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Will most suitable spawning grounds for coastal fishes be impacted by climate change? A larval drift modelling approach

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ABSTRACT

For many fishes, their early life stages are transported (passively) by currents between spawning areas and coastal nurseries, but also potential dispersal towards new habitats. Therefore, species have developed strategies to enhance the recruitment success, including the selection of appropriate spawning grounds. However, increased temperature due to climate change may lead to changes in hydrodynamics, shorter larval drifts, and earlier spawning, and consequently the location of the most suitable spawning grounds may change. We investigated whether the location of the most favourable spawning areas (allowing higher rates of larvae reaching coastal nurseries) was stable over time, and if differences could be found between environmentally contrasted years. We used a larval drift model taking into account hydrodynamics, larval characteristics and behaviour for three commercially exploited fish species (sole *Solea solea*, flounder *Platichthys flesus* and seabass *Dicentrarchus labrax*) in the Western Europe (encompassing the Bay of Biscay, the Celtic Sea and the English Channel). According to our model, we conclude that despite contrasting environmental conditions, the location of spawning grounds allowing the best chance of recruitment to nurseries for the offspring was fairly similar. However, even if the location of the main spawning grounds is stable over time, their relative effectiveness varies greatly between years. This would suggest that natural selection may favour the emergence of homing behaviour. This stability in this fish essential habitat location could facilitate protection measures. Going further, it could be interesting to study the variations occurring in spawning grounds (in terms of recruitment success, and retention/dispersion) during the course of a spawning season.

1. Introduction

The effects of climate change on the marine environment are both complex and difficult to predict (Peck et al., 2018; Rijnsdorp et al., 2010). Apart from temperature, climate change affects weather patterns (both frequency and intensity), sea ice cover, CO₂ concentrations, pH and salinity (Sriskanthan and Funge-Smith, 2011). Thus, the whole marine ecosystem is affected by climate change through the physiology, behaviour and population dynamics of species (FAO, 2011). For example, the Atlantic Meridional Overturning Circulation (AMOC), a major ocean current transporting warm waters towards the Northern Atlantic, is known to be gradually collapsing (Boers, 2021; Boulton et al., 2014; Thornalley et al., 2018). At the population level, fish thermal niches are shifting (Poloczanska et al., 2013; Santiago et al., 2016) leading to a tropicalization phenomenon (poleward shifts in the

center of distributions of a large number of species; Cheung et al., 2012; Costa et al., 2014). As temperature also leads to a quicker development for many fishes, it may induce a mismatch between predators and their preys (Keller et al., 2020).

Climate change also affects the reproductive cycle and spawning behaviour of fishes in numerous ways. Indeed, higher-than-optimal temperatures can affect every stage of the life cycle and are associated with changes in physiology at multiple levels (Alix et al., 2020). Furthermore, ocean acidification brings additional mortality in early life stages which are the most sensitive (Koenigstein et al., 2018). Higher temperature induces a shift towards earlier spawning (Fincham et al., 2013), changes in gamete development (resorption of oocytes in the worst cases) and egg quality (Donelson et al., 2010; Luo et al., 2017).

MEO mature adults spawn on the continental shelf, in areas that are distant from juveniles nurseries (typically shallow coastal areas), and

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have their eggs and larvae mainly passively transported by oceanic currents (Houde, 2008). The dispersal to nursery areas is critical since they provide high food abundance, good conditions for a rapid growth and a low predation rate on juveniles (Cabral et al., 2022 and references therein). Most of the eggs are not able to recruit, and estimates of larval mortality may be quite high. By conducting a literature review on marine fish populations, Le Pape and Bonhommeau (2015) estimated that survival-to-maturity rates as low as 1 in 100,000 are frequently observed. Recruitment of MEO species is highly stochastic and environmentally driven, making larval dispersal extremely sensitive to many parameters (Swearer et al., 2019; Treml et al., 2015). Many species have developed spawning strategies to enhance recruitment success that critically rely on environmental conditions such as temperature and oceanic conditions (Mullon et al., 2002). In this context, climate change might be particularly challenging to those species recruitment strategies.

Even though spawning locations are known to have major impacts on recruitment (Treml et al., 2015) and their location to be the result of adaptation to local conditions (Bailey et al., 2005), little is known about the inter-annual variability of the most suitable spawning grounds, i.e. those ensuring the best chance to recruit to a nursery area. On one hand, if the location of the most favourable spawning grounds are variable among years, it might be beneficial for species to adapt their spawning grounds based on annual environmental cues to maximize their fitness. In fact, marine taxa are able to track geographic shifts of isotherms over time to adapt to their occupied niche (Pinsky et al., 2013). On the other hand, if the location of most favourable spawning grounds remain stable over years, a homing behaviour would be an evolutionary advantage (Ciannelli et al., 2015). However, the modifications brought about by climate change and especially an enhanced temperature, such as phenological shifts (Fincham et al., 2013), altered currents (Bashevkin et al., 2020), or increased mortality rates (Alix et al., 2020; Dahlke et al., 2020), could have a detrimental impact on such a strategy.

In this context, the study of larval drift is of major interest in order to understand how changes in parameters may affect recruitment success. Because eggs and larvae are tiny propagules spawned in large numbers, it is near impossible to study and quantify their dispersal *in situ* (Levin, 2006). Some studies used geochemical trace elements in otoliths (Almany et al., 2007), genetic markers (Randon et al., 2021) or tracked drifters (Vendrami et al., 2021) to understand hydrodynamics and larvae transport. However, they are financially costly and only provide local insights of dispersal for a given time period and at a local scale. Therefore, biophysical modelling is often used to study larval drift and recruitment success (Swearer et al., 2019 and references therein). Biophysical models are widely used from evaluating the effects of management policies (Walker et al., 2020) to the prediction of recruitment (Henriksen et al., 2018) notably under climate change scenarios (Lett et al., 2010; van de Wolfshaar et al., 2021). This latter is of particular interest for fishes with a high fisheries interest in order to explore the sustainability of fisheries and the effects on exploited stocks.

