierce, 2017) for netCDF files reading and processing, ‘reshape’ 0.8.7 (Wickham, 2007) and ‘dplyr’ 0.7.8 (Wickham et al., 2018) for data reorganization, ‘magrittr’ 1.5 (Bache and Wickham, 2014) for function construction, ‘rgdal’ 1.3-1 (Bivand et al., 2018) for geoprocessing and ‘ggplot2’ 3.1.0 (Wickham, 2016) for plotting. Furthermore, we plotted the mean current velocity of the WMOP for each species across its planktonic period assessed from the otolith data with the same methodology, using a ‘viridis’ R package scale (Garnier, 2018) for colour scale construction.

For each individual, we calculated the mean dispersal distance and orientation considering the backtracking simulations originating in coastal waters. The angle of each particle was defined in relation to the Northwest in each sampling locality to avoid that the range of potential orientations within any location included the zero value, and thus this parameter always increases as the direction changes clockwise. In order to evaluate the effect of PLD and hatching date on mean dispersal distances and orientations we performed generalized lineal mixed model (GLMM) tests with the R package ‘lme4’ 1.1-23 (Bates et al., 2015). We first built an analysis with all data considering species and locality as random factors (Dispersal distance/Dispersal orientation ~ PLD + Hatching date + Species + Locality). Additionally, we carried out an analysis for each species separately to assess the mean dispersal distance and orientation as a function of PLD and hatching date while defining localities as a random factor (Dispersal distance/Dispersal orientation ~ PLD + Hatching date + Locality).

To assess the effect of oceanographic discontinuities on dispersal patterns we considered three sampled areas and seven source zones for simulated particles. We defined the three sampled areas as the three oceanographic regions separated by the oceanographic discontinuities along the study area (Figure 1):

(1) Alboran Sea: from the Gibraltar Strait (GS) to the Almeria-Oran Front (AOF), (2) West Algerian Basin: Iberian Peninsula area from the AOF to the Ibiza Channel (IC), and (3) Balearic Sea: Iberian Peninsula area from IC to Gulf of Lion. On the other hand, we delimited the seven potential source coastal areas (Figure 1): (1) Atlantic Ocean (Atlantic particles arriving through GS), (2) Alboran Sea (from GS to AOF), (3) West Algerian Basin (Iberian peninsula from AOF to IC), (4) Algerian coast (northern Africa from AOF towards the east), (5) Balearic Sea (Iberian peninsula from IC to Gulf of Lion), (6) Balearic Islands and (7) Liguro-Provençal Basin (from the Gulf of Lion towards the northeast). For each species we tested for differences in individual mean dispersal distances between areas using a Kruskal-Wallis test and a Dunn post-hoc test in R. We evaluated with the same test the variability of oceanographic transport across the IC and AOF in different years (2014-2017) during the whole pelagic period for each species (considering Hatching date and PLD according to our data). We plotted in a chord diagram the links between the source and sample areas with the R package 'circlize' 0.4.9 (Gu et al., 2014).

3 Results

3.1 Hydrographic setting and backtracking trajectories

We generated a total of 1,413,000 backtracking trajectories from which we kept a total of 410,627 trajectories originating in coastal waters (Figure 3), to be used in further analyses. Individual mean dispersal distance and orientation were calculated with these remaining trajectories, with standard deviations inside individuals around 48.3 km (min 0.3 km, max 370.6 km) for dispersal and 3.5 rad (min 0.4 rad, max 5.9 rad) for orientation. We observed that most settlers had their natal origin in the same oceanographic region where they were born (57.2%-99.9%), indicating a high level of self-recruitment at the regional level, with some differences across species and regions (Figure 4, Table S2). In the Balearic Sea, the simulations indicate that most of the settlers were from the same region

(85.3% ± 15.3), but some could also have arrived from the Liguro-Provençal area (14.5% ± 15.0), and a small fraction from the Balearic Islands (0.3% ± 0.6), without any contribution from other source areas. The WMOP maps showed that the Northern Current (Figure 1) exhibited a constant pattern (Figures S1). This current followed the continental slope of the North-western Mediterranean Sea from the Ligurian Sea towards the Balearic Sea and recirculated when it reached the Ibiza Channel. As expected, the proportion of settlers from the Liguro-Provençal area varied across localities and decreased from the northernmost locality (e.g. Colera) to the southernmost one (e.g. Ametlla) (Figure 3). Differences among species were found from settlers originating in the Liguro-Provençal basin with a higher frequency in *D. vulgaris* and *C. chromis* (Figure 4, Table S2). Differences among species were also found for settlers originating in the Balearic Islands as for *D. puntazzo* and *D. vulgaris,* which were able to cross the Balearic Front from the Balearic Islands to the continental coast in higher frequency (Figure 3, Table S2).

