



Sensitivity to life-history parameters in larval fish drift modelling predictions for contrasting climatic conditions

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ABSTRACT

Many marine fish species display a long larval drift between offshore spawning grounds and coastal nursery areas. This drift, whose efficiency drive the renewal of the population, critically depends on many environmental factors and on the spawning behaviour of species. Given the complexity to collect field data on fishes early life stages, modelling has proved to be one of the most valuable tool to explore such questions. However, these complex models require many parameters, many of which are uncertain, making a comprehensive sensitivity analysis a crucial step before drawing conclusions on the effects of environmental drivers. This study focused on the larval drift of five species archetypes mimicking five commercially important fish species with contrasted spawning strategies and larval ecology, in five different sub regions over Western Europe, from the Iberian coast to the North Sea. Using an hydrodynamic model (MARS3D) coupled with an individual-based model, and by building a simulation design suitable for such sensitivity analysis, we assessed the relative influence of extrinsic (years and region's hydrodynamics) and intrinsic (spawning grounds' depth, spawning period, vertical migration, developmental rate, daily mortality and tolerance to temperature) factors and their two-ways interactions on recruitment success to nurseries. The thermal tolerance of species was one of the leading factors, suggesting that this is a critical parameter, especially when modelling species recruitment success at the edge of their distribution range. On the other hand, other parameters such as the nycthemeral vertical migration, that are often discussed in such larval drift simulation exercise, have proved to have a more limited influence for an analysis at such a large spatial scale. Overall, when studying larval drift on a large scale, local hydrodynamics and inter-annual variations hold most of the explained variance in the recruitment success, confirming the importance of repeating simulations over multiple years before exploring the connectivity among spawning and nursery areas.

1. Introduction

Species dispersal is a key process to ensure connectivity among habitats, populations, and the colonisation of new habitats. For a large number of fish species, high dispersal mainly occur in the pelagic larval stage when individuals drift under the influence of ocean currents (Houde, 2008). Larval drift takes place between spawning areas and nurseries, in which juveniles spend their growth phase. Estuaries and coastal areas are often used as nursery areas, as there is a high food availability, a low predation pressure and good conditions for juvenile growth (Cabral et al., 2022, and references therein). Since the drift is mainly passive, species exhibit diverse spawning strategies to maximize

the amount of larvae reaching nursery areas (here considered as recruitment), differing in the selection of spawning grounds and timing of spawning events. A spawning area closer to coastal areas and/or a short larval duration may maximise the probability of recruitment to nearby and suitable nursery areas (retention), but may, however, limit dispersal and diminish the inter-subpopulation connectivity or ability to colonize new habitats (dispersion). This trade-off between a short larval drift maximising survival and a longer drift favouring dispersion and enhancing population adaptability to environmental changes is often referred as the retention/dispersion trade-off (Strathmann et al., 2002; Warner and Cowen, 2002). Many environmental factors affect larval dispersion, including climatic and physical oceanographic factors