Most studies using biophysical models to predict recruitment considered spawning grounds to remain in the same location over environmentally contrasting years (Lacroix et al., 2018; van de Wolfshaar et al., 2021), although other studies found that main spawning sites may change locations over time (Hidalgo et al., 2012). This article aims to test whether the potential spawning areas that ensure a good recruitment success are spatially constant even among years with contrasted environmental conditions. The objective is to provide insights on which spawning behaviour would be the most beneficial for populations, and on the potential effects of climate change. We focused on three MEO fish species: the common sole *Solea solea*, the European flounder *Platychthys flesus* and the European seabass *Dicentrarchus labrax*. Those are well-documented species of high fisheries importance. As they show differences in their life-history traits, they were used as ecological archetypes to infer and extrapolate to a wider diversity of species. We simulated the larval drift of these three species with a Lagrangian

particle tracking module embedded in a hydrodynamic model (Lazure and Dumas, 2008), and identified potential spawning areas generating high recruitment success. Then we compared the location of the most efficient spawning areas across years with contrasted abiotic conditions. This study was conducted on three fish species and on a large study area covering the northeast Atlantic side, from the southern Bay of Biscay to the English Channel through the Celtic Sea.

2. Material and methods

2.1. Determining groups of contrasted years

The study area focuses on the western Europe (from 41°N to 55°N and 18°W to 9.5°E), encompassing three sub-regions: the Bay of Biscay, the English Channel and the Celtic Sea (see Fig. 1d). The sub-regions delimitations are from the FAO fishing area 27 (<https://www.fao.org/fishery/en/area/27/en>). Apart of the Celtic Sea FAO divisions, our so-called Celtic Sea includes the Irish Sea, the West and South of Ireland, the Porcupine Bank and the Bristol Channel.

To determine groups of years with contrasted abiotic conditions, a Principal Component Analysis was performed on a 21 years environmental dataset (1999–2019). Each year was characterised by several parameters: two atmospheric pressure indices, i.e. North Atlantic Oscillation (NAO) and East Atlantic pattern (EA), sea surface temperature and precipitation in each sub-region. Atmospheric pressure anomalies inform on the general climatic conditions, as they are associated with strong wind and current patterns. NAO index indicates the intensity and location of the North Atlantic jet stream and storm track extending from eastern North America to western and central Europe. Strong positive phases of the NAO are associated with warmer years and stronger currents (Barnston and Livezey, 1987) which affect larval development and transport. However, the NAO is not necessarily a good indicator of abiotic conditions in the Bay of Biscay (Valencia et al., 2009). The EA was also considered in this analysis since it is the second most prominent mode of low-frequency variability in the North Atlantic and is more southward shifted when compared to the NAO (Borja et al., 2008). The NAO index and EA pattern data were extracted from the Climate Prediction Center (NOAA, USA) (<https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>). The sea surface temperature and precipitations data were issued from Copernicus (<https://doi.org/10.48670/moi-00153>, Hersbach et al., 2019). For precipitations and sea surface temperatures, winter values from December to March (that correspond fairly to the beginning of the spawning seasons of the studied species; detailed further in next sections) were averaged for each area separately (Bay of Biscay, English Channel, Celtic Sea). A hierarchical clustering based on PCA coordinates was then carried out to detect groups of years with similar environmental conditions.

2.2. Modelling larval drift

For each year from 1999 to 2019, we simulated larval drift to identify potential spawning areas generating high recruitment success. The larval drift model couples two submodels: a hydrodynamic model and an individual-based model.

2.2.1. Hydrodynamic model

We used MARS3D hydrodynamic model (Lazure and Dumas, 2008). We adopted a set-up similar to the one described in Petton et al. (2023) in the same study area as Savina et al. (2016). The model is forced by river discharges, meteorological data (wind fields, air temperature, atmospheric pressure, cloud cover and relative humidity from Meteo-France ALADIN, ARPEGE and ARPEGERHR models depending on years) and inter-annual variability at open boundaries for temperature and salinity from MERCATOR (GLORYS2V2, GLORYS_PSY2V4, rejeu, GLORYS_PSY2V4 or GLORYS_PSY4V3 depending on years). The model resolution corresponds to a grid of 2.5 km horizontally, and 40

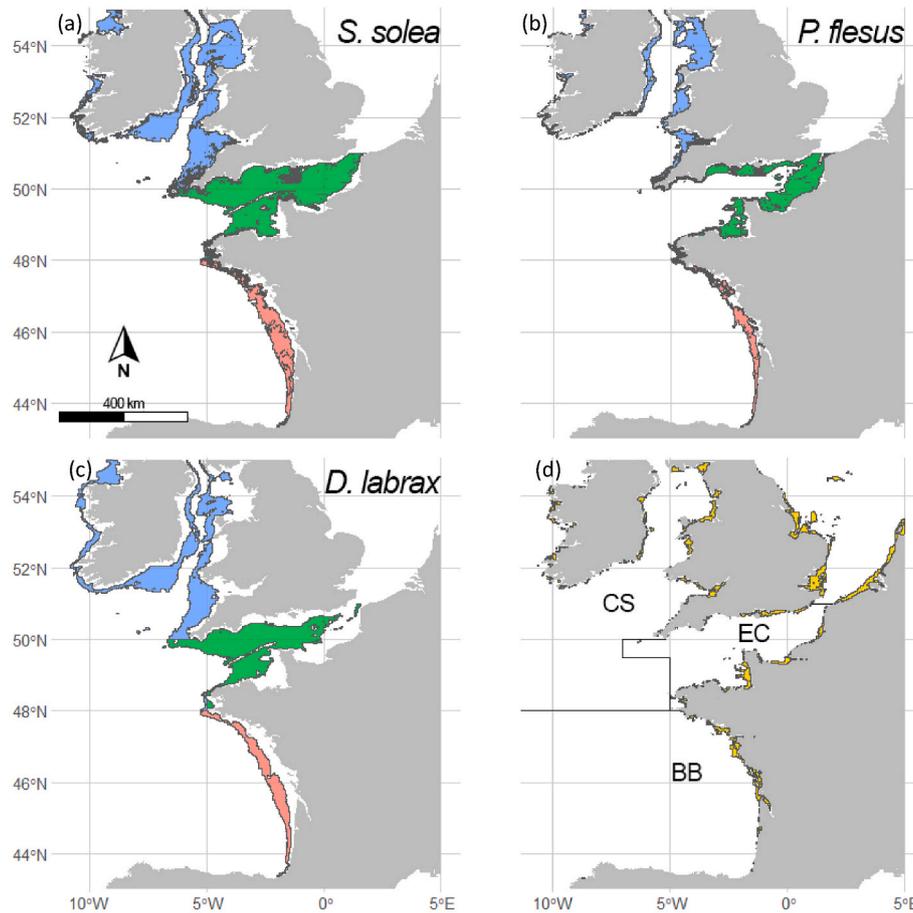


Fig. 1. Spawning (a, b and c, according to species) and nursery areas (d, for all species; coastal areas with less than 20 m depth) considered in the modelling for the three species. Sub-regions are symbolised by different colours: red for the Bay of Biscay (BB), green for the English Channel (EC) and blue for the Celtic Sea (CS). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

generalized sigma layers in the vertical with a time-step of approximately 2 min.

