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Abstract

Connectivity between spawning grounds and recruitment areas of marine fish species drives population structure and dynamics, and may be affected by climate-induced changes in oceanographic processes. We analysed the variability in recruitment success of larvae to estuarine nursery areas along the Iberian Atlantic coast of four fish species with distinct spawning grounds and periods (*Solea solea*, *Solea senegalensis*, *Platichthys flesus* and *Dicentrarchus labrax*). Concomitantly, we explored the variations in connectivity patterns between "cold" and "warm" year archetypes. We used a three-dimensional Lagrangian transport particle-tracking model integrating time series of velocity, temperature and salinity fields archived from the Regional Ocean Modelling System. We simulated individual larval dispersal, over extended spawning periods, from multiple coastal spawning areas to estuarine recruitment areas over 20 years (1989 - 2008). Overall, high inter- and intra-annual variation were found for all species. Nonetheless, highest overall average recruitment estimates were obtained for *S. solea* and *D. labrax* (with 7.3% and 5.7% of the particles released in spawning areas reaching a recruitment area, respectively) compared to *S. senegalensis* and *P. flesus* (3.4% and 1.7%, respectively). Recruitment estimates were overall higher at earlier spawning dates but peak values occurred at later spawning events. Regarding spawning origin, particles that recruited to the northern part of the Iberian coast were mainly from southern source areas. For estuarine systems located in southern Portugal, the relative contributions of northern and southern coastal spawning areas were more balanced, or with a preponderance of northern spawning areas (namely for *S. senegalensis* and *D. labrax*). Recruitment was higher in "warm" years compared to "cold" years, except for *P. flesus* for which nil recruitment was registered in the southern Iberian coast during "warm" years. Larvae also travelled farther in "warm" years compared to "cold" years. Ultimately, understanding how oceanographic conditions govern larval recruitment to estuarine nursery areas is pivotal to forecast the potential impacts of climate change on species with segregated life histories, and will underpin long term management and safeguarding of estuarine nursery role.

Highlights

- Simulation of fish larval dispersal from coastal spawning areas to estuaries.

- Analysis of 4 species over 20 years (1989 - 2008) along the Western Iberian coast.

- High intra- and interannual variability in larval dispersal and recruitment.

- Average recruitment estimated between 1.7% and 7.3% of released larvae.

- Recruitment and connectivity patterns differed in "cold" and "warm" year archetypes.

- Higher recruitment and larval transport in "warm" years for three out of four species.

1. Introduction

Connectivity shapes population structure, dynamics and evolution of fish species, bridging the gap between spatially segregated life history stages that many fish species present during ontogeny. Many marine species undergo large displacements during early life stages (particularly during the planktonic larval phase) due to dispersal events, which are critical for population connectivity and recruitment success (e.g. Curry and Roy 1989, Houde 2008, Carr et al. 2017).

Shallow coastal areas and estuarine systems act as nursery areas for several marine fishes. However, these species generally spawn on the continental shelf, and thus their reproductive success (measured as the number of eggs, larvae or juveniles that survive and reach suitable habitats for ontogenetic development) is contingent on hydrodynamic processes and regulated by environmental factors, as early life history transport is mainly passive (e.g. Paris et al. 2007, Duffy-Anderson et al. 2015). This high dispersion phase is present in the life cycle of most marine-estuarine opportunist fishes (*sensu* Elliott et al. 2007 and Potter et al. 2015) and is critical in terms of population dynamics and connectivity (e.g. Houde 2008, Leis et al. 2011, Duffy-Anderson et al. 2015, Le Pape and Bonhommeau 2015).

Spawning locations are assumed to be relatively stable, resulting from selective factors restricting spawning to areas that favour the transport of eggs and larvae towards suitable coastal areas (Hinckley et al. 2001, Hufnagl et al. 2013). However, to champion this assumption, there is still a clear need for long term studies and data analysis. Whilst some spawning areas may correspond to defined areas that are stable over time, spawning still occurs throughout vast areas of the continental shelf (e.g. Rijnsdorp et al. 2015, Brunel et al. 2018, Ganias et al. 2018), and varies in extent and/or nature according to geographical area (e.g. Duffy-Anderson et al. 2015). Timing of spawning, batch frequency and size may also be extremely variable, even within the same species, and may reflect the ability of individuals to recognise the most suitable environmental conditions to maximize reproductive success (Duffy-Anderson et al. 2015).

After spawning, eggs and early larval stages are mainly dispersed by the action of ocean currents and wind which can have a dominant role in early development stages (van der Veer et al. 2000, Le Pape et al. 2003, Vinagre et al. 2007, Jennings and Ellis 2015, Teodósio et al. 2016). Despite their weak locomotion ability, larvae, especially late larval stages, may promote directional movements through vertical migrations in the water column. These abilities have been documented for a large number of fish species but are usually more effective in processes driving the ingress of late larvae and early juveniles into estuaries rather than counteracting ocean currents (see Teodósio et al. 2016 for a review). Ecological processes acting in nursery areas may also affect year-class strength but are

generally less important compared with the ones influencing larval stages, since nurseries provide good conditions for survival (Duffy-Anderson et al. 2015, van der Veer et al. 2015).

The reproductive success and population persistence of marine-estuarine opportunist fishes largely depend on long term trends in oceanographic conditions that safeguard the connectivity between spawning areas (adult individuals) and nursery areas (juveniles), otherwise, these processes would be largely stochastic thereby preventing the establishment of delimited spawning areas. In general, these species have similar life cycles: adults occur along the continental shelf from the coast down to 200 m depth, and juveniles concentrate in estuarine systems until ca. 2 years old (Jennings and Pawson 1992, Koutsikopoulos and Lacroix 1992, Pickett et al. 2004, Cabral et al. 2007, Pawson et al. 2007, Vasconcelos et al., 2011). The interannual variability of their recruitment is high, and it is often hard to establish relationships with environmental conditions. Nonetheless, both density-independent factors, acting mainly during the pelagic larval phase, and density-dependent ones, especially important within nursery grounds, have been recognised as drivers of year-class strength variability (Le Pape et al. 2003, Cabral et al. 2007, Le Pape and Bonhommeau 2015, van der Veer et al. 2015). Le Pape and Bonhommeau (2015) reviewed the available knowledge on mortality of early life stages of several marine fishes and outlined that recruitment variability of early life stages is several orders of magnitude higher compared with post-settlement/early juvenile phases.

Because several constraints hinder the direct estimation of egg and larvae abundance, modelling tools are increasingly used to effectively evaluate recruitment success of early life stages of fishes, with individual-based models linked to oceanographic models successfully characterizing larval drift and connectivity between spawning grounds and nursery areas (e.g. Hufnagl et al. 2013, Savina et al. 2016, Hinrichsen et al. 2017, Lacroix et al. 2013, Tanner et al. 2017, Beraud et al. 2018). These studies have highlighted the importance of physical factors, such as water temperature, ocean currents, wind and river plumes in driving recruitment variability, and allow us to anticipate how climate change can impact population dynamics. Indeed, climate change may introduce additional variation to the recruitment success of these species by affecting different phases of their life cycles. Climate warming, ocean acidification, changes in ocean currents and wind patterns, and even sea level rise in shallow coastal areas may impact marine-estuarine opportunist fish populations (Gillanders et al. 2011).

The Atlantic Iberian coast is often considered as the northern limb of the Eastern North Atlantic Upwelling System (Canary Upwelling system) (Barton et al. 1998) and is a region of strong mesoscale activity and seasonal variability, and thus very likely to be sensitive to climate change (Pires et al. 2013). However, other authors prefer to separate the Iberian upwelling system, since the pressure gradients responsible for the upwelling-favourable winds are different from the Canary Upwelling

System (Sydeman et al. 2014). These areas respond to two different pressure systems and have distinct upwelling trends (Sydeman et al. 2014). Miranda et al. (2012) and Pires et al. (2013) applied climate and oceanographic models to estimate future oceanographic conditions (projections for 2100) in the continental shelf of the Atlantic Iberian coast and their results suggest an increase of about 1°C in sea surface temperature in spring and summer (seasonal upwelling) and of 2ºC in the rest of the year, while sea surface salinity may decrease c. 0.2. Moreover, the predominant poleward flow in winter is projected to weaken in the future but an intensification of coastal upwelling may occur in summer (Pires et al. 2013, Miranda et al. 2012), especially in the north of the western Iberian coast, which may buffer the effect of global warming (Miranda et al 2012). Barton et al. (2013) and Syderman et al. (2014) highlighted a contemporary weakening in the wind when annually averaged wind trends were analysed. However, it is expected that interannual variability will increase, which will have a profound impact on the marine ecosystem (Miranda et al. 2012).