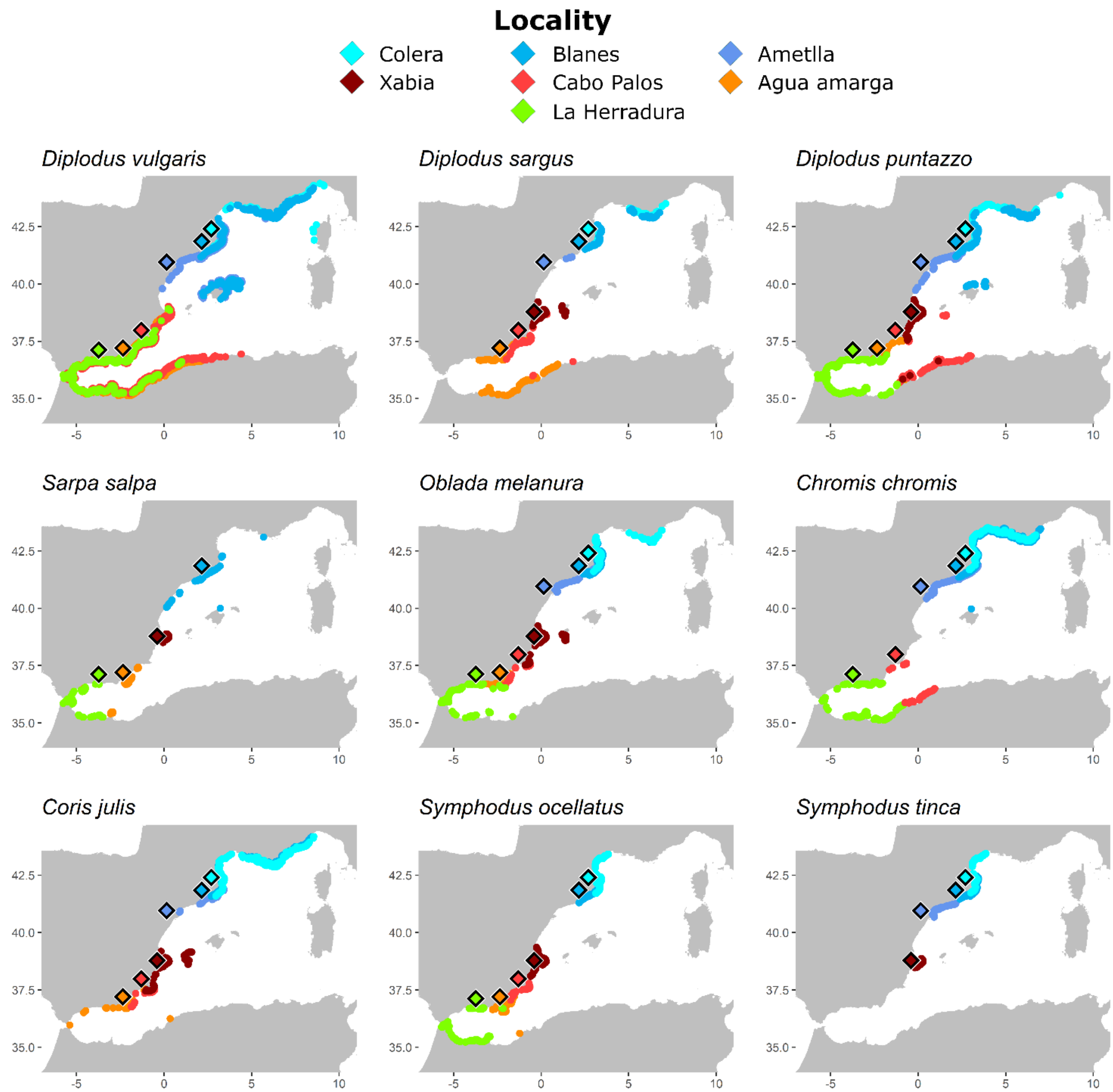

Figure 3. Potential coastal origin (dots) of the settlers captured in the different sampled localities (diamonds) as assessed by backtracking simulations for each species.