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affecting hydrodynamics (Dubois et al., 2016; Hidalgo et al., 2019) or also mortality that can be due to thermal tolerance or predation. In addition, spawning grounds and spawning seasonality might result from adaptation to these constraints to maximise offspring survival (Mullon et al., 2002). The behaviour of larvae (e.g. vertical migration) can also affect the resultant drift (Fiksen et al., 2007; Ospina-Alvarez et al., 2012). Thus, the influence of extrinsic (climate, topography) and intrinsic (spawning strategy, larval behaviour) factors on larval drift are of major interest to explore how retention/dispersion and connectivity would respond to modifications induced by inter-annual variability (Lett et al., 2010). Direct acquisition of observations on larval drift is almost impossible due to the difficulty of tracking and identifying many tiny propagules in the open sea. Indirect methods can be useful to assess continuity and/or fluxes between individuals from different areas, such as geochemical trace elements in otoliths (Almany et al., 2007; Tanner et al., 2016) or genetic markers (Randon et al., 2021; Reis-Santos et al., 2018). However, these methods are not suitable to infer dispersion drift patterns between spawning grounds and nursery areas for a large-scale study. For this purpose, biophysical models appear to be a suitable tool to explore dispersal patterns and connectivity between subpopulations. These models usually integrate two components: a hydrodynamic model that describes the environmental conditions affecting drift (e.g. currents, temperature, salinity), which is coupled with an individual-based model describing larval behaviour of the species considered. Their major advantage is their ability to integrate the main processes that can have an effect on larval drift, larvae development and/or behaviour, at both large and small scale. Thus, they play a major role in understanding drift, but also in predicting it in the context of climate change (van de Wolfshaar et al., 2021) or to evaluate the effects of management policies (Walker et al., 2020). However, the use of these tools raise several challenges. First, it is difficult to validate model outputs due to the lack of observational data on larval abundance (regular monitoring or opportunistic surveys are available for a few geographical areas, but even in these cases, there are major limitations regarding species or spatial and temporal dimensions). On the actual larval drift, there is a lack of information regarding parameters and complex interactions regarding environmental conditions (with only a few cases for which experimental data exists e.g. Fonds, 1979, and even in these situations experimental conditions are very far from environmental ones). Moreover, larval drift is extremely complex and modelling it involves making choices about which processes or factors to represent. For instance, in flounder, it has been shown that the density of eggs laid by a female depends on the salinity in which it was living in the days before laying (Solemdal, 1967). Trying to stick as closely as possible to real conditions (of both hydrodynamic and biological processes) leads to over-complicate the model and to drastically increase the number of parameters, leading to an increased uncertainty. Furthermore, the impact of model's parameters on outputs is often extremely asymmetrical, with some parameters having a huge influence on results, while the one from other is quite negligible. Modelled predictions on connectivity and recruitment have been proven to be sensitive to small changes in larvae vertical position in the water column (including larvae density or motion, Paris et al., 2007), spawning period (both timing Romero-Torres et al., 2017 and frequency Kough & Paris, 2015) or location of spawning grounds (Treml et al., 2015).

Sensitivity analysis of complex models, such as larval drift models, are difficult to implement due to a potential large number of parameters, the difficulty of accounting their interactions, and even to constraints regarding computation time. Specific methods based on the construction of appropriate simulation designs have been proposed (Favre et al., 2013) to optimise the number of simulations needed to obtain information on parameters influence and their interactions on the outputs. Sensitivity analysis have already been conducted to assess the importance of model configuration (Hufnagl et al., 2017; Huret et al., 2010; Monroy et al., 2017; Simons et al., 2013). However, such methods have rarely been used for biophysical larval drift model on life-history traits

and their sensitivity analysis have generally been limited to a specific parameters using a one-factor-at-a-time strategy and specific to a single area or species. In this work, we performed a sensitivity analysis to evaluate the impact of several parameters on results of larval drift modelling for five commercially important fish species, with contrasted spatial distributions, spawning strategies and larval period duration, in a large scale study covering the western European shelf. These species may be considered archetypes of species with similar life-history traits. We considered years with contrasting climatic conditions in order to encompass the various possible abiotic conditions. The results obtained are particularly important when building and parametrizing larval drift models allowing to highlight critical structural aspects and to support methodological procedures under high uncertainty levels.

2. Methods

2.1. Studied fish species

We selected five fish species: the common sole *Solea solea*, the Senegalese sole *Solea senegalensis*, the European flounder *Platichthys flesus*, the European plaice *Pleuronectes platessa* and the European seabass *Dicentrarchus labrax*. They share a common life cycle, with adults occurring in the continental shelf where spawning takes place and a larval drift phase before arriving to coastal nurseries, where juveniles spend their first years of life. These species differ, however, in their geographical range of their distribution and preferred habitats in the continental shelf, as well as in spawning period, larval period duration and development rates. Several other fish species have similar life-history traits and that is why these selected species may be considered as ecological archetypes and may be used to infer and extrapolate results to a wider diversity of species. The main life-history traits regarding the studied species are synthesized in Table 1.