In this study, we analysed the long-term variability in recruitment success of larvae to estuarine nursery grounds (i.e. the number of particles reaching recruitment areas after the respective larval duration period) of four of the main fish species that use estuaries as nurseries along the Western Iberian coast. Specifically, we simulated individual larval dispersal and determined the number of larvae reaching coastal areas influenced by river plumes over 20 years (1989 - 2008). Based on environmental variables (SST, Meridional Wind Stress, rainfall, NAO index and East Atlantic Index), we identified the most contrasting years over the study period (hereafter referred to as "cold" and "warm" year archetypes) to explore the potential effects and implications of climate change on the dispersal trajectories and larval recruitment success of fish species with distinct spawning grounds and periods.

2. Methods

2.1. Oceanographic and climate conditions in the western Iberian coast

Oceanographic conditions in the Western Iberian Margin are characterized by multiple cores with seasonally varying flows. In the summer, upwelling-type shelf circulation with associated equatorward surface currents, cold water fronts, filaments and eddies dominate, inducing the occurrence of cold waters near the coast and a southward flowing upwelling jet over the shelf (Haynes et al. 1993; Peliz et al. 2002; Relvas and Barton, 2002). Winter circulation is dominated by the Iberian Poleward Current (IPC) over the upper slope and outer shelf. Two other cores are also important for the circulation in this area: the equatorward centred Upper Slope Countercurrent, just beneath the IPC, and a deeper core at Mediterranean Water levels (600–1200 m) (Haynes et al. 1993; Relvas and Barton 2002; Peliz et al. 2002, Teles-Machado et al. 2016).

Based on Regional Ocean Modelling System outputs (see section 2.2) and on climate and meteorological data (sources: Portuguese Institute for Sea and Atmosphere and National Oceanic and Atmospheric Administration), a preliminary characterization of environmental conditions was made for the period 1989-2008. Sea surface temperature varied according to latitude, with values from the south Portuguese coast ca. 2°C higher than northern areas. Annual mean values varied between 14.8°C and 18.2°C and showed a slightly increasing trend over time, in all latitudinal areas. The highest SST mean values were registered in 1990, 1997 and 2006, and the lowest in 1991 and 1992 (Figure S1a). The interannual variation was similar for all the latitudinal areas considered (Figure S1a). Meridional Wind Stress presented a decreasing trend from 1989 to 2008, although interannual variability was high (Figure S1b). Northern areas presented the highest values (mainly positive values) and differed most from lower latitude areas that presented almost exclusively negative values (Figure S1b).

Rainfall differed considerably according to latitude. Southern areas presented lower values (around 500 mm for the majority of the years) and less interannual variation. In northern areas, the variation patterns were more pronounced and rainfall was generally above 1000 mm per year. Nonetheless, there was a fair concordance regarding wet (e.g. 1989, 1996, 2006) and dry (e.g. 1992, 1998, 2005) years for the four latitudinal areas considered (Figure S2a).

The North Atlantic Oscillation (NAO) is the major atmospheric mode that determines regional temperature, precipitation and storm tracks. Under positive NAO conditions, increased precipitation and warm anomalies occur in northern Europe, while negative NAO conditions induce average temperature and more precipitation in southern Europe (Hernández et al. 2020). The East Atlantic (EA) pattern is the second main atmospheric mode influencing conditions in the North Atlantic, with

positive EA associated with above-average surface temperatures and precipitation in northern Europe, and below-average values in southern Europe. Negative EA values induce opposite conditions (Rodriguez-Puebla et al. 1998; Comas-Bru & McDermott 2014). The NAO index presented a decreasing trend in the time series (1989-2008), which contrasted the increasing trend seen in East Atlantic Index values. However, interannual variability was high, even for consecutive years. Positive NAO index values were obtained mainly from 1989 until 1995 (also in 2000 and 2002), while the lowest values were registered in 1996, 2001 and 2005 (Figure S2b). For the EA index, values from 1989 until 1997 were predominantly negative (except for 1994) and positive from 1998 to 2008 (except for 1999 and 2004). The highest value was obtained in 1998 and the lowest in 1995 (Figure S2c).

2.2. Hydrodynamic model

The Regional Ocean Modelling System (ROMS) was used (Shchepetkin and McWilliams, 2005), with 2-way nesting capabilities (Debreu et al. 2012). This model has been successfully applied to the Iberian shelf, with several improvements made over time (e.g. Peliz et al. 2003, Teles-Machado et al. 2016). Model configuration was similar to the one described by Teles-Machado et al. (2016), and incorporated the processes driving the western Iberian margin circulation, the outflow of the main rivers and the exchanges with the Mediterranean. The model consists of a set of nested grids of varying resolution, the smallest of which covers 2.3 km and corresponds to the grid used in this study. Atmospheric forcing had a 27 km resolution and was obtained from a Weather, Research and Forecast dynamic simulation, downscaling of an ERA-Interim reanalysis (Soares et al., 2012). The simulation covered the period from 1989 to 2008, with an archive time of 5 days.

2.3. Life history traits of selected fish species

Four fish species (i.e. common sole, *Solea solea*, Senegalese sole, *Solea senegalensis*, European flounder, *Platichthys flesus*, and European seabass, *Dicentrarchus labrax*) were considered in this study as ecotypes of different spawning and larval development patterns, and as proxies to explore intra- and inter-annual variation in larval dispersal trajectories, determine potential recruitment success, and discuss future implications of climate change on marine fish with inshore (coastal and/or estuarine) nursery areas. The selected fish species are predominantly marine, occurring in the continental shelf, where spawning takes place. Eggs and larvae are pelagic and drift mainly by currents and wind action, during the initial phase of development. Larval concentration in coastal areas and estuaries is critical for survival, and estuarine areas, in particular, have a key role as

nursery grounds where juveniles find suitable environmental conditions for rapid growth with low mortality (Cabral et al. 2007). In the present study, relevant data on the egg and larval life history stages of each species were obtained from the literature and used to parametrize the particle-tracking model, namely spawning location, spawning period, planktonic larval duration (PLD) and lethal temperatures for eggs and larvae (Table S1, Supplementary material). *S. solea* represents a temperate winter spawner species; *S. senegalensis* a sub-tropical spring spawner species, for which the northern limit of distribution is near the spatial coverage of this study; *P. flesus* a cold-temperate fish species, that spawns in winter but for which its larval thermal tolerance range lies within the study area; and *D. labrax* a coastal demersal fish, that also spawns in winter, but closer to the coast and at lower depths compared to the previous three species (Table S1, and references therein).

2.4. Eggs and larvae dispersal model

To model the dispersal of fish eggs and larvae, Ichthyop (version 3.3) was used (Lett et al., 2008). Ichthyop is a three-dimensional particle-tracking model written in Java and designed to study transport processes and their effects on plankton dynamics. This tool simulates Lagrangian transport integrating input time series of velocity, temperature and salinity fields archived from ROMS. ROMS velocity fields were interpolated at 3 h time steps and a horizontal dispersion factor was included following Peliz et al. (2007). Ichthyop is an Individual-based model that accounts for stochasticity, in particular by randomly assigning the location of each particle within pre-defined spawning areas. The movement of particles simulated by the model includes horizontal and vertical advection, horizontal and vertical dispersion, egg buoyancy and larval migration, with some of these processes optional and parametrized by the user (Lett et al. 2008).

In each simulation, 1000 virtual eggs (particles) were released per day (near the bottom for *S. solea*, *S. senegalensis* and *P. flesus*; at the surface for *D. labrax*) in eight contiguous spawning areas along the continental shelf at the depth intervals specified for each species, and during a four-month period corresponding to the spawning season of each species (Figure S3, Table S1). For each species, simulations were carried out for each, from 1989 until 2008, starting at the first spawning event, with spawning events every day during four months, and ending when the larval stage of the final batch of eggs/larvae completed its larval period. Particle densities were similar within each one of the eight sampling areas, with the initial release location randomly assigned within each spawning area. Twenty-one estuarine recruitment areas were considered, from Xallas estuary, in the North, to Guadalquivir estuary, in the south (Figure S3). For each simulation, an output file was generated registering particle locations and status at a pre-defined pace of time (24 hours). The size of the

recruitment areas adjacent to the 21 estuaries was based on river flow (mean flow above or below 150 m^3 s^{-1}) with recruitment areas set as 15 km by 15 km for Minho, Douro, Tejo, and Guadalquivir estuaries, and 7.5 km by 7.5 km for all remaining areas. Particles reaching recruitment areas after 75% of the species-specific PLD were considered to have recruited (it was assumed that at this development stage they would have the ability to settle or actively enter estuaries; e.g. Teodósio et al. 2016). Two sets of simulations were conducted: one without vertical migration of larvae and the other with larvae larger than 4 mm (corresponding roughly to first feeding and metamorphosing larvae) occupying the first 5 m of the water column during the night and down to 40 m depth during the day (or the maximum water column depth in shallower shelf zones) (Tanner et al. 2017). The purpose of thee two sets of simulations was to compare outputs and to evaluate their similarity, since key parameters regarding larvae behavior are not known for some of the species considered in this study.