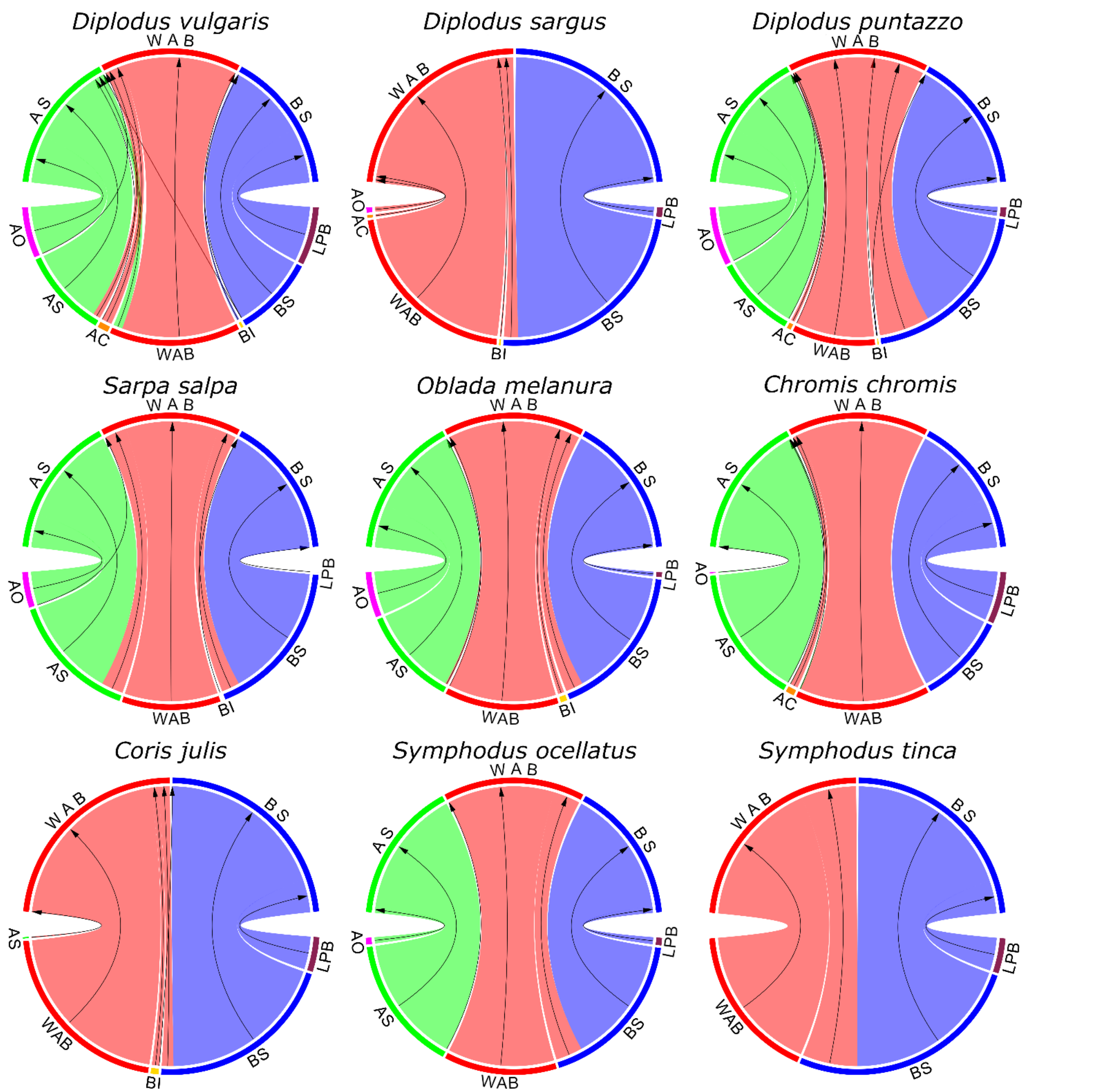

Figure 4. Dispersal plots for all nine species to the sampled areas of settlers (upper half of each circle) from their potential source coastal areas (lower half of each circle) according to the backtracking simulations. Arrows indicate larvae directionality and bottom bar colours delimit the source areas. AO: Atlantic Ocean (pink), AS: Alboran Sea (green), AC: Algerian Coast (orange), WAB: West Algerian Basin (red), BI: Balearic Islands (yellow), BS: Balearic Sea (blue), LPB: Liguro-Provençal Basin (purple). Circle and upper bar colours indicate sampled settlement areas.