2.2. Hydrodynamic model and spatial and temporal dimensions considered

We used MARS3D hydrodynamic model developed at IFREMER (Model for Application at Regional Scale, Lazure & Dumas, 2008) to force the larval drift. The configuration was similar to the one used by Savina et al. (2016), covering a large region ranging from the northern Iberian coast to the south of the North Sea (from 41°N to 55°N and 18°W to 9.5°E). The model has a 4 km horizontal resolution with 30 vertical generalized sigma layers. We used a time step of about 2 min to handle tidal currents on the continental shelf. Meteorological data were provided by Meteo-France (ARPEGE). River discharges were similar to Savina et al. (2016). Inter-annual variability at open boundaries for temperature and salinity provided by a global circulation model solution ORCA from the OPA-NEMO model (Michel et al., 2009). The wide spatial range considered is suitable to explore inter- and intra-species differences, according to the biological and ecological parametrization that was used. In what concerns the temporal dimension, we run simulations for five environmentally contrasted years. To select and characterize these years we used the North Atlantic Oscillation (NAO). The NAO is an important index that informs on the climatic conditions in the North-Atlantic (Barnston and Livezey, 1987). This index indicates heights and pressure anomalies over the North Atlantic, Eastern United-States and Western Europe. High NAO is generally associated with warmer temperatures and stronger currents (Hurrell and Van Loon, 1997; Pingree, 2005). As such, it can affect larval supply to nursery grounds (Rochette et al., 2012).

To focus on five environmentally contrasted years, we carried out a clustering analysis of the NAO index over the last decades (source: <https://www.cpc.ncep.noaa.gov/>) and selected five years (2010, 2011, 2012, 2016 and 2018) showing different index values thus representing a wide range of abiotic conditions in our study area (Dupuis et al., 2006).

Table 1

Parameters used in the modelling for the five species of interest. Growth equations for the pelagic larval duration (PLD) are [a] $D = \alpha T^{-\beta}$, [b] $D = e^{\alpha+\beta T}$ and [c] $D = 10^\alpha / 10^{\beta T}$. 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>S. solea</i>	<i>S. senegalensis</i>	<i>P. flesus</i>	<i>P. platessa</i>	<i>D. labrax</i>	References	
Spawning grounds bathymetry	30-90m deep; soft sediments		20-50m deep; soft sediments	20-40m deep; soft sediments	50-90m	5, 11, 16, 17, 18	
Spawning period	January-April	February-July	February-June	December-May	January-April	1, 5, 6, 10, 15, 16	
Lethal temperatures	<8.75°C or >16°C	<12°C	<8°C or >15°C	<2°C or >12°C	<9°C or >17°C	11, 14, 19	
Stage duration D	Egg	$\alpha = 274.64$; $\beta = 1.5739$		$\alpha = 12.65$; $\beta = 0.33$	$\alpha = 114.18$; $\beta = 0.95$	$\alpha = 6.47$; $\beta = -0.129$	2, 4
	YSL	$\alpha = 137.92$; $\beta = 1.4619$		$\alpha = 516.5$; $\beta = 1.83$	$\alpha = 469.6$; $\beta = 1.14$	$\alpha = 1.89$; $\beta = 0.077$	
	FFL	$\alpha = 3560.1$; $\beta = 1.9316$		$\alpha = 20$; $\beta = 0$		$\alpha = 25$; $\beta = 0$	
	ML	$\alpha = 1146.1$; $\beta = 1.9316$		$\alpha = 300$; $\beta = 1$	$\alpha = 223.5$; $\beta = 1.25$	$\alpha = 22.5$; $\beta = 0$	
Size (mm)	Egg	1.28	1.00	1.00	1.55	1.35	3, 7, 8, 9, 13, 16
	YSL	3.00	2.40	2.50	/	3.50	
	FFL	4.25	3.34	4.00	7.00	5.50	
	ML	12.00	5.75	8.50	11.50	11.00	