2.5. Potential recruitment estimates, climate conditions and statistical analyses

Overall dispersion of particles, both recruited and non-recruited, and based on the geographical coordinates of particles at the end of the PLD, was plotted for each species, and presented as the density of particles estimated using a kernel estimator. For each species, recruitment success (i.e. the percentage of particles reaching recruitment areas after their respective PLD, among all released particles) was calculated per month and year. A connectivity diagram was produced, presenting the overall percentage of recruited particles to each recruitment area by spawning area of origin.

To evaluate differences according to climate and oceanographic conditions, "cold" and "warm" year archetypes were identified in the 20-year time series using multivariate ordination techniques. A principal components analysis (PCA) based on the correlation matrix of climate variables (SST, Meridional Wind Stress, rainfall, NAO index and East Atlantic Index) was used to evaluate similarities among years. The PCA ordination diagram of the first two principal components accounted for 63% of the variance, and the first principal component of the ordination was positively correlated with SST, wind and rainfall, and highlighted two contrasting clusters of years that were used as case studies of "cold" and "warm" year archetypes(Figure S4). "Cold" years (i.e. 1989, 1992, 1994 and 2004) presented the lowest values of SST, Meridional Wind Stress and rainfall, while "warm" years (i.e. 1996, 1997, 2001 and 2002) the highest (see Figure S5). Differences regarding East Atlantic index and NAO index were less evident, with NAO index values generally higher in "cold" years compared to "warm" years.

For each species, differences in recruitment success estimates in "cold" and "warm" year archetypes were compared. Dispersal distances of recruited particles (distance between spawning and recruitment area) were calculated using the great-circle distance and compared ("cold" vs. "warm" years). Differences in both recruitment success and dispersal distances in "cold" and "warm" year archetypes were evaluated through an analysis of variance (using year archetype and month as factors), after assessing required assumptions of normality and homocedasticity.

All statistical and graphical analyses were performed in R software (R Core Team 2018) and using packages: dplyr, ggplot2, ggpubr, KernSmooth, lm, lubridate, ncdf4, raster, RColorBrewer, sf, tidyr, viridis.

3. Results

3.1. Particle dispersion patterns

Overall particle dispersion patterns were considerably different according to species (Figure 1). For *S. solea*, particles were concentrated in coastal areas all along the Iberian Atlantic coast, with decreasing densities as the distance to shore increased. The distribution of particles was more fragmented for *S. senegalensis*, with some high-density areas close to several estuarine systems (e.g. Minho, Ria de Aveiro, Tejo, Mira and Ria Formosa). For this species, an offshore concentration of particles was registered SW off the Portuguese coast and along the Spanish SW coast of the Gulf of Cadiz. The dispersion pattern obtained for *P. flesus* showed low or null density in southern areas (south to 38°N) and concentrations in coastal areas in northern areas, especially in northern Spain. For *D. labrax*, higher density areas occurred nearshore throughout the Iberian coast, with a hotspot in the southern Portuguese coast.

3.2. Recruitment variation patterns by year and spawning period

High intra- and interannual variability in the recruitment success of particles was registered for all the species (Figure 2). *S. solea* and *D. labrax* presented the highest values (overall, an average of 8.0% and 9.6% of the particles released reached a recruitment area, respectively) compared to the other species (4.0% and 1.7% for *S. senegalensis* and *P. flesus*, respectively). Although the interannual variation pattern was not entirely consistent across all four species, in 1997, the highest recruitment estimates were recorded for all the species (higher than 10%, except for *P. flesus* with ca. 4%).

For *S. solea*, the highest recruitment values were mainly registered for spawning events during January and February (mean values of 11% and 9%), while estimates obtained for March and April were near 7%. Nonetheless, peak values were obtained for these late spawning events, namely in 1997 and 2000 (Figure 2). A contrasting pattern was obtained for *S. senegalensis*, with highest recruitment values generally recorded for spawning events occurring in April and extremely low values in June and July (Figure 2). For *P. flesus*, the highest values were estimated for February, with recruitment estimates for spawning events during April almost nil (Figure 2). *D. labrax* presented a pattern similar to *S. solea*, with highest recruitment values obtained for spawning events during January and February, and slightly lower values for March and April, that nonetheless presented peak values for particular years (e.g. 1997, 2000) (Figure 2).

3.3. Connectivity between spawning zones and recruitment areas

Among species, spawning areas that contributed most to estuarine recruitment areas were rarely in the same latitude, with complex connectivity patterns both in space and time (Figure 3). For estuaries north of the Mondego, recruited particles originated mostly from areas to the south of the recruitment areas, while for estuarine systems located in the southern Iberian coast, contributions from areas to the north an south of the recruitment areas were more balanced. In the case of *S. senegalensis* there was some preponderance of particles originating from north of the recruitment areas. For P. *flesus*, almost no recruitment was registered south of the Mondego estuary (Figure 3). Spawning areas responsible for the highest contributions of particles reaching recruitment areas differed according to species. For *S. solea*, highest recruitment values were observed in Minho, Douro, Tejo, Mira, Ria Formosa and Guadalquivir recruitment areas (Figure 3). The spawning zones 3 and 4 generated increased numbers of successful recruits, with values two times higher or more than the remaining areas. Recruitment origins are relative to the nearest spawning zones, but most of the estuaries receive particles from 3 or more spawning areas (adjacent north and south to the spawning zone located at similar latitude than the considered estuary) (Figure 3). For *S. senegalensis*, highest recruitment values were obtained in Tejo, Ria Formosa and Guadalquivir estuary (Figure 3). For *P. flesus*, spawning zones 2 and 3 were the ones that contributed most to recruitment, which was higher in the Umia, Verdugo and Minho estuaries (Figure 3). For *D. labrax*, estuaries with the highest percentage of recruited particles were the Minho, Tejo, Mira, Ria Formosa and Guadalquivir estuaries (Figure 3).

3.4. Climate effects on recruitment patterns

The patterns obtained for the four species according to climate conditions ("cold" and "warm" year archetypes) presented some similarities: potential recruitment was higher in "warm" years compared to "cold" years (mean values of 10.5% vs 5.0%, for *S. solea*; 2.5% vs. 1.5%, for *P. flesus*; and 8.0% vs 3.0%, for *D. labrax*), except for *S. senegalensis* for which values were similar (mean values of 4.5% and 4.4%, respectively for "warm" and "cold" years). The differences between potential recruitment in "warm"and "cold" years archetypes were significant for *S. solea* and *D. labrax* ($F>8.0$, p-value<0.05) and not significant for S. senegalensis and P. flesus ($F<1.0$, p-value>0.05). For this last species, potential recruitment values in "warm" year archetypes were higher in northern areas, but extremely low or nil south to 39° N (due to temperatures higher than critical lethal limits), which impacted the non-significance of these differences in the statistical analyses. Overall distances over which recruited particles dispersed in "warm" and "cold" year archetypes were not significantly different ($F<3.3$, p-value>0.05), except for *P. flesus* ($F=14.1$, p-value<0.05), for which distance travelled by particles were higher in "warm" year archetypes and were originated from southern

areas. However, for most of the species the distance over which recruited particles dispersed and their prevailing origins also differed according to latitudinal area (spawning zones and recruitment areas). For *S. solea*, in "cold" years and in northern estuaries (from Xallas to Minho), the origin of recruited particles was mainly located between 0 km and 200 km south of their recruitment area. From the Minho estuary southward, the contribution of particles originating north or south relative to recruitment areas was more symmetrical and generally within 200 km (Figure 4). For the Tejo and Mira estuaries, particles were mainly from northern areas, up to 400 km away. For "warm" years, distances travelled by particles were larger and their origin was farther south, when compared to "cold" years, and with a high proportion of recruited particles originating as far as 300 km south (Figure 4). This pattern is particularly evident for recruitment areas from the Xallas to the Tejo estuaries, while for southern estuaries the number of particles originated in northern or southern spawning areas relative to recruitment areas was more balanced (Figure 4). *S. senegalensis* presented a similar pattern to that described for *S. solea*, except for relative importance of the contribution of northern areas from the Douro estuary southwards, both in "cold" and "warm" years. For these estuaries south of Douro, particles predominantly originated in northern areas relative to their recruitment areas, with distances travelled reaching up to 400 km (Figure 5). For *P. flesus*, in "cold" years, recruited particles were predominantly from sources located south of their recruitment areas, until the Mondego estuary, particles travelling between 0 km to 300 km (Figure 6). For the reduced number of *P. flesus* larvae that recruit to estuaries south of the Mondego, particles originated up to 300 km north from the recruitment estuary. For "warm" year archetypes, distances travelled by particles were larger and recruitment levels were higher compared to cold years, but only for estuarine systems north of the Douro. Extremely low levels of recruitment were estimated in "warm" years south of the Douro estuary, with no particles registered south of the Mondego estuary. Finally, for *D. labrax* a similar pattern to the one described for *S. solea* was obtained, with a predominance of recruited particles with a southern origin in the northern part of the coast for "cold" years, and a preponderance of northern origins for estuaries south of the Tejo estuary in "warm" years (Figure 7). For all the species, the relevance of recruitment areas, in terms of the number of particles that reached these areas, was similar in "cold" and "warm" year archetypes (Figures 4 to 7).