2.2.2. Individual-based model and species-specific parameters

An individual based model was coupled to MARS3D to describe particle transport and developments along calculated currents. We modelled three fish species: the common sole *Solea solea*, the European flounder *Platichthys flesus* and the European seabass *Dicentrarchus labrax*. These three species have a similar life cycle, with adults spawning on the

continental shelf, eggs and larvae dwelling before recruiting to coastal or estuarine nursery areas. However, they differ in their spawning locations, timing, planktonic larval duration and development (Table 1). Based on the information contained in Table 1, seabass experience a longer larval drift, with spawning occurring in deeper waters. In contrast, flounder spawns later and closer to the coast. Sole shares particularities with both.

The individual-based model relies on a Lagrangian module for particle transport (Huret et al., 2010) and takes into account multiple

Table 1

Parameters used in the modelling for the three species of interest. Growth equations for the pelagic larval duration (PLD) are $\alpha T^{-\beta}$ for *S. solea* and *P. flesus*, $D = \exp^{\alpha+\beta T} / 24$ for *D. labrax* egg stage and $D = 10^{\alpha} / 10^{\beta T}$ for *D. labrax* yolk-sac-larvae stage. Sizes are attributed at the beginning of each stage, and between two stages the size increases linearly until the next stage is reached. YSL: Yolk sac larvae, FFL: First feeding larvae, ML: Metamorphosing larvae.

Parameter	<i>Solea solea</i>	<i>Platichthys flesus</i>	<i>Dicentrarchus labrax</i>	References	
Spawning ground	30–90 m deep soft sediments	20–50 m deep soft sediments	50–90 m deep	Dambrine et al. (2021); Skerritt (2010); Tanner et al. (2017)	
Spawning period	December–May	February–June	December–April	Amara et al. (1994); Billard and Monod (1997); Eastwood et al. (2001); Skerritt (2010)	
Lethal temperatures	<8.75 °C or >16 °C	<8 °C or >15 °C	<9 °C or >17 °C	Koutsikopoulos and Lacroix (1992); Pickett and Pawson (1994); Yin and Blaxter (1987)	
Stage duration D	Egg	$\alpha = 274.64; \beta = 1.5739$	$\alpha = 12.65; \beta = 0.33$	$\alpha = 6.47; \beta = -0.129$	Barbut et al. (2019); Beraud et al. (2018)
	YSL	$\alpha = 137.92; \beta = 1.4619$	$\alpha = 516.5; \beta = 1.83$	$\alpha = 1.89; \beta = 0.077$	
	FFL	$\alpha = 3560.1; \beta = 1.9316$	$\alpha = 20; \beta = 0$	25 days	
	ML	$\alpha = 1146.1; \beta = 1.9316$	$\alpha = 300; \beta = 1$	22.5 days	
Size (mm)	Egg	1.28	1.00	1.35	Fonds (1979); Munk and Nielsen (2005); Skerritt (2010)
	YSL	3.00	2.50	3.50	
	FFL	4.25	4.00	5.50	
	ML	12.00	8.50	11.00	

factors such as the development rate of each particle, its swimming behaviour, its size and density (Huret et al., 2010). The model uses a random walk for vertical mixing. The location, growth rate, larval stage, survival as well as the temperature encountered by every particle were saved on a daily basis.

2.2.3. Larval stages, growth and behaviour

Individuals go through four developmental stages: egg, yolk-sac larvae (YSL), first-feeding larvae (FFL) and metamorphosing larvae (ML). Each stage has its own developmental rate. For *S. solea* and *P. flesus* the equation was taken from Barbut et al. (2019): $D = \alpha T^{-\beta}$. In this equation and all those following: D stands for the stage duration in days, T for temperature, and α and β are specific values for each stage and are indicated in Table 1. For *D. labrax* equations were taken from Beraud et al. (2018) with $D = e^{\alpha+\beta T}$ for eggs and $D = 10^\alpha/10^{\beta T}$ for the larval stages. As in Boussouar et al. (2001), those equations were converted into instantaneous variation of stages. Therefore, we obtained the expression of maturity in stage i at time t as:

$$m_i(t) = \int_{t_i}^t \frac{1}{D_i(T(s))} ds$$

The stage is completed and the particle switches on to the next life stage when $m_i > 1$.

Meanwhile, particle sizes, which affect buoyancy and thus position in the water column, were assumed to increase linearly between predefined stage sizes for each species (summarized in Table 1):

$$Size_i(t) = Size_i(t-1) + (Size_{i+1} - Size_i) \cdot m_i(t)$$

With $Size_i$ the size forced at the beginning of the current stage and $Size_{i+1}$ the size at the next developmental stage. Active vertical swimming was incorporated to the model. The first two life stages (eggs and YSL) are passive, and consequently only buoyant. For FFL and ML, we implemented a diurnal migration: the particles swam towards the surface during the night, and swam towards the bottom, up to 40 m deep, during the day (based on Champalbert and Koutsikopoulos, 1995 as in Barbut et al., 2019; Cabral et al., 2022; Tanner et al., 2017). Swimming speed corresponded to one body length per second.

2.2.4. Mortality

Two types of mortality were included in the model. The first one is due to the thermal tolerance of each species. An individual instantly died when it encountered its lethal temperature (Table 1). The second type of mortality builds up with each passing day of drift. It accounts mainly for predation, which is very difficult to estimate. We assumed a constant instantaneous natural mortality M : at each time step, a particle survives with probability $\exp(-M \times \Delta t)$. For *S. solea* and *P. flesus* that have similar pelagic larval durations (around one month, Paoletti et al., 2021; Sims et al., 2004), we used the same M equals to 0.04 day^{-1} (as in Rochette et al., 2012). It is close to what can be found in the literature (0.035 day^{-1} in Horwood, 1993 for soles and 0.048 day^{-1} in Barbut et al., 2019 for plaices). *Dicentrarchus labrax* have a longer pelagic larval duration, between 50 and 70 days. To ensure that the overall probability of survival to natural predation are of the same order of magnitude among species, we used this stage duration as a mortality proxy (as in Beraud et al., 2018). Based on the mortality chosen for sole and plaice, this led us to a mortality of 0.02 day^{-1} for seabass, as:

$$\tau_{labrax} = \tau_{solea-flesus}$$

$$e^{-\Delta t_{labrax} \cdot M_{labrax}} = e^{-\Delta t_{solea-flesus} \cdot M_{solea-flesus}}$$

$$M_{labrax} = \frac{\Delta t_{solea-flesus} \cdot M_{solea-flesus}}{\Delta t_{labrax}}$$

$$= \frac{30 \times 0.04}{\frac{50+70}{2}} = 0.02 \text{ day}^{-1}$$

2.2.5. Spawning releases

For each species, spawning areas and spawning periods were determined based on literature (Table 1, Fig. 1).