The number refers to the following references: 1: Amara et al. (1994), 2: Barbut et al. (2019), 3: Bedoui (1995), 4: Beraud et al. (2018), 5: Dambrine (2020) and Dambrine et al. (2021), 6: Devauchelle et al. (1987), 7: Dinis et al. (1999), 8: Fernández-Díaz et al. (2001), 9: Fonds (1979), 10: Imsland et al. (2003), 11: Koutsikopoulos et al. (1989), 12: Koutsikopoulos and Lacroix (1992), 13: Munk and Nielsen (2005), 14: Pickett and Pawson (1994), 15: Rijnsdorp (1997), 16: Skerritt (2010), 17: Tanner et al. (2017), 18: Wegner et al. (2003), 19: Yin and Blaxter (1987).

2.3. Individual-based model

The individual-based model coupled to MARS3D was similar to the one used in Huret et al., 2010. It simulates the pelagic dispersal of individuals from nurseries to spawning grounds, while taking into account their development and their swimming behaviour. It also uses a random walk for vertical mixing, mainly due to turbulence generated by wind (Huret et al. 2010). This random walk is based on the eddy diffusivity, consistently with Visser (1997). Every day, the model saved the location, growth rate, larval stage, survival, as well as the temperature encountered by every particle.

2.3.1. Spawning, particles (larvae) release

The potential spawning areas were obtained from information in the literature on the preferred depth of spawning areas, as well as on the substrate nature (Table 1, Fig. 1). Across our study area, spawning periods of the five species reported in the literature vary according to latitude. For simplicity, we considered a single extended spawning period for each species across the entire study area that encompasses all spawning seasons reported in the literature. Five spawning events were regularly distributed within each spawning period. For each species, on each of these spawning dates, 1200 particles were randomly released into the spawning area of each region (Iberian coast, Bay of Biscay, Celtic Sea, English Channel and North Sea; see Fig. 2 for regions) i.e. 30,000 particles per species and per spawning period over the whole area. Eggs were released at the bottom of the water column for flatfish species and randomly in the vertical dimension for *D. labrax*.

2.3.2. Larval development and behaviour

• Larval stages

During their drift, particles evolve through four developmental stages: eggs, yolk-sac larvae (YSL), first-feeding larvae (FFL) and meta-

morphosing larvae (ML). The developmental rate was taken from Barbut et al. (2019) for *S. solea*, *P. flesus* and *P. platessa* (eq.1) and from Beraud et al. (2018) for *D. labrax* (eq.2 for eggs & eq.3 for larvae). Information regarding *S. senegalensis* being scarce, we used the same formula for this species as for *S. solea*. The duration of each stage was related to temperature with the following equations:

$$D = \alpha T^{-\beta}, \quad (1)$$

$$D = e^{\alpha+\beta T}, \quad (2)$$

$$D = 10^\alpha / 10^{\beta T}, \quad (3)$$

D stands for the stage duration and T for temperature. Values for α and β for each stage are indicated in Table 1.

To take into account the temperature encountered, D was computed for each particle at each timestep. These equations were then transformed into instantaneous variation of stages as in Boussouar et al., 2001 where they obtained the expression of maturity in stage i at time t as:

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

Where T is the temperature. The stage completion was achieved when $m_i > 1$.