3.5. Differences between the simulations without or with larvae vertical migration

The results obtained from the two sets of simulations, i.e. without or with larvae vertical migration, were very similar, and thus the figures regarding the simulations with larvae vertical migration parametrized in the model are presented as supplementary material.

4. Discussion

The main differences in larval dispersal patterns among the four species were linked to their spawning periods and location of spawning grounds, as well as oceanographic processes along the Iberian coast. Despite the oceanographic complexity of this region, the prevailing currents in winter months are governed by the Iberian Poleward Current that flows northwards along the coast (Peliz et al. 2002, 2003). This could support the higher dispersion northwards of all the winter spawner species (i.e. *S. solea*, *P. flesus* and *D. labrax*); whilst the lack of *P. flesus* larvae in southern areas is explained by temperatures above its thermal limit (15°C) (von Westernhagen 1970). The more widely dispersed pattern registered for *D. labrax* may be due to a longer larval duration compared to the other two species. The profoundly different larval distribution pattern obtained for *S. senegalensis*, which spawns later than the former species, may be related to upwelling events that typically are more intense in late spring and summer periods (Peliz et al. 2002, 2003, Miranda et al. 2012, Pires et al. 2013). Most oceanographic studies conducted in the Iberian Atlantic coast highlighted a pronounced spatial and temporal variability, according to different scales (e.g. Peliz et al. 2002, 2003, Teles-Machado 2014), which surely interfere with larval dispersion processes and that could be responsible for the high intra- and inter-annual variability that was found among the four species analysed.

Recruitment estimates obtained for *S. solea*, *S. senegalensis*, *P. flesus* and *D. labrax* presented a marked temporal and spatial variability reflecting the variation of oceanographic processes, and responses to "cold" and "warm" year archetypes. Although the larval dispersal model predicted a strong concentration of larvae in coastal areas, a large proportion of particles did not reach recruitment areas. Tanner et al. (2017) modelled larval dispersal dynamics of *S. solea* along the Portuguese coast, and the obtained estimates of larvae reaching recruitment zones were within the range of our results (from 4.2% to 8.5%). Nonetheless, most studies on marine fish larval dispersal in Europe present higher estimates of recruitment (often higher than 50%) but focus on more closed marine areas, such as the Celtic Sea, North Sea or the Baltic Sea, where bathymetry is quite low and putative nursery areas may be found almost in all the directions of dispersion from spawning areas (e.g. Rochette et al. 2012, Hinrichsen et al. 2018, Corell and Nissling 2019, Deschepper et al. 2020). Contrastingly, studies conducted in open shelf waters, such as the one in the Northwest Pacific by Stockhausen et al. (2018), that modelled the recruitment of rockfishes (*Sebastes* spp.), reported a large proportion of larvae failing to reach inshore areas (>80%). In the Mediterranean Sea, Gargano et al. (2017) also estimated that most of the larvae of *Mullus barbatus* were transported to areas unsuitable for settlement and concluded that the dispersal process induced a strong loss of potential

settlers. These results were also corroborated by Koeck et al. (2015) in the same area for several fish species.

In a context of highly variable oceanographic conditions, wide spawning grounds combined with extended spawning period or batch-spawning represent a more successful reproduction strategy compared to a localised and unique (or limited) emission of gametes. Although the first month of the spawning period generated the highest potential recruitment, for several dates throughout the spawning season recruitment estimates were still high (> 15% of larvae reaching recruitment areas). A multi-cohort nature of juveniles recruiting to estuarine areas has been reported and may have the effect of a more balanced resource partitioning and a reduction of niche overlap (Cabral 2000, Martinho et al. 2008, Wouters and Cabral, 2009, Vasconcelos et al. 2010).

Regarding connectivity patterns and their interannual variation, the recruitment areas for which the highest potential recruitment estimates were obtained were fairly consistent throughout time (1989-2008), as were the spawning areas that contributed most to recruitment. Despite the high interannual variability of oceanographic processes in the Iberian Atlantic coast (e.g. Peliz et al. 2002, Miranda et al. 2012), the analysis of a long time-series (20 years) allowed us to determine the main trends over this period, although with some divergent estimates in atypical years. In what concerns the northern or southernmost spawning areas, a border effect is likely, with estimates of potential recruitment and dispersal distances underestimated (presumably more pronounced for the southern limits of the study area, taking into consideration the prevailing larval drift northwards). Nonetheless, the highest recruitment levels originated in spawning areas 2 and 3 for almost all the species (these two areas accounted for 40% to 72% of recruited larvae). Although fisheries data should be considered with caution, because even if it may reflect resource abundance it strongly depends on several other factors (e.g. fishing effort, fleet composition, targeted species), zones 2 and 3 (from 40°N to 42°N, see Figure S3) are also those with the highest landings of soles, flounder and seabass in the Portuguese coast (representing about 50% of total landings for soles, 80% for flounder and 60% for seabass; source DGRM). Furthermore, the landings of these species present a marked seasonal pattern, with fish mainly landed in winter (ca. 50% of the annual harvest), that correspond to the spawning periods of sole, flounder and seabass (Teixeira et al. 2011).

Available data on the relative importance of estuarine nursery areas along the Portuguese coast only partially support the obtained model's predictions. Vasconcelos et al. (2010) evaluated the importance of six estuarine systems (Douro, Ria de Aveiro, Mondego, Tejo, Sado and Mira estuaries) for *S. solea*, *S. senegalensis*, *P. flesus* and *D. labrax*, based on fishing surveys conducted in July 2005 and 2006, with results differing according to species: the Tejo was the most important for *S. solea*, *S. senegalensis* and *D. labrax*, and the Douro for *P. flesus*, when considering the estimates of the total

numbers of juveniles. However, these abundance patterns may vary considerably among years (e.g. Cabral et al. 2007, Martinho et al. 2009, Bento et al. 2016). As outlined by Tanner et al. (2017) the comparison of larval abundance in coastal areas with juvenile densities within the estuarine nursery areas may be misleading, as these authors also found a weak relation between larval supply and juvenile abundance in estuaries. Larval supply should influence juvenile abundance in estuaries but there are a series of factors, such as habitat and food availability, predation and competition, that will affect larvae and juveniles differently (Tanner et al. 2017). Moreover, there is a major time gap between studies evaluating larval processes and those focusing on juveniles in nursery grounds, that hinder the establishment of relationships, particularly due to the scarcity of knowledge regarding factors affecting nursery colonization processes.

For the four species, the levels of self-recruitment, i.e. larvae recruited to a certain area originated in the nearest spawning area, was not particularly high, but if the contributions of the adjoining areas are considered, these estimates increase greatly. These results are fairly concordant with connectivity matrices obtained by Tanner et al. (2017), for *S. solea*, where connectivity varied with year (from 2004 to 2009) and latitudinal area, with differences in the preponderance of northward or southward larval origin in recruitment areas along the coast (six estuaries). Mean dispersal distances of larvae obtained in the present work were similar to the ones reported for the same species in Northern European waters but connectivity patterns were profoundly different. Savina et al. (2016), for *S. solea* in northern France, and Barbut et al. (2019), for six flatfish species in the North Sea, reported low connectivity between larvae populations and a considerable self-recruitment. However, and as outlined above, the oceanographic context of these areas are very different. In both studies, discrete spawning grounds were considered but oceanographic or geomorphological features such as the English Channel, shallow banks, and regional patterns of wind, tidal waves and currents may induce barriers, bottlenecks or a prevailing directional dispersal, tightly linked to larvae origin.

According to our larval dispersal model predictions, "warm" years, characterized by higher wind intensity and rainfall, favoured recruitment, except for *S. senegalensis*. The spawing period of this species is mainly in Spring, when oceanographic conditions may be quite different and less related with the variables used in the analysis. In particular, the coastal oceanography along Portuguese coast in Spring and Summer months is markedly influenced by upwelling events (Haynes et al. 1993; Peliz et al. 2002; Relvas and Barton, 2002), which may confound the effect of "warm" and "cold" year archetypes. For *P. flesus*, the southern limit of its distribution lies on the Portuguese coast (ca. 39°N) and thus the recruitment of this species in warm years is limited to northern areas, which explains the lack of significant differences in overall rates of recruitment between "warm" and "cold" year archetypes.