The Western Algerian Basin also had a high proportion of self-recruitment (80.1% ± 11.3) but coupled with some incomes from other source areas (Figures 3-4). The transport across the Ibiza channel connected the Balearic Sea and the Western Algerian basin. We found a considerable potential contribution of settlers from the Balearic Sea, crossing the Ibiza Channel (13.9%± 12.6). The higher pass of larvae from the northern to the southern side of the Ibiza channel was detected in *S. tinca* and *D. puntazzo* (Figure 4, Table S2). A small contribution from the Balearic Islands was observed (1.0% ± 1.8), being higher in *O. melanura* and *C. julis* (Figure 4). Moreover, for the three *Diplodus* species and *Chromis chromis* we detected a certain amount of settlers (3.4% ± 3) from the Algerian coast (Figure 4), specially arriving at Cabo de Palos and Agua amarga sites (Figure 3). Finally, the potential proportion of settlers from the Alboran Sea through the Almeria-Oran Front was small (3.1% ± 5.3).

The Alboran Sea was characterized by the presence of two anticyclonic gyres between Gibraltar Strait and Almeria-Oran Front. The western gyre was strong and present during the larval period of all species while the eastern gyre was milder (Figure S1). Therefore, the gyres and the AOF delimited a sub-basin that appeared to be badly connected with the rest of the Western Mediterranean Sea. However, Almeria-Oran Front decreased its strength when the eastern anticyclonic gyre faded in autumn-winter (2014-2015) allowing a transport of settlers in both directions, as it was observed during the larval period of *Diplodus vulgaris* (Figures 4, S1). A high number of settlers in the Alboran Sea were self-recruits (75.3%± 17.8), nonetheless, we found a good number of potential incoming settlers from the Atlantic Ocean through the Strait of Gibraltar (23.3%± 16.9), common in most of the species (Figure 3). Thus, we can consider that the three sampling regions are three hydrodynamic units.

3.2. Influence of early life traits on dispersal distances and orientation

The global GLMM for dispersal distances explained a high proportion of the variance found in our data (R^2=0.814). In this model, all variables (PLD, hatching date, and the two random factors, locality and species) had a significant effect (Table 1). Most of the variability was explained by the random factors, as the variance explained by the fixed factors was only R^2=0.045. The species-specific GLMM showed that PLD positively and significantly affected dispersal distance in all species (Table 2). The hatching date had a significant effect on dispersal distances in most species with a few exceptions as for *Diplodus vulgaris*, *Sarpa salpa* and *Coris julis* (Table 2). The sign of the correlation changed in some cases, for instance species such as *Diplodus sargus* and *Symphodus tinca* presented significant negative correlations while the rest were positively correlated. Interestingly, these two species reproduce in spring suggesting that individuals hatching early in the season disperse over larger distances. The species with significant positive correlation (*Diplodus puntazzo*, *Oblada melanura*, *Chromis chromis* and *Symphodus ocellatus*) reproduce, at least partially, in summer, suggesting that individuals hatching later disperse larger distances. For all species differences between localities were significant and the full models presented high R^2 values. We observed different contribution of the random factors across species as compared with the variance explained by their fixed factors (Table 2). For instance, in *Symphodus tinca* the variance explained by PLD and hatching date was very high (R^2=0.72) while in *S. ocellatus* was very low (R^2=0.08).

Table 1. Results of the generalized lineal mixed model (GLMM) for the dispersal distance and dispersal orientation We show the significance of the influence (p-value) of the fixed (PLD and Hatching date) and random (Species and Locality) factors on dispersal distance and orientation as well as the adjusted R^2 o the models including all factors (Full model) or only fixed factors.

Factors		Dispersal distance	Dispersal orientation
Fixed	PLD	**< 2.2E-16**	0.395
	Hatching date	**1.20E-05**	**2.05E-04**
Random	(Species)	**< 2.2E-16**	**< 2.2e-16**
	(Locality)	**< 2.2E-16**	**< 2.2e-16**
R^2	Fixed factors	0.045	0.007
	Full model	0.814	0.52

Table 2 Results of the generalized lineal mixed model (GLMM) for the dispersal distance and dispersal orientation for each one of the studied species. We show the β coefficient of the influence of the fixed factors (PLD and Hatching date), in bold when there is a significant effect. We also indicate the influence (p-value) of Locality on dispersal distances and the adjusted R^2 of the full model and only for fixed factors.