• Growth

Individual sizes affect the speed at which the particle rises and falls through the water column. Thus, it is one of the components affecting the vertical position of the particle, along with its density and the water mixing. The growth of an individual is based on two submodel. First, a submodel describes how the stage maturation (see previous point) that indicates how close an individual is to achieve a larval stage transition. This is based on the Boussouar et al., (2001) equation and accounts for the effect of the temperature on the development. Then, to convert this

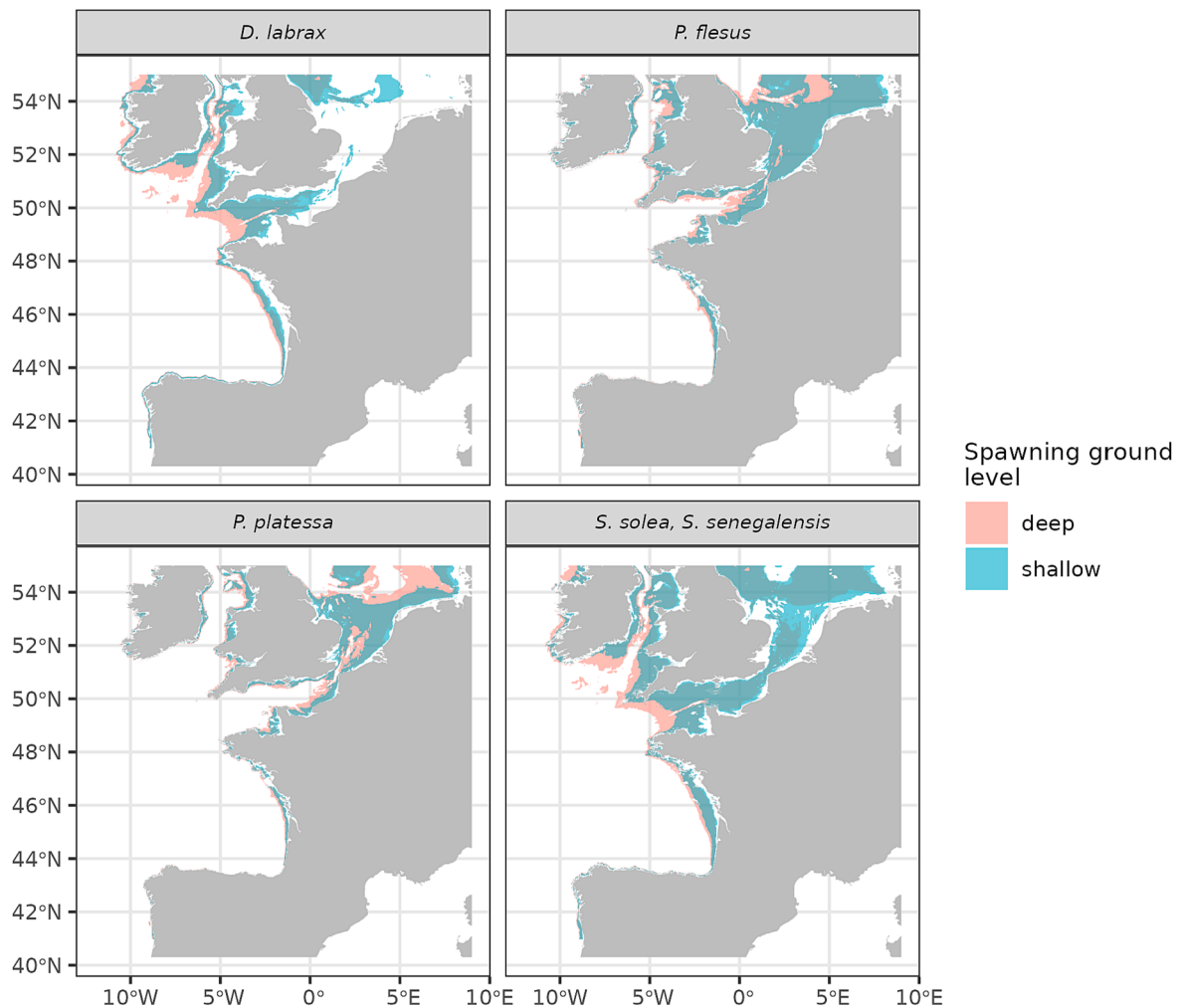


Fig. 1. Location of spawning areas considered in the modelling. Spawning areas were computed based on the species preferential spawning areas depths and bottom sediments (Table 1). The bathymetry was extracted from MARS3D, and sediments originated from EMODnet Geology project (2019). The high and low modalities had this depth range respectively increased by 10% or reduced by 10% (Table 2).