Connectivity patterns obtained for the four species showed evidence of a common trend: larval origin was predominantly from southern spawning areas in the North (north to about 40°C), while for southern recruitment areas larval origin was more balanced. Indeed, the Iberian Poleward Current may be more pronounced in northern areas, while in the south Atlantic Iberian coast equatorward flows appear (Pires et al. 2013). Furthermore, several studies on oceanographic processes of the western Iberian coast highlighted the influence of some canyons, such as the Aveiro canyon (ca. 40.5°N) that may affect circulation through the creation of eddies (Peliz et al. 2003) that may superimpose to currents along North-South direction.

Lacroix et al. (2018), in a study conducted in the North Sea, also predicted a 70% increase in dispersal distance of larvae in a warming scenario. The ecological significance of larger distances of larval trajectories, at higher velocities, are not evident, and with conflicting evidence regarding their ability to boost or hinder feeding ability and/or predator avoidance. Mahjoub et al. (2012) studied the impact of turbulence on *D. labrax* feeding activity and highlighted negative effects on prey ingestion by *D. labrax* in more turbulent water flow and for non-evasive prey. However, climate-induced impacts may be extremely difficult to predict due to a large number of effects and their interactions, with the literature presenting disparate results (e.g. Britten et al. 2016, Lacroix et al. 2018, Young et al. 2018). One of the probable effects of sea warming will be earlier spawning, as reported for *S. solea* (Horwood 1993; Fincham et al. 2013), but different results were also obtained, namely for flounder, for which the spawning migration setting is triggered by the difference between estuarine and coastal waters temperature (Sims et al. 2004). Additionally, river plumes may modulate warming in coastal waters (Costoya et al. 2016). The increase in interannual variability and uncertainty regarding upwelling strength and seasonality (Miranda et al. 2012, Barton et al. 2013, Pires et al. 2013, Syderman et al. 2014) may also have a profound regional effect that may be differentiated from wide-scale climate change forecasts. Lacroix et al. (2018) also suggested that an earlier spawning may reduce pelagic larval duration (as much as 22%), in response to the reduced temperature experienced by early hatched larvae, which can reduce dispersal and connectivity (e.g. Young et al. 2018). So, despite the evidence of higher connectivity for the Iberian coast in our results, other ecological and oceanographic related aspects may interfere and thus enhance or constrain connectivity in other geographical areas. Physiological studies are also needed to predict consequences for larval development and survival under different conditions. If the temperature increase exceeds the physiological tolerance range or optimum, a decrease in larval survival rates may be observed (e.g. Arula et al. 2015, for *Clupea harengus*). Some of the studied species, namely soles, may be sensitive to increased temperature and/or hypercapnia, with impact at the metabolic

rates (Pimentel et al. 2015), while the development of seabass larvae seems not to be affected by projected ocean acidification scenarios (Crespel et al. 2017).

Direct quantification of larvae abundance through ichthyoplankton surveys in coastal areas would contribute to validate model estimations, but surveys are scarce in Iberian waters and the available literature suggests that neither species composition, nor abundance patterns are similar in coastal and estuarine areas (e.g. Primo et al. 2012, Ramos et al. 2016). Teodósio et al. (2016) proposed the "sense acuity and behavioural hypothesis", describing biophysical processes of larval recruitment into estuaries, and have demonstrated that via a hierarchy of sensory cues (odor, sound, visual and geomagnetic cues) successful recruitment of Sparidae larvae may increase up to 32%. There is also additional empirical evidence that for one of the species considered in the present study (*S. solea*), settlement occurs before estuarine colonization, explaining why these species are not particularly abundant in estuarine plankton (Amara et al. 2000). This is seconded by the fact that in France, and in northern areas of their distribution, nursery areas for soles and flounders are located in the estuarine-coastal continuum (e.g. Amara et al. 2000, Le Pape et al. 2003). Why these coastal nurseries are usually not reported in the southern areas of distribution of these species is still unexplained, but the particularities of the Iberian coast, with an extremely narrow continental shelf, high hydrodynamics and lower temperatures in summer even when compared to northern areas may be among the main causes.

The coupling of oceanographic and larval dispersal models is a useful approach to explore relationships between physicochemical and biological conditions but these methods also have limitations, especially regarding active dispersal processes and ontogenetic changes. Our purpose was to compare the dispersal patterns of early-life stages of four species of marine-estuarine opportunist fish species over a long period. The lack of data for some of these species, concerning larval development and its relationships with environmental factors, did not allow a more comprehensive parametrization of the individual-based models (e.g. Larvae&Co, Lacroix et al. 2018; DisMELS, Stockhausen et al. 2018). Whilst these models may integrate a wide set of parameters, their estimates are often obtained in experimental conditions and/or values are inserted from related species, which may also have drawbacks. As a consequence, the parametrization of larval dispersal models can become inadequate or arbitrary. In all studies that have modelled larval dispersal for the four species considered in the present work, parameters were never obtained from observational data but based on experimental studies. The few available observational studies are relative to *S. solea*,regarding swimming activity (e.g. Castelbon et al. 1991, Champalbert et al. 1991) and larval development (Fonds 1979). However, these studies were designed and implemented in conditions (larvae obtained from hatcheries, either starvation or artificial feeding ad libitum, fixed

and limited temperature conditions, single variables experiments, vertical movements measured in less than 1m tanks, among other limitations) where extrapolation may be strongly constrained. For these reasons, and also to ensure that a similar procedure for four species considered was applied, neither larval growth nor larval vertical migration parameters were included in the model. Furthermore, the relevance of the inclusion of larval vertical migrations in the model may be mitigated due to vertical mixing of water layers, which may be dominant over larval migration ability (in our model's simulations, particles were as deep as 60m, being 25% of particles generally found below 5-10 m depth), and also to the the fact that recruitment success corresponded to reaching recruitment areas (coastal areas adjoining to estuaries mouth) at 75% of the duration of the larval period. Most of the larvae reaching these coastal areas were still as early stages (often before first-feeding larvae stage), for which no vertical migrations have been documented.

Some authors also emphasize that variability between different ocean circulation models is high, although the transport directions and connectivity rates were comparable (Hufnagl et al. 2017). In that regards, the impacts of spawning and nursery area delineations on the results may not be negligible. For *S. solea* and *P. flesus* the existing volume of information is considerably higher compared to the other two species, with discrete spawning areas well characterized in the North Sea and other northern areas of distribution (e.g. Lacroix et al. 2013, Hinrichsen et al. 2018). In our study, lacking detailed baseline information, a continuous spawning ground along the coast was prefered, fragmented only where sediment type is not favourable for these species.

Overall, larval dispersal modelling is a powerful tool to evaluate impacts at the population level of different oceanographic and climate scenarios. In the present study, it highlighted contrasting larval dispersal patterns of four marine-estuarine opportunist fish species, as well as outlining differences in connectivity patterns in "cold" and "warm" year archetypes and thus of the potential impacts of climate change. However, knowledge of key biological and environmental aspects are still lacking and can be used to further advance these modelling approaches. Observational data would be particularly important to validate model predictions (Hufnagl et al. 2017, Lefcheck et al. 2019), especially relative to ichthyoplankton abundance and adult fish tagging surveys. Further research should also focus on estuarine colonisation processes by larvae or early juveniles that are poorly known for several marine species that use estuaries as nurseries.