Species	Dispersal distance ~ PLD + Hatching date + (Locality)					Dispersal orientation ~ PLD + Hatching date + (Locality)				
	PLD	Hatching date	Locality	R^2 fixed	R^2 full	PLD	Hatching date	Locality	R^2 fixed	R^2 full
Diplodus vulgaris	**19.56**	0.31	**1.46E-06**	0.24	0.47	0.02	**0.55**	**7.58E-16**	0.03	0.58
Diplodus sargus	**20.85**	**-1.15**	**< 2.2e-16**	0.33	0.87	-0.02	0.44	**1.68E-10**	0.05	0.53
Diplodus puntazzo	**8.80**	**1.66**	**< 2.2e-16**	0.03	0.67	-0.09	0.50	**< 2.2e-16**	0.01	0.67
Sarpa salpa	**18.11**	2.21	**1.21E-04**	0.14	0.40	-0.14	-0.22	**1.01E-06**	0.00	0.54
Oblada melanura	**12.75**	**2.45**	**< 2.2e-16**	0.10	0.71	**-0.32**	**-1.64**	**< 2.2e-16**	0.14	0.69
Chromis chromis	**18.42**	**2.60**	**< 2.2e-16**	0.11	0.67	-0.20	-0.48	**7.24E-16**	0.01	0.57
Coris julis	**6.25**	-1.53	**1.70E-06**	0.13	0.62	0.11	-0.54	**1.53E-12**	0.03	0.53
Symphodus ocellatus	**18.47**	**0.54**	**< 2.2e-16**	0.08	0.85	0.01	0.43	**6.20E-12**	0.02	0.44
Symphodus tinca	**19.53**	**-1.88**	**4.33E-02**	0.72	0.79	0.35	0.57	**2.55E-06**	0.01	0.52

Dispersal distances among hydrodynamic units were significantly different for most species, as assessed with the Kruskal-Wallis and post-hoc Dunn tests (Figure 5, Table S3). Individuals settling in the Alboran Sea showed the largest dispersal distances. The patterns in the other two basins varied across species. Settlers of the three *Diplodus* species had significantly longer dispersal distances in the West Algerian Basin than in the Balearic Sea, whereas *Oblada melanura, Chromis chromis*, *Coris julis* and *Symphodus ocellatus* had the reverse pattern (Figure 5). *Sarpa salpa* and *Symphodus tinca* showed no differences in mean travelled distance by recruits from these two basins.