We assumed an extended spawning period for simplicity encompassing all the possible spawning dates found in the literature across the whole study area (Table 1). For many species, spawning events are triggered by specific temperature or photoperiod thresholds (Devau-chelle and Coves, 1988; Fincham et al., 2013; Oliveira et al., 2009). In our study, we opted for fixed spawning seasons across all years and regions. However, this choice raises concerns about eggs spawned either too early or too late, potentially facing lethal environmental conditions. To mitigate the impact of high mortality resulting from individuals spawned in unfavourable conditions, we decided to eliminate the most precarious segments of the spawning period. Consequently, the retained spawning period should encompass only conditions conducive to viable larvae development across the entire study area. Therefore, to ensure optimal conditions for larval survival and growth we removed 20 % of the spawning period at the beginning and at the end of it, and distributed 15 spawning dates evenly over the resulting period. On each of these spawning events, 10,500 particles were randomly distributed over the whole study area (3500 in each main sub-region Bay of Biscay, English Channel and Celtic Sea). In total, we computed the larval dispersal from 157,500 particles per species and per year.

2.2.6. Recruitment success

Nursery areas were set as areas located within the 20 m isobath (as proposed by Savina et al., 2016). A particle was considered as recruited when it successfully reached a nursery area alive (i.e. it has survived to lethal temperature and natural mortality) in one of its two last developmental stage (first-feeding or metamorphosing larvae).

2.3. Statistical analysis

2.3.1. Identifying successful spawning areas

For every year and species, spawning locations and the recruitment success of each particle were retrieved. A binary kernel-based smoother was used in order to make an estimation of the probability of success or failure everywhere in the area. This kernel is estimated by fitting a kernel for positive outcome and a kernel for negative outcome and then computing the proportion among both (Jensen, 2015). This provided for each year and species a map displaying probabilities of recruitment success. Kernel values were placed in a grid of 5 km cells. To identify zones of high recruitment success on those kernel maps, we carried out hot-spot analyses, using Getis-Ord G_i^* (Getis and Ord, 1992), an analysis commonly used in niche overlap studies (Colloca et al., 2009; Katara et al., 2021; Rissler and Smith, 2010). Such analyses compare the sum of a particular variable (here recruitment success probability) in a local neighbourhood network (here using the 4 nearest neighbours) against the overall sum of the area of interest. By using spatial auto-correlation statistics such as Moran's I, local hot-spots can be detected. We conducted those analyses in each of our sub-regions, and selected positive ($z_{G_i^*}$ score >0) and significant (p -value <0.05) hot-spots cells in our grid (Julian, 2013). Therefore, we obtained for each year and species a binary map displaying the location of hot spots of successful modelled spawning areas.

2.3.2. Comparison of effective spawning areas between contrasting year groups

To assess how the spatial distribution of favourable spawning areas varies depending on environmental conditions, we compared the hot-spots maps within groups and among groups of years resulting from the cluster analysis. To assess the similarity among maps, we used the

Schoener's D index. It is used to compare two density maps, point by point. This index lies between 0 (maps are completely different in every points) and 1 (maps are purely identical). This index was used in two different ways.

First, we calculated Schoener's D index on hot-spots binary maps for each pairs of years belonging to the same years group and looked at the resulting distributions of indices. This was used to assess the homogeneity in the location of the most favourable spawning areas between years having the same abiotic conditions.

Then, we looked more globally at the stability of spawning areas between different environmental conditions. For each year group, we stacked the binary maps showing where the most favourable spawning areas were located (we added each binary map to one another, and divided by the number of binary maps used). Therefore, we obtained a recurrence map for each year group, in which each cell has a value (between 0 and 100%) standing for the proportion of years when the grid was considered as a hot spot. These recurrence maps were compared for each sub-region using Schoener's D index. To assess the significance of this difference, we made bootstraps. We made random year groups, and calculated the difference between their recurrence maps for each sub-region. In total, 1000 random year groups were formed, leading to a Schoener's D index distribution. In the end, the hypothesis of spawning area stability was rejected when the Schoener's D index corresponding to the year groups formed using PCA was within the lowest 5% of the Schoener's D index distribution values obtained in the bootstrap with randomly formed year groups. The whole method process is summarized in Fig. 2.

3. Results

Annual recruitment rate means and trends were different according to species and sub-regions (Fig. 3). For *P. flesus*, the recruitment values in the three sub-regions were fairly on the same order of magnitude. For sole and seabass however, the recruitment values in the Bay of Biscay were significantly higher than the estimates obtained for the English Channel and Celtic Sea (as indicated by the Kruskal-Wallis tests on Fig. 3). The Bay of Biscay also displayed a higher inter-annual variability in the recruitment rate. In fact, significant differences in the variability in recruitment rates were found through a Levene test (for sole and seabass $p < 0.05$ when comparing the Bay of Biscay with the English Channel or the Celtic Sea). Recruitment's inter-annual variation pattern for *S. solea* and *D. labrax* were strongly synchronous (also among sub-regions), and very different from the pattern obtained for *P. flesus* (Fig. 3).