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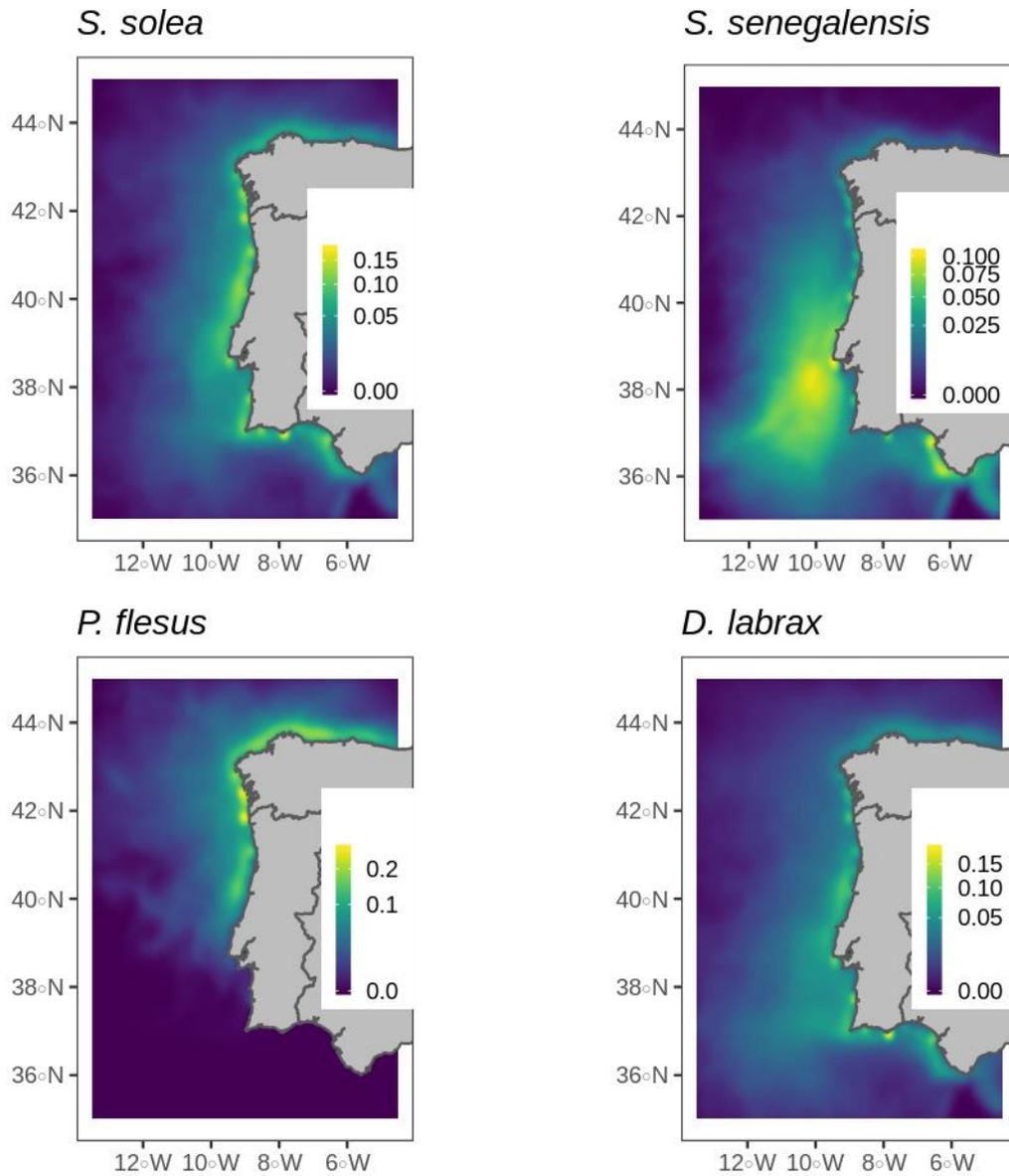**Figures and tables** (Figures and tables numbered with S will be as supplementary material)