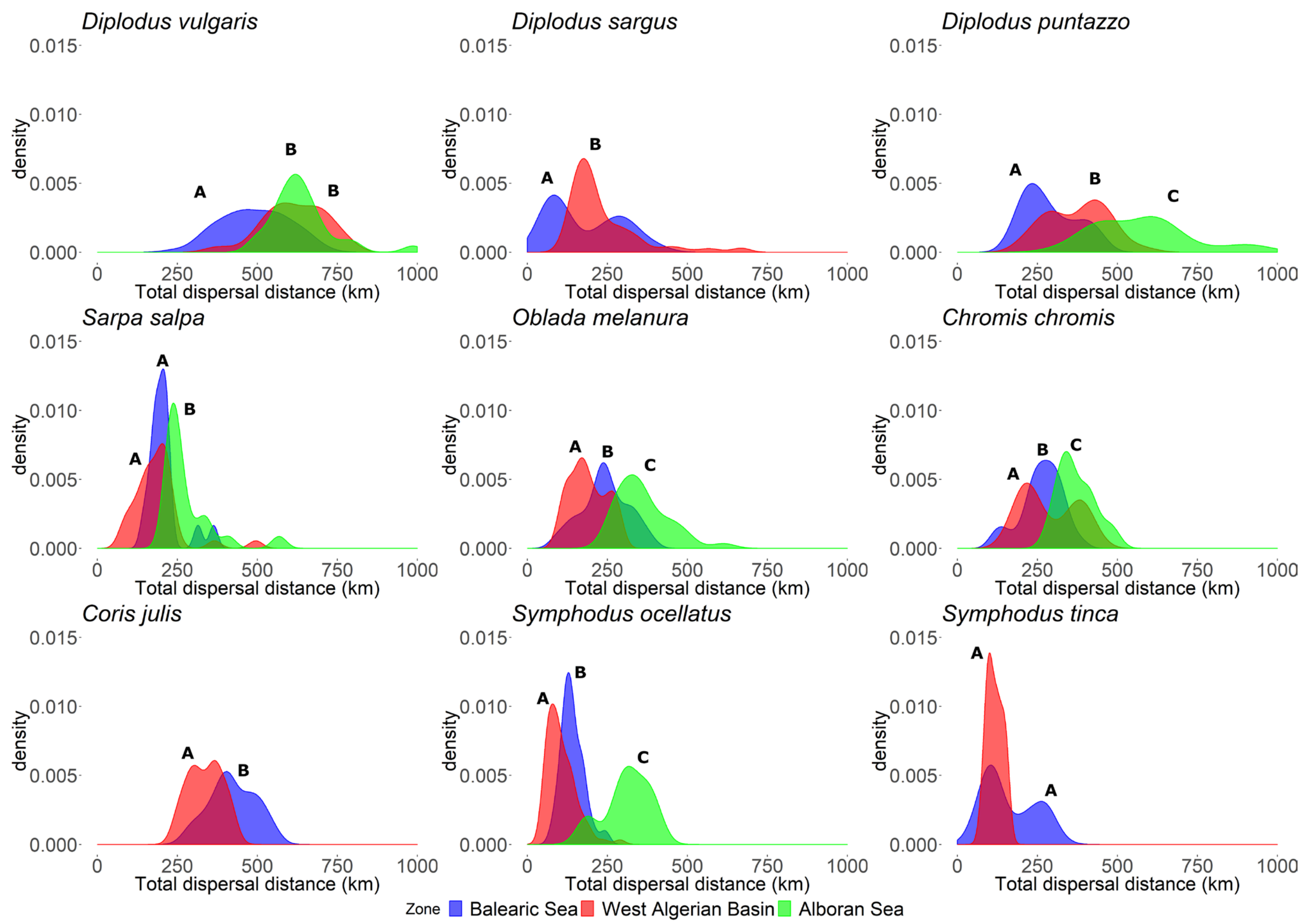

Figure 5. Dispersal distance distributions of the individuals sampled in the three hydrodynamic units based on the individual backtracking simulations for each species. Different letters within each species indicate statistically significant differences in larval dispersal distances between hydrodynamic units (post-hoc Dunn tests).

Dispersal orientation was significantly affected by hatching date and the two random factors (locality and species), but not by PLD (Table 1). The full model explained a good proportion of the variance (R^2=0.52) although mainly due to the random factors, since the effect of the fixed factors was small (R^2=0.007). For the species-specific GLMM significant differences in dispersal orientation were found among localities for each species (Table 2). However, significant effects for PLD were only found in *O. melanura,* the correlation being negative with dispersal orientation. Thus, individuals in this species with longer PLD originate preferentially northwards, since the 0 angle is directed to north-west and consequently small values suggest a northern origin. The angles between 315-360 degrees which indicate a northern origin could be misleading. However, only 5.34% of individuals have values in this range and therefore should not have a relevant impact on our results. The hatching date in these analyses were only significant for *O. melanura* and *D. vulgaris,* with negative and positive correlations respectively (Table 2). Consequently, in all species but *O. melanura*, the variance explained by the fixed factors on dispersal orientation was small although the full model explained a good proportion of the variance with regressions ranging from R^2=0.44 in *S. ocellatus* to R^2=0.69 in *O. melanura*.

Overall, the variance explained by PLD and hatching date on dispersal distance and orientation was small within species. However, at the individual level these two factors can have different effects in the final dispersal. For instance, individuals of *O. melanura* from Xabia with the same hatching date but different PLD had different displacement direction and longer dispersal distances with longer PLD as expected (Figure S2). Individuals from the same locality with the same PLD but different hatching date, changed also dispersal direction and distance (Figure S2). This pattern suggests that at a fine scale (*e.g.* locality scale) hatching date and PLD can have an important role in determining the origin of settlers mediated by changes in environmental conditions that at a larger scale remains undetectable.

The oceanographic transports during 2014-2017 showed monthly, seasonal and interannual variability across both the IC and AOF, with more stable net transports across the AOF and a higher variability across the IC (Figure S3). For each species, during its whole pelagic period, the K-W tests did not show significant differences across years in the AOF, while significant differences were observed in the IC (Table S4).

4 Discussion

Here, we measured the dispersal abilities (and thus, potential connectivity) in nine common fish species in the Mediterranean Sea by individual-based simulations. We show that the three sampled areas defined by the oceanographic discontinuities, Balearic Sea, West Algerian Basin and Alboran Sea, present low exchange of recruits in all species and should be considered three hydrodynamic units. Nonetheless, for some species we observed a higher directional exchange among them due to the temporal decrease in the front strength. We found significant influence of early life traits (PLD and hatching date) and sampling area in dispersal distance and orientation between and within species. Our results demonstrate that individual based information on life-history traits is fundamental to model dispersal and evaluate connectivity at a fine and regional scale.