temperature dependent maturation level ($m_i(t)$) into a length, we postulated that stage transition occur at constant length (Table 1) and that length increases linearly with maturation in the stage:

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

With $Size_i$ being the size forced at the beginning of the current stage and $Size_{i+1}$ being the size set for the next developmental stage. As such, the size includes both the effect of the larval development rate and of the temperature.

- Nycthemeral vertical migration

Active movements and positioning throughout the water column changed along larvae development. The density of the eggs and YSL was assumed to be equal to that of the surface water. Their vertical position was calculated from Stoke's equation, taking into account the particle's properties (diameter, density), as well as the water's (density, viscosity, turbulence) as described in (Petitgas et al., 2006). While for FFL and ML a vertical behaviour was included in the model (based on Champalbert and Koutsikopoulos, 1995). Particles of these larval stages migrate towards surface at night and towards the bottom during the day. The speed of this vertical migration was restricted by their size as they move at a speed set as one body length per second. From now on, the term vertical migration refers only to nycthemeral migrations and does not take into account tidal migrations.

- Survival to thermal conditions

Based on literature, we defined for each species a tolerated temperature range for each species (Table 1); particles died when they encountered a temperature outside these ranges.

- Recruitment

Drift lasted for at most 70 days. Larvae could settle in nurseries as long as they did not encounter any lethal temperature, reached at least the third stage (first feeding larvae) and passed through an area considered as a nursery (a coastal area shallower than 20 m deep; Fig. 2) (as proposed by Rochette et al., 2012 and Savina et al., 2016). This implies that particles can be considered as efficiently recruited even though they did not reach the end of their larval stage duration (which is based on temperature as described in Table 1, and set with 70 days as a maximum).

- Mortality

A mortality of 0.09 day^{-1} was applied (Savina et al., 2016) to limit the overestimation of recruitment due to long drifts, i.e. for particles recruiting after t days, we assumed that numbers were given by $e^{-0.09 * t}$ individuals. The longer the drift (either because of slower larval development or because of unsuitable current transport), the lower the