The PCA performed to evaluate environmental conditions for the different years of the 1999–2019 time-series revealed three different groups (Fig. A1). The first group is mainly characterised by low SST and

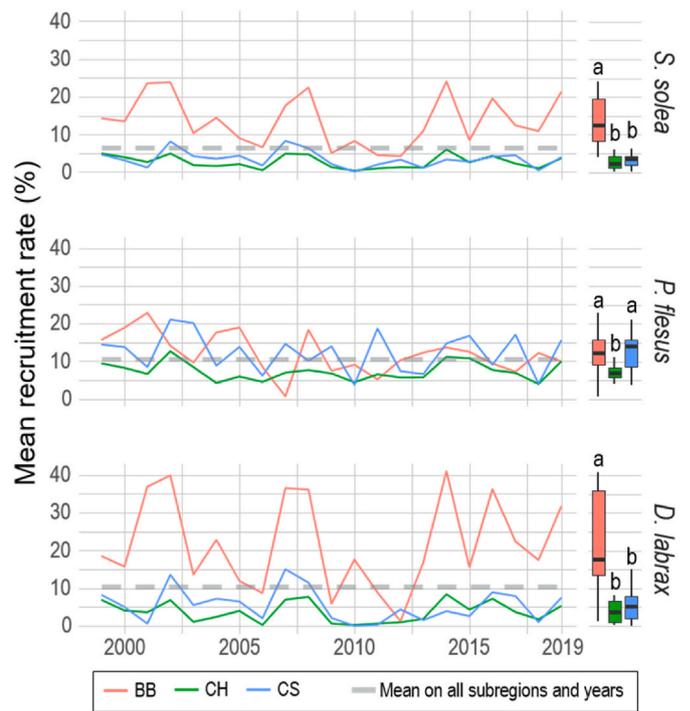


Fig. 3. Average recruitment rate through the years for the three species of interest (*Solea solea*, *Platicthys flesus*, *Dicentrarchus labrax*), for each sub-region (BB - Bay of Biscay; CH - English Channel; CS - Celtic Sea). The grey dotted lines represent the recruitment mean for each species, considering all years and sub-regions. Boxplots of mean recruitment rate for each region are on the right. Letters correspond to Kruskal-Wallis tests (p -value < 0.05).

NAO index, i.e. a “cold years” group that contains eight years (2000, 2001, 2006, 2009, 2010, 2011, 2013, 2018). The second group includes years with low precipitation, i.e. a “dry years” group, containing five years (2003, 2004, 2005, 2008, 2012). The last group merged the eight remaining years (1999, 2002, 2007, 2014, 2015, 2016, 2017, 2019) with high SST and NAO i.e. a “warm years” group. The recruitment rate calculated for these three types of years showed a similar pattern for all species and regions: “cold years” have the lowest recruitment rate, “warm years” the highest and “dry years” intermediate values between these two groups (Fig. 4).

To go further and check the similarity in the location of favourable spawning areas among years belonging to the same group, we compared the Schoener's D index between pairs of years belonging to the same group of environmentally contrasting years (Fig. 5). Globally, there is a

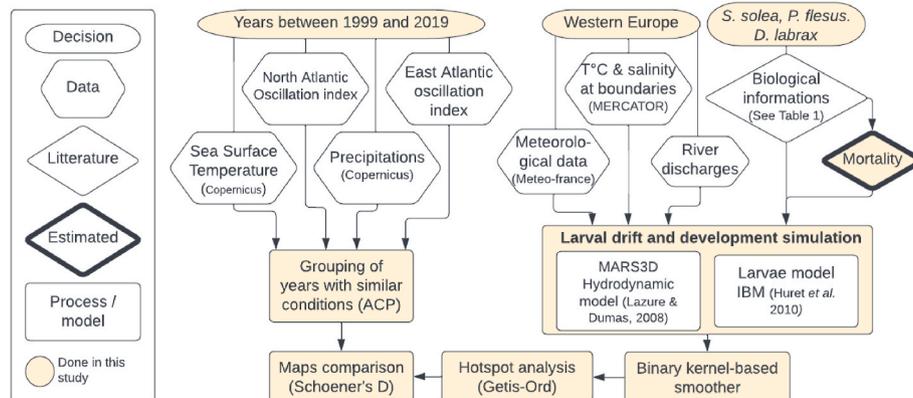


Fig. 2. Flowchart of the methods used to assess the stability of potential spawning areas ensuring a good recruitment success among years with contrasted environmental conditions.

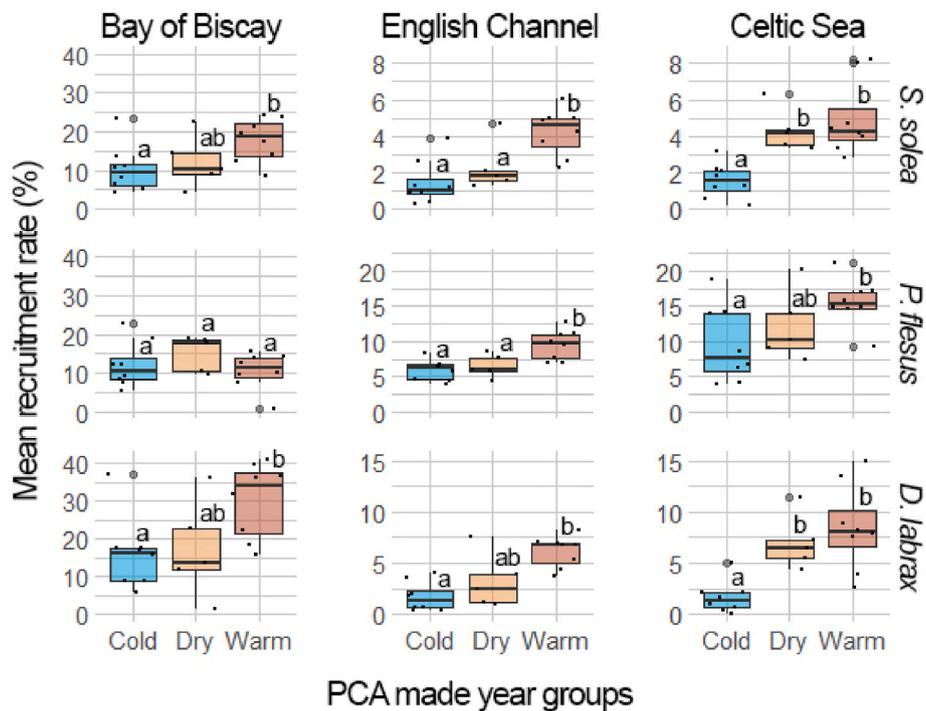


Fig. 4. Average recruitment rate for each group of environmentally contrasting years (that resulted from the PCA) within each sub-region and for each species (*Solea solea*, *Platichtys flesus*, *Dicentrarchus labrax*) to confirmed spawning areas are red, while theoretical ones are blue. Each point represents a year. Letters correspond to Kruskal-Wallis tests ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