The low level of larval exchange among hydrodynamic units in all species suggests that self-recruitment is the common mechanism of larval replenishment in Mediterranean coastal fishes. Using molecular techniques, such as microsatellite loci, high levels of self-recruitment had been found in some fish species in the western Mediterranean (e.g. *Tripterygion delaisi*, *Serranus cabrilla*) suggesting that a high proportion of the larvae remained close to, or never left, their natal spawning area (Carreras-Carbonell et al., 2007; Schunter et al., 2011a). Similar results were observed in coral-reef fishes (e.g. Buston and Elith, 2011; Jones et al., 2005, 1999; Swearer et al., 1999). For instance, Almany et al., 2007 found by stable isotope analyses that for species with both short (<2 weeks *Amphiprion percula*) and long (>1 month, *Chaetodon vagabundus*) PLD ca. 60% of settled juveniles were spawned at Kimbe island (Papua New Guinea), further confirmed by parentage analyses (Berumen et al., 2012; Planes et al., 2009). Similar high level of self-recruitment was observed by parentage analyses within a network of marine reserves on the Great Barrier Reef in *Plectropomus maculatus* and *Lutjanus carponotatus* (Harrison et al., 2012). Nevertheless, with the same assignment technique, other species showed a smaller proportion of self-recruitment in the same area, e.g. *Amphiprion polymnus* (Saenz-Agudelo et al., 2012) indicating a certain variability in these patterns probably species specific.

In our work, we found that the two oceanographic discontinuities present in the study area (Ibiza channel and Almeria-Oran front) determined the presence of three hydrodynamic units (Balearic Sea, West Algerian Basin and Alboran Sea) with low larval exchange in all species. Other studies have found different and larger hydrodynamic units in the same area, when simulating particle movement in different years and considering species-unspecific PLD models (Rossi et al., 2014). Temporal changes in currents and front strength in different species can account for changes in larval exchange. This seems the case of *D. vulgaris* reproducing in winter where the AOF allowed more larval exchange in both directions according to our backtracking modelling. This front had been previously reported to decrease its strength or even disappear in winter (Fernández et al., 2005; Renault et al., 2012; Tintore et al., 1988). In our study, we observed that the decrease in strength in winter of 2014-2015 was due to the fading of the eastern anticyclonic gyre in the Alboran Sea, allowing the transport of particles in both directions (Figures S1, Table S2). Nonetheless, a previous genetic study with *D. vulgaris* found strong genetic differentiation across this front (Galarza et al., 2009) suggesting that interannual variation might be relevant. Oceanographic variability across years and seasons (Botsford et al., 2009) can modify the level of self-recruitment. Inter-annual changes in gene flow across the AOF have been reported for other species such as the crab *Liocarcinus depurator* (Pascual et al., 2016), or the sea urchins *Paracentrotus lividus* (Calderón et al., 2012) and *Arbacia lixula* (Pérez-Portela et al., 2019), where temporal genetic population differentiation was associated to changes in water circulation patterns across years. Nonetheless, we did not observe significant changes in potential larval transportation across this oceanographic discontinuity during the analysed period (2014-2017) suggesting that this front is more permanent despite the reported interannual variation.

Oceanographic variability was also detected across the Ibiza Channel, where the meridional water transport was observed to change at weekly, seasonal and interannual scales (Balbín et al., 2014; Heslop et al., 2012; Pinot et al., 2002). We observed a high proportion of settlers in the West Algerian Basin coming from the Balearic Sea in *Symphodus tinca*, whereas in *S. ocellatus*, from the same genus and with similar PLD, the proportion was lower (Figure 4). Given that these two species reproduce at different seasons, temporal seasonality in front strength can account for the capacity to cross the Ibiza Channel. This higher capacity of *S. tinca* in crossing southwards the IC is in accordance with the lower genomic differentiation found in this species in comparison to that found in *S. ocellatus* (Torrado et al., 2020). Different patterns of genetic differentiation have been reported across IC for different fish species, for instance no genetic differentiation was found for *Epinephelus marginatus* (Schunter et al., 2011b), whereas strong genetic differentiation was detected for *Serranus cabrilla* (Schunter et al., 2011a). Moreover, temporal variation has been detected in the northern site of the IC for *Liocarcinus depurator* further indicating that annual changes might promote differential exchange and connectivity (Pascual et al., 2016). This area is a highly dynamic transition area with variable transport in strength and direction as we have observed at different temporal scales (Figure S3) affecting dispersal patterns in all species. Therefore, the three hydrodynamic units defined in the western Mediterranean Sea by these two oceanographic discontinuities should not be considered as closed systems, but as a net with seasonally and yearly variability in connections.