Figure 1 – Overall particle densities (square root scale) that resulted from the larval drift model for each species: a. *Solea solea*; b. *Solea senegalensis*; c. *Platichthys flesus*; d. *Dientrarchus labrax*.
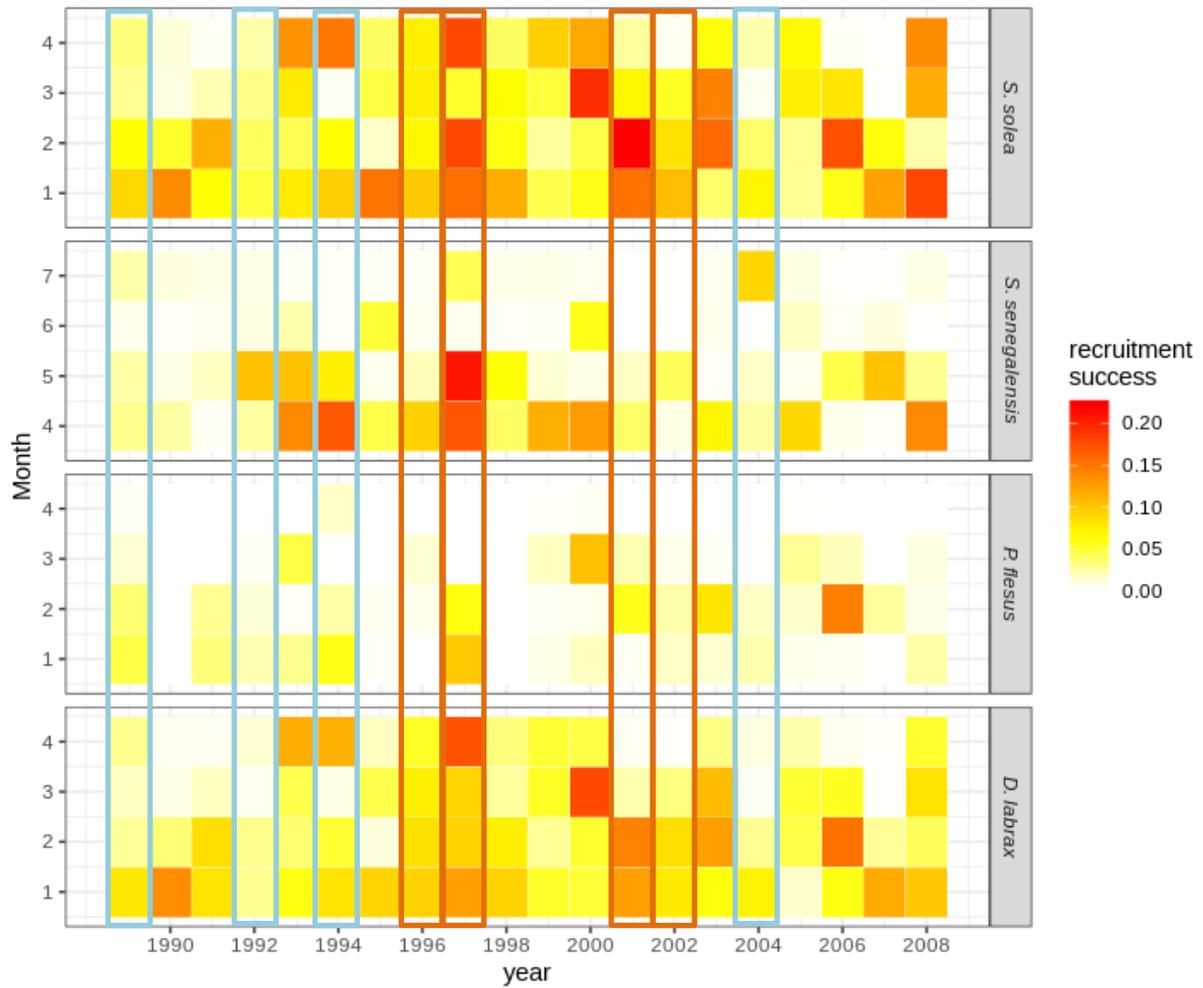
Figure 2 –Recruitment success (proportion of released particles reaching recruitment areas) per month and year, for *S. solea*, *S. senegalensis*, *P. flesus* and *D. labrax* (blue and red rectangles indicate "cold" and "warm" year archetypes, respectively).
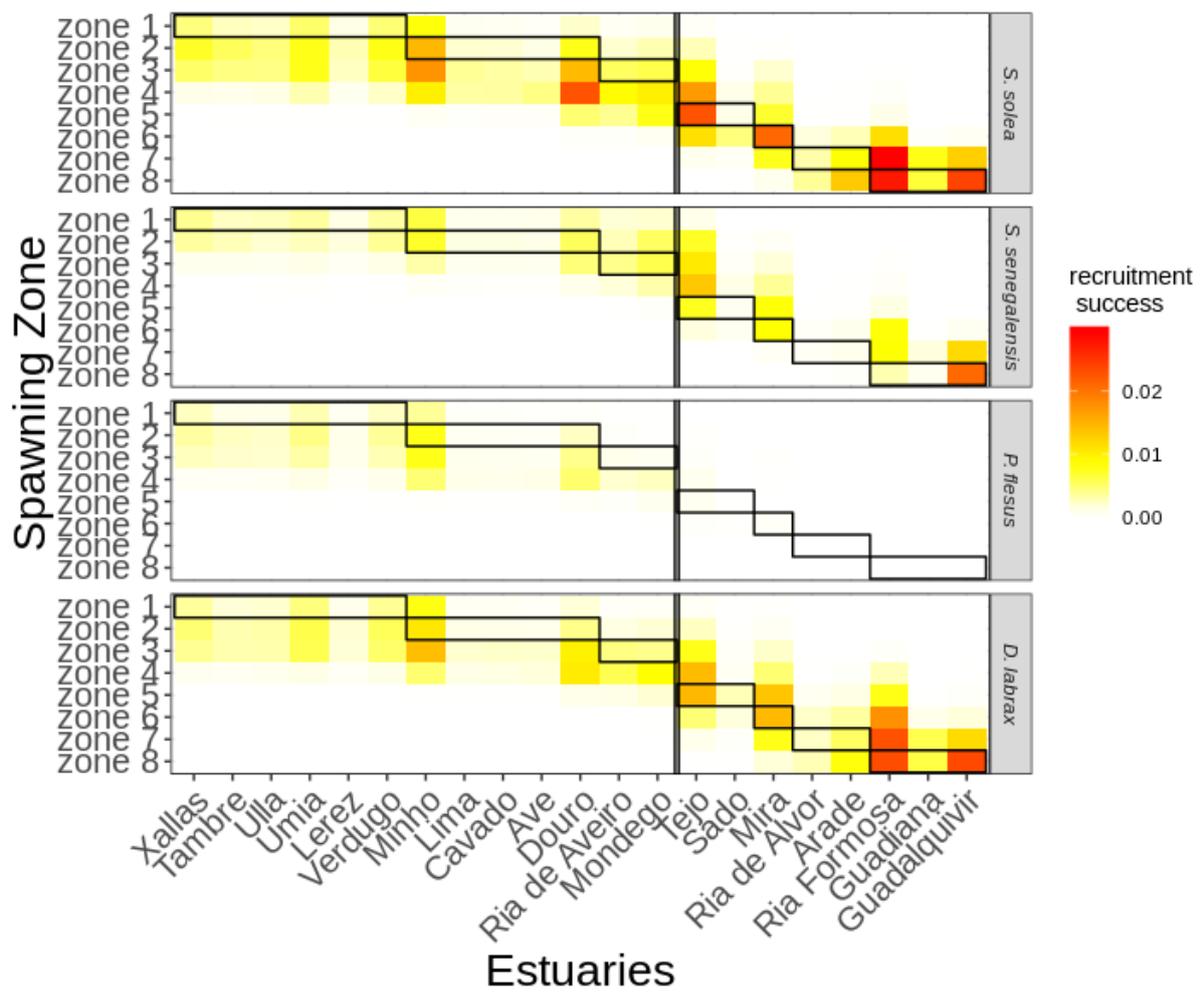
Figure 3 – Proportion of particles reaching recruitment areas according to spawning area for S. solea, S. senegalensis, P. flesus and D. labrax. Bordered rectangles (in black) represent the estuaries that are in the same latitudinal range of each spawning area.
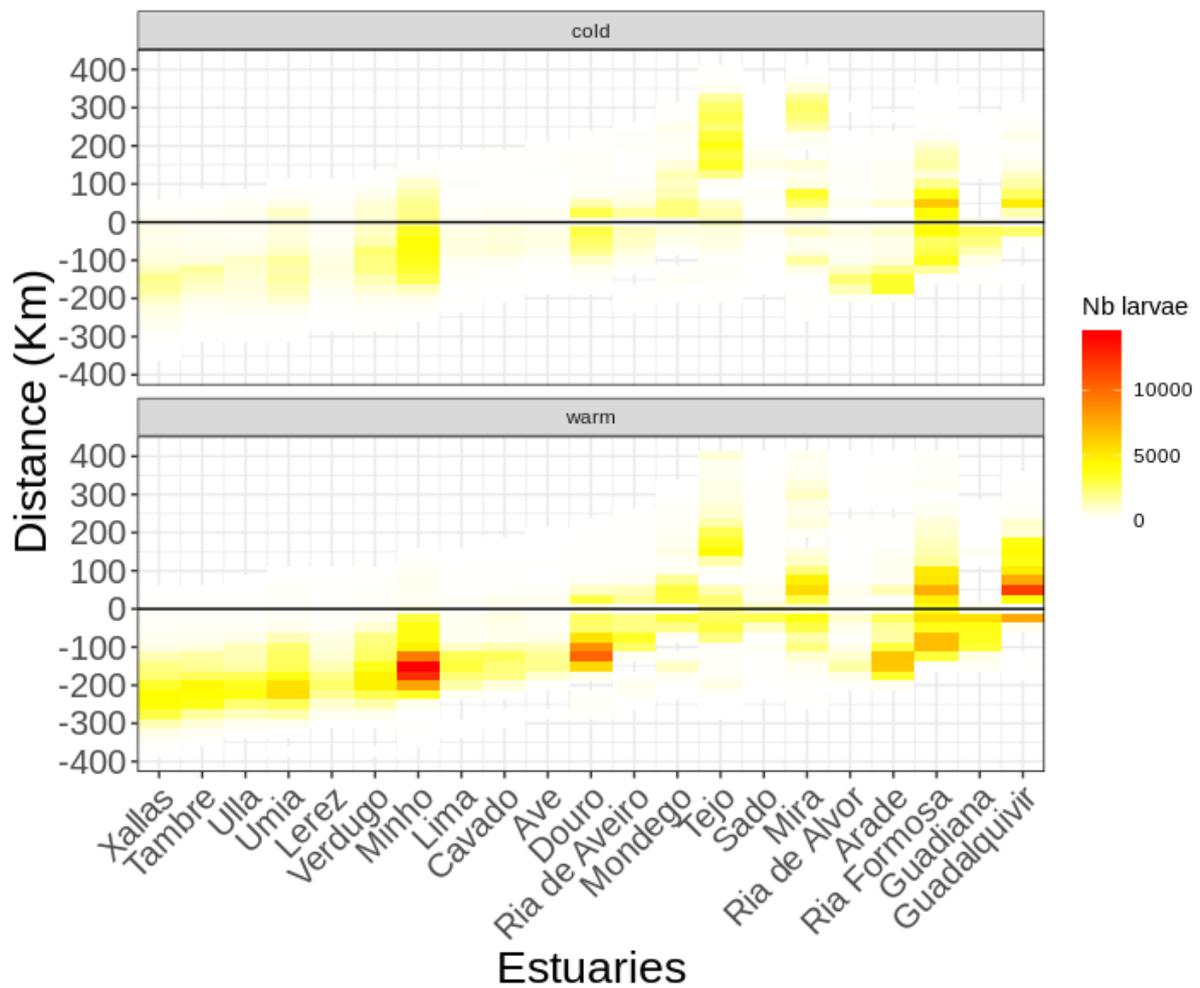
Figure 4 – Number of recruited larvae of S. solea for each recruitment area, according to origin distance, for "cold" and "warm" year archetypes (positive values represent northward dispersal in relation to their origin, while negative values indicate southward dispersal).