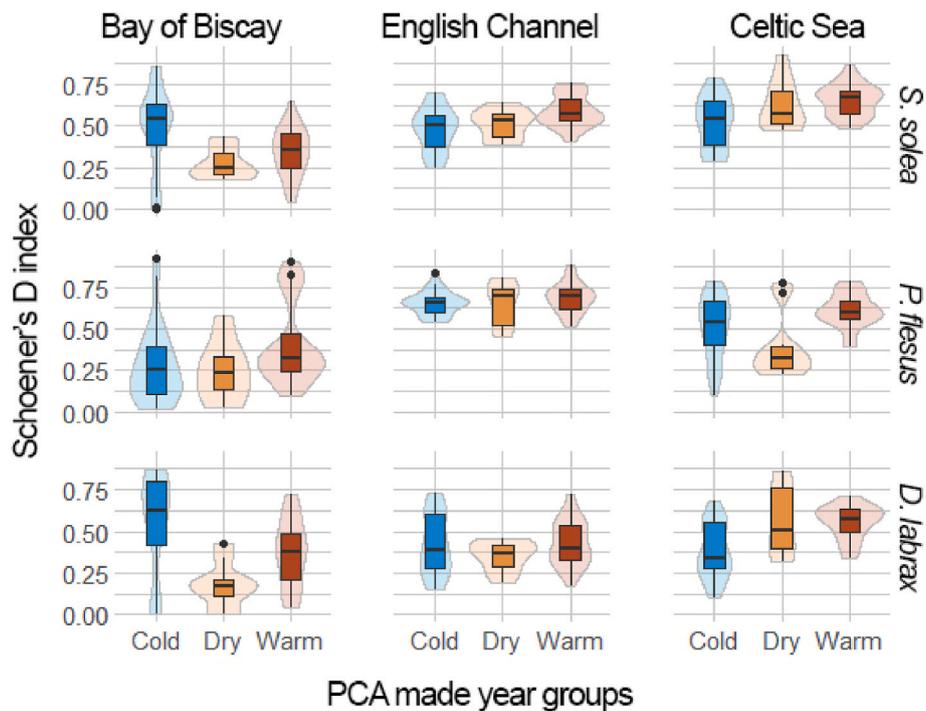


Fig. 5. Differences in the location of favourable spawning areas between two years belonging to the same group of environmentally contrasting years (Cold, Dry or Warm year groups) for the three species of interest (*Solea solea*, *Platichtys flesus*, *Dicentrarchus labrax*). Differences were assessed using the Schoener's D index (1 = maps are the same, 0 = maps are entirely different). The number of observations being the number of possible combinations without repetitions, for the Cold and Warm year groups $n = 28$ and for the Dry year group $n = 10$.

high variability in the location of favourable spawning areas between years having the same abiotic conditions. One would have expected low inter-annual variability within groups (meaning that all the years contained in the same abiotic conditions group would show similar

locations of favourable spawning areas) which is not the case here. This variability is particularly high (low Schoener's D index) in the Bay of Biscay, while the English Channel shows more consistent effective spawning area locations (as in Fig. 3). In the Bay of Biscay, there is

relative stability within the cold year group for sole and sea bass. For dry years, there is an inverted pattern for these two species between the Bay of Biscay and the Celtic Sea.

The location of the most favourable spawning areas are shown for all years combined and for each years group in Fig. 6. Main suitable spawning zones remain almost similar from one group of abiotic conditions to another. The bootstrap was used to check whether the differences among groups (quantified with the Schoener's D index) were statistically significant (Fig. 7). This confirmed that the actual location of spawning grounds was not sensitive to changes in environmental conditions, as only two of the 27 comparisons tested were significant (*P. flesus* in the Celtic Sea between dry and warm years p -value = 5×10^{-2} and *D. labrax* in the Bay of Biscay between cold and dry years p -value = 4.9×10^{-2}).

4. Discussion

Using a larval drift model and comparing three species with different spawning strategies, we explored whether the most suitable spawning areas were varying over time and more specifically, whether recruitment success varied between cold and warm years. Results show that there is no major change in the location of the most favourable spawning areas among years. However, the global efficiency of these areas is highly variable. While results vary among species, recruitment success tends to increase in warm years, probably because of different hydrodynamic patterns.

The overall recruitment success was highly variable depending on the species and region of interest. This stochasticity of recruitment success is a well known phenomenon (Cabral et al., 2021; Catalano et al., 2021; Palatella et al., 2014). Indeed, fish larvae are sensitive to many environmental parameters and suffer high mortality, and as such, recruitment to juvenile stage is a key reason of population dynamics variability (Snyder et al., 2014). Despite this stochasticity, synchronous peaks in terms of recruitment success were seen and that recruitment success was different among group of years. This confirms the influence of overall climatic conditions, here characterised by NAO, EA and SST in the recruitment success. Since our study is on a large scale, we used large scale integrative indices to summarize environmental conditions, but it might be worthwhile looking at more local indices to have a better understanding of the influence of environmental conditions in each sub region. In this study, a pattern arises where the recruitment success is overall the biggest in warm years and the smallest in cold years. It is not unusual to find better recruitment in warmer years (Cabral et al., 2021). This results both from overall modifications of oceanic currents (Boers, 2021) and on modifications of larval development (Borja et al., 2019; Henderson and Seaby, 2005). Indeed, the main reason for the higher recruitment in our model in our so-called "warm" years is certainly due to the currents. During these years, the strong positive NAO index induces a strong westwards flux (Hurrell and Deser, 2010), which would greatly favour recruitment, especially in the Bay of Biscay.

Overall in literature, the development rate is often mentioned as an explanation for better recruitment success in warmer years (Henderson and Seaby, 2005) however this supposes that enough food must be available (Huebert et al., 2018). In fact, food availability also has a major influence on survival (Houde, 2008), spawning period of larvae (Pinto et al., 2021) and may also influence the location of their spawning habitat (Bakun, 2006). Indeed, the peak abundance of larvae and preys are not necessarily synchronous, thus sometimes leading to a mismatch between both (Hinckley et al., 2001; Lima et al., 2022). During warmer years, the spawning period gets longer with warming temperature (Motos et al., 1996), and coupled with the later spring the overlap between larval and prey abundance is prolonged, enhancing the potential recruitment success (Kristiansen et al., 2011). In this sense, the timing of reproduction is essential.

As we have seen, modelling is a valuable tool in order to decompose the recruitment success according to several environmental parameters,

and to explore how species might behave when threatened by all the climate-induced modifications. Others methods cannot achieve this level of understanding on a large scale as *in situ* methods using ichthyoplankton sampling would need tremendous efforts to catch, identify and follow propagules in order to provide the same information (Swearer et al., 2019). Although modelling has its own limits as it requires many data on larval duration, larval development rates, vertical migrations and other behaviours or mortality that are difficult to collect because of the limited field data, models can still provide a rough picture and be a relevant tool to explore climate change scenarios (Lacroix et al., 2018).