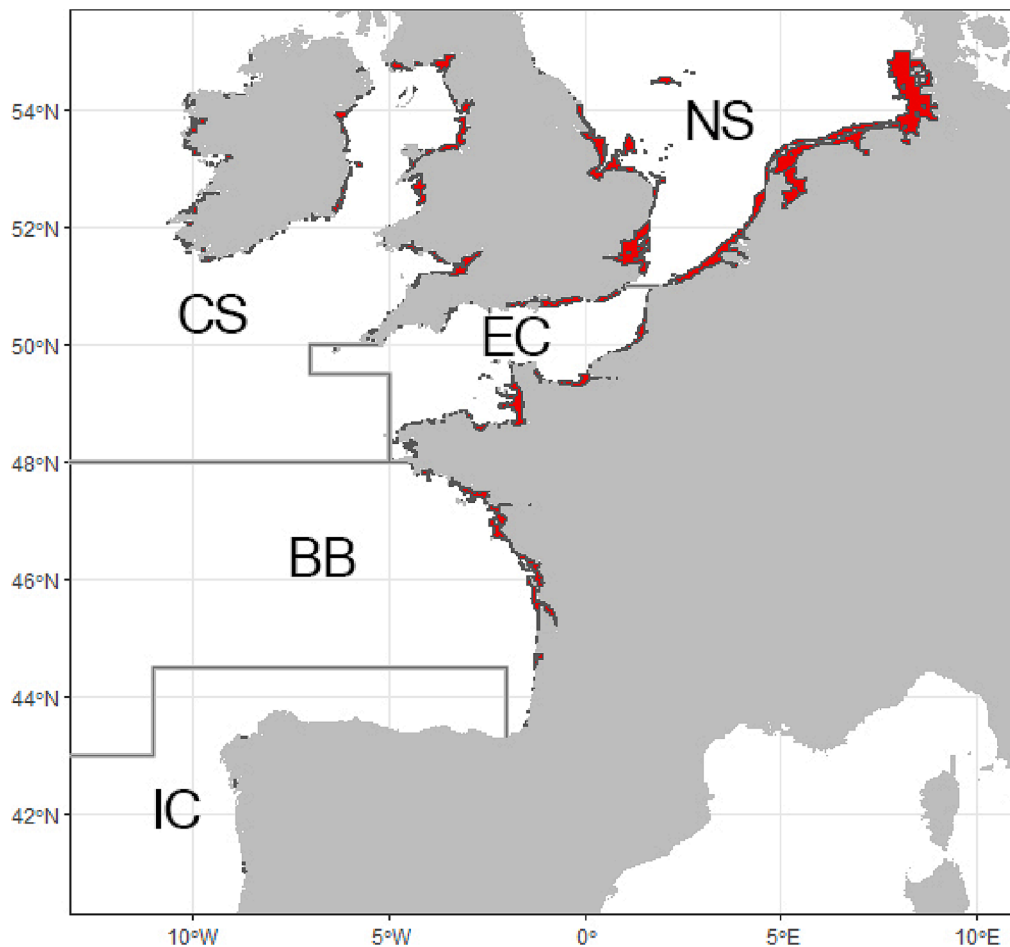


Fig. 2. Sub-areas and nursery location considered in the modelling. All species shared common nursery areas (depth < 20 m, bathymetry extracted from MARS3D). The study area was divided into five sub-areas, following the ICES statistical rectangles: the Iberian coast (IC), the Bay of Biscay (BB), the Celtic Sea (CS), the English Channel (EC) and the North Sea (NS).

survival probability is. These calculations were made *a posteriori* after model simulations. As the larval drift duration depends on both the development rate and the current transport, the probability to survive until recruitment vary among trajectories. Here, we do not account for any post-settlement mortalities since we focus only on the larval drift efficiency.

2.4. Sensitivity analysis

2.4.1. Simulation design

A sensitivity analysis was conducted to assess the impact of parameters on the proportion of larvae (particles) that reached a nursery (denoted Y). The analysis was conducted on seven parameters that could potentially affect recruitment, among which the annual conditions along with six model parameters (X): the development rate, the presence of a vertical migration, the spawning season, the mortality due to lethal temperature, the daily natural mortality (applied *a posteriori*), and the spawning grounds depth. Apart from the year and the presence of a vertical migration, a low and a high value were set based on a 10% range of variation (Table 2) for parameters values set based on literature (Table 1).

A fractional factorial design was built with a resolution V (allowing the estimation of main effect and second order interaction of parameters): each row being a simulation and each column indicating whether the values of parameters to be used (Fig. 3). Fractional factorial design of simulations are orthogonal. This design led to plan of 16 simulations, which was repeated separately for each year and species, and for both

global mortalities (Fig. 3).

All the strong assumptions included in the model are summarised in Table 3.

2.4.2. Data analyses

All statistical analysis were performed using R version 4.0.3 (R Core Team, 2020). The statistical individual used throughout these analyses in each simulation was the sum of the numbers of particles on which mortality was applied, divided by the total number of eggs from a same batch (i.e. same species, same simulation in the experimental design, same release date and release location) that successfully recruited, whatever the nursery areas in which they arrived. For each species, and for each sub-area, generalized linear models were conducted to test the influence of the selected model parameters and their two-way interactions (the six parameters of the simulation design plus years) on the proportion of recruitment. We used GLM with a quasi-likelihood family (Weddeburn, 1974) with a logit link a variance of $\mu(1-\mu)$ to fit to the positive recruitment values. This family and link function were used to mimic a binomial family (this variance function and