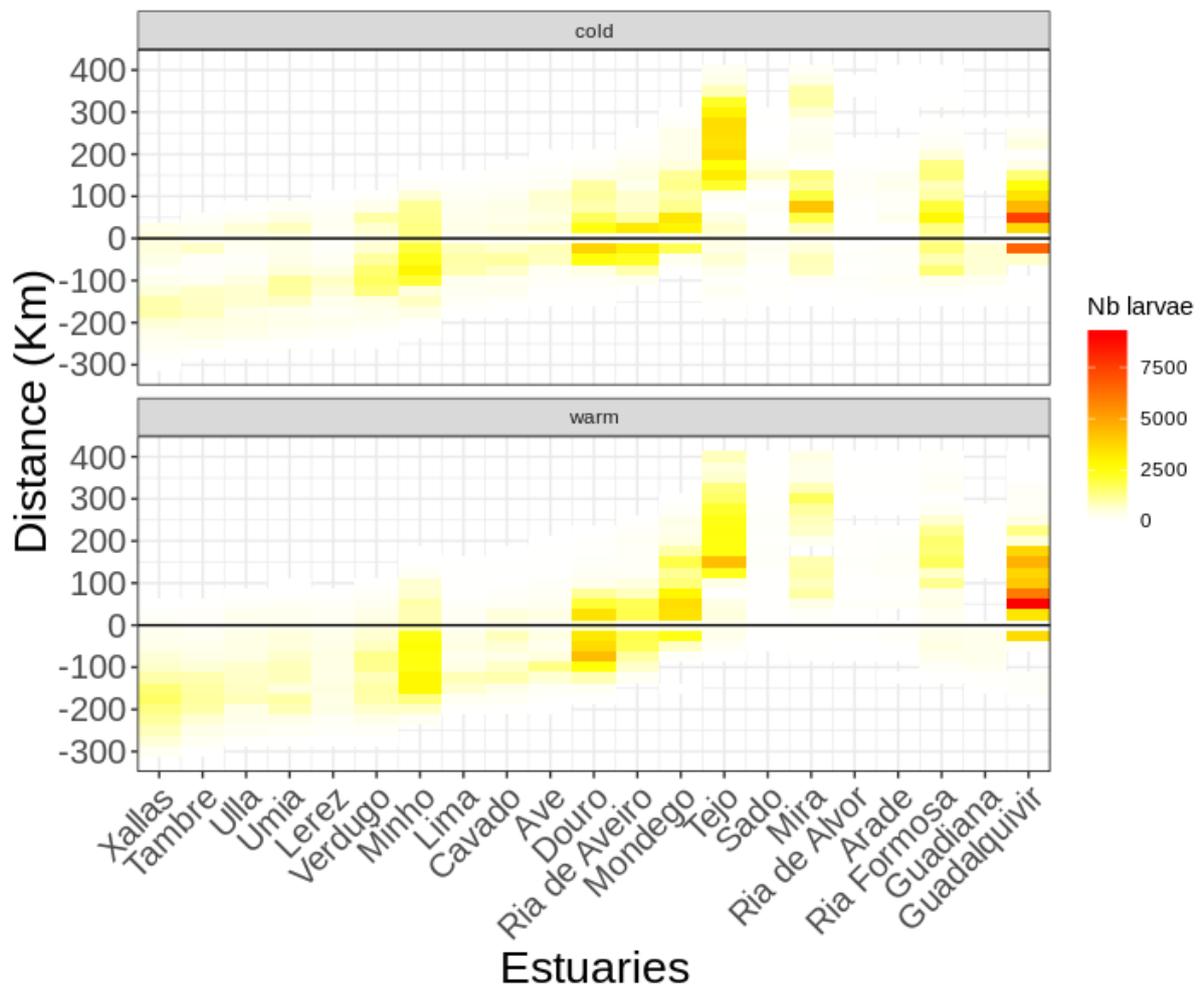
Figure 5 – Number of recruited larvae of S. senegalensis for each recruitment area, according to origin distance, for "cold" and "warm" year archetypes (positive values represent northward dispersal in relation to their origin, while negative values indicate southward dispersal).
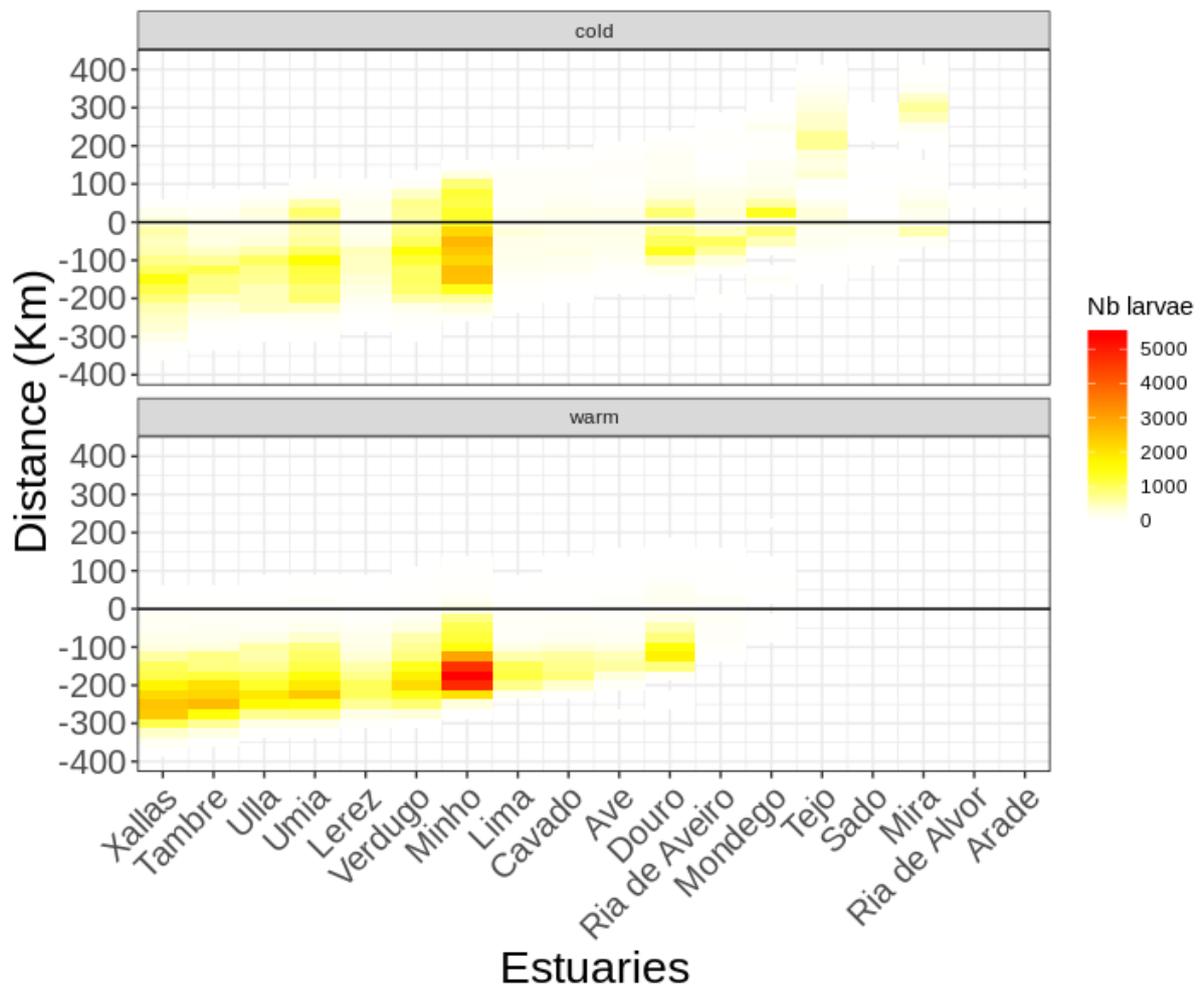
Figure 6 – Number of recruited larvae of P. flesus for each recruitment area, according to origin distance, for "cold" and "warm" year archetypes (positive values represent northward dispersal in relation to their origin, while negative values indicate southward dispersal).
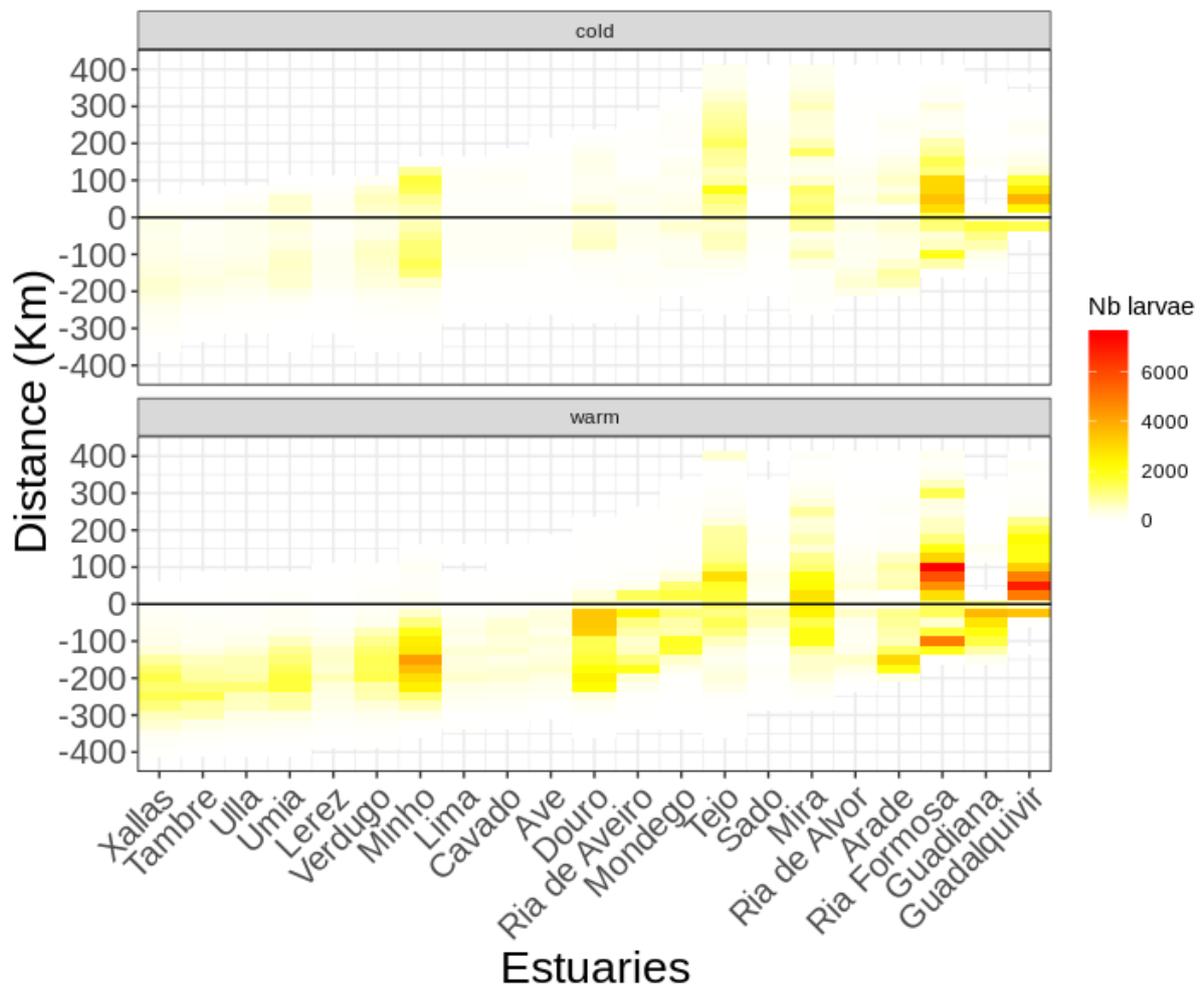
Figure 7 – Number of recruited larvae of D. labrax for each recruitment area, according to origin distance, for "cold" and "warm" year archetypes (positive values represent northward dispersal in relation to their origin, while negative values indicate southward dispersal).