In this context, using a bioenergetics individual-based development model coupled with plankton forcing might be a relevant solution (Huebert et al., 2018). The food-availability aspect can be included in particle-drift through DEB models, focusing on the energetic intake and how it is allocated in individuals (Dambrine et al., 2020; van de Wolfshaar et al., 2021).

For all species, the recruitment rate changes greatly across regions suggesting that local hydrodynamics hold great influence (Barbut et al., 2020). For instance, the Bay of Biscay ensures better recruitment success for the sole and the seabass than the two other regions. Although this is not the case for flounder, which is probably related to the thermal tolerance of this species since the Bay of Biscay is at the southern edge of its distribution area, the habitat becoming less and less favourable with warming years (Cabral et al., 2001; Vinagre et al., 2009). Another explanation for this lower recruitment could be related to the strong NAO in warmer years as explained earlier. During the winter, the westerly current induced by positive NAO is even stronger (Hurrell and Deser, 2010), which would explain why flounder with its late spawning would benefit less from this westward recruitment compared to the two winter spawning species.

Interestingly, these two species which have the most similar spawning strategies (sole and seabass) also display similar results in terms of recruitment rate and in the location of the most favourable spawning areas. It confirms that biological traits also play a fundamental role in the recruitment success (Barbut et al., 2019; Peck et al., 2009). The European flounder is yet again the exception between the three species, as differences among regions are less important for this species than for the other ones. Their shallowest spawning grounds, closest to the shore (Skerritt, 2010) are likely to limit the influence of local hydrodynamic configurations, enabling a more stable recruitment over years even though the difference between abiotic conditions are paramount (Bashevkin et al., 2020). Therefore to go further we could hypothesize that deep spawning fishes (>50 m deep) such as cod *Gadus morhua* (Cohen et al., 1990), mackerel *Scombrus scombrus* (Priede et al., 1995) or red mullet *Mullus barbatus* (Güçü and Bîngel, 2022) may be more sensitive to climate-induced modifications than fish species with a short larval duration and a short distance between the spawning grounds and the nurseries (Bashevkin et al., 2020).

The most favourable spawning areas are stable through time in our modelling despite contrasting environmental conditions. This is consistent with the fact that areas enhancing recruitment success are restricted to particular hydrodynamic features (Munk et al., 2009). As these specific areas ensure good offspring survival, it supports the emergence of a homing behaviour that was observed in our species (Exadactylos et al., 2003 for sole; Le Luherne et al., 2022 for seabass) which is quite common in fish species (Ciannelli et al., 2015). These habitats are likely to ensure a good retention of particles towards suitable spawning grounds, the success of the strategy critically depends on the persistence of the connected nursery grounds, even though dispersion towards new nursery areas might occur in specific environmental conditions (Borja et al., 2008; Peck et al., 2009).

In this analysis, we used theoretical spawning grounds based on depth and sediment type. As such, it is interesting to check whether the most suitable spawning areas are consistent with documented existing ones. Some of them are accurate, mostly for the European flounder. For instance only the European flounder have shown effective spawning

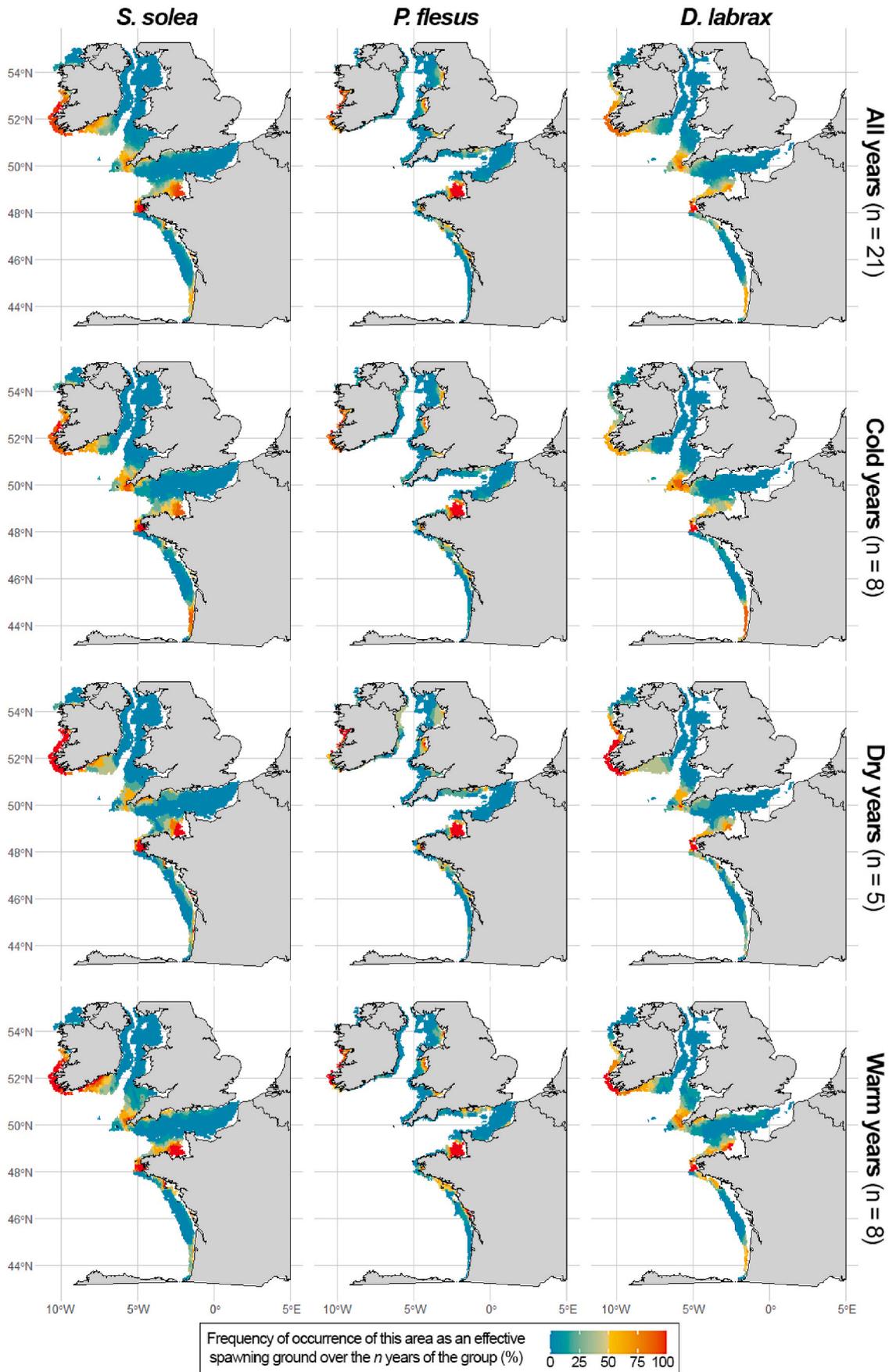


Fig. 6. Frequency maps showing the most suitable spawning locations estimated by our model for the three species (*Solea solea*, *Platichthys flesus*, *Dicentrarchus labrax*) and for each year group individually.