Nevertheless, large-scale circulation patterns are not the unique factors influencing larval dispersal. In our study, we found a global relationship between early-life traits and dispersal distances and orientations. Our results demonstrate that species with longer PLD have greater dispersal distances, in accordance with previous studies (e.g. Pascual et al., 2017; Siegel et al., 2003). Moreover, hatching date also influenced dispersal distances as indicated in our global analysis, which could be related to temperature in modifying PLD through changes in larval growth rate, as with increasing temperature larvae grow quicker to their settlement size (Raventos et al., 2021; Schunter et al., 2019). Nonetheless, different impact of hatching date was obtained at the intraspecific level, with no influence for the two species with larger PLD (*D. vulgaris* and *C. julis*) and for *S. salpa*. Moreover, the regression coefficient changed in sign across species with those reproducing in spring showing negative correlations with distance so that individuals hatching earlier experience colder temperatures, show longer PLD than individuals hatching later in the season and consequently disperse larger distances. Similarly *D. puntazzo* reproducing in autumn presents a positive correlation that could be also explain with its relation to temperature. On the other hand, those species reproducing in summer (*O. melanura*, *C. chromis* and *S. ocellatus*) have positive correlations, indicating that individuals hatching later have larger dispersal distances. Since temperature increases over time along this period with a corresponding decrease of PLD (Raventos et al., 2021), the effect of hatching date on dispersal distance is probably due to interaction of other factors as could be, for example, changes in productivity affecting feeding resources (Robitzch et al., 2016), but further research is necessary to unveil the causes.

The dispersal distances also varied at intraspecific level among our hydrodynamic units. These differences seemed to be related with two main factors: (1) differences in circulation patterns and oceanographic currents strength to which the larvae were exposed in each area, and (2) the distance and direction of available source areas of larval hatching. For instance, the larvae in the Alboran Sea had for most species longer dispersal distances than larvae in the other two areas. These longer distances were mostly due to the presence of one permanent and one semipermanent eddy in this zone (Tintore et al., 1988; present study) making larvae to travel longer distances before reaching the coast. Thus, longer dispersal distances do not imply more connectivity across hydrodynamic units since eddies can strongly contribute to self-recruitment by promoting larval retention within these areas. Moreover, eddies can further impact on populations, since they can generate recruitment peaks in punctual moments (Sponaugle et al., 2005) and increase larval development rate and settlers' survivorship (Shulzitski et al., 2016, 2015). Furthermore, the communication between Balearic Sea and Balearic Islands was probably mediated by temporal eddies occasionally formed in this area (e.g. Amores et al., 2013; Pascual et al., 2002) which can coincide with some species' larval periods as observed in our models.

We found that hatching date can also significantly affect dispersal orientation in the global model, and subsequently the geographic origin of settlers. However, at the intraspecific level this significance was only observed in two species, *D. vulgaris* and *O. melanura* with positive and negative correlations, respectively. It is improbable that the significance in these correlations are due to sampling biases, as in six of the nine studied species we have similar number of sampling sites (6-7 localities). Furthermore, we are working at the individual level, dealing with a mean number of 150 individuals per species. Thus, individuals hatching early in the season show preferentially a southern origin in *O. melanura* while a northern origin in *D. vulgaris,* although this factor explained a small proportion of the model. For instance, we observed that individuals from the same locality (Xabia near the Ibiza channel) and the same PLD, but born at different dates, had a different hatching area, originating northwards or southwards. This variability could be related to daily current variations, common in coastal waters (Fernández et al., 2005), modifying dispersal orientation as observed in other species through direct dispersal assessment by parent-offspring analysis (Schunter et al., 2014). Thus, the hatching date of the individual can be more important than previously thought at a fine scale.

5 Conclusions

The use of oceanographic models together with PLD general information have been used in previous studies at a regional (Andrello et al., 2013; Barbut et al., 2019; Rossi et al., 2014), and global scale (Andrello et al., 2017). These studies have generated conservational strategies recommending the use of these units or cells (Boero et al., 2016) and recommended their use to establish Marine Protected Areas (MPAs) network strategies and fisheries policies (Kerr et al., 2010). In our study, both individual hatching date and PLD have been confirmed as factors to have in mind to design more precise larval dispersal models. We can conclude that having good individually otolith-inferred information about these parameters helps to a better definition of recruit's origin area and in defining hydrodynamic units. This more accurate information could be highly valuable for the identification of natural management units and can be useful when considering conservation strategies such as those establishing networks of Marine Protected Areas or in defining conservation measures at regional scales.

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