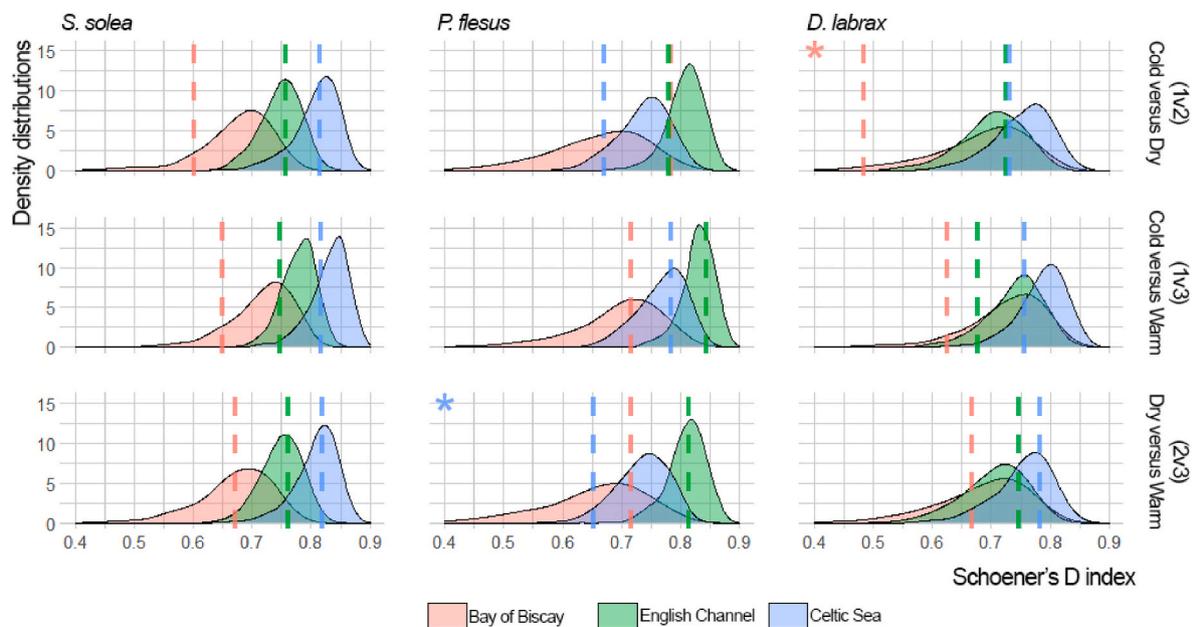


Fig. 7. Differences between the effective spawning ground frequency maps of environmentally defined year groups for the three species (*Solea solea*, *Platichthys flesus*, *Dicentrarchus labrax*). Differences were assessed using the Schoener's D index (1 = maps are the same, 0 = maps are entirely different). The density distributions correspond to the Schoener's D indices distributions obtained with the bootstrap when years groups were randomly composed (1000 iterations). Dotted lines correspond to the Schoener's D indices calculated when the year groups corresponded to those created in the PCA. Significance was assured when the Schoener's D index corresponding to the PCA groups belonged to the lowest 5 % of values in the distribution, and is represented by asterisks.

areas in the Irish Sea as supposed to (Armstrong, 2001). This is not the case for the other two species, probably because the modelled effective spawning areas in the Celtic Sea around the south west of Ireland were too intense and statistically obscured those in the Irish Sea. This difference between modelled and reality is found in several areas of the study, such as the Bay of Biscay, where for sole and seabass, the known spawning area located in front of the Gironde estuary (Alglave et al., 2022) is not detected (although the spawning area in the south is). This is likely due to the nursery definition we used, as we set all areas with less than 20m depth as nurseries, as used in many larval drift modelling (as in Savina et al., 2016 with areas less than 20m deep, Rochette et al., 2012 < 25m deep or also Hinrichsen et al., 2018 < 30m deep as nurseries). Even though nurseries are not restricted to estuaries, all areas less than 20m deep are not necessarily displaying all the conditions ensuring a good juvenile growth. Our study confirms that the effectiveness of a spawning area depends crucially on the quality of the nurseries to which it is connected, which can also change of location when facing perturbations (Støttrup et al., 2017). In order to obtain more accurate results in terms of recruitment success, it is essential to define where the nurseries and/or the spawning grounds for the fish species concerned are located.

We already have a glimpse of how complex climate change effects will be (Rijnsdorp et al., 2010), and it may have huge variability at small scale (Cerini et al., 2023). In order to predict the potential effects of climate change, it is important to make more global models including full-life cycle (as in Walker et al., 2020), food-web interactions, fisheries exploitation, potential invasive species, etc (see Peck et al., 2018 for more). However, the efforts to model everything is paramount, without saying that every step has its own uncertainty, many data are yet to be found/approximated, and as seen here each region and each species can react in a non-analogue way therefore introducing a lot of complexity in these forecasts.

5. Conclusion

According to our model and the assumptions we made to build it, we can conclude that despite contrasting environmental conditions, the location of spawning grounds allowing the best chance of survival for

the offspring does not change. However, even if the location of the main spawning grounds is stable over time, their relative effectiveness varies greatly from one year to the next. Indeed, the recruitment success is much higher during years showing high atmospheric pressure indices, probably due to easier (westward current) and faster (development) transport to the nurseries. This work highlights the benefits of modelling in this domain, whilst emphasising the importance of defining realistic nurseries when building larval drift models. Going further, it could be interesting to study the variations occurring in spawning grounds (in terms of recruitment success, and retention/dispersion) during the course of a spawning period.

CRediT authorship contribution statement

Violette Silve: Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Henrique Cabral:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Martin Huret:** Writing – review & editing, Software, Resources, Methodology. **Hilaire Drouineau:** Writing – review & editing, Visualization, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

None of the paper's authors have any competing interests to declare.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2023.108584>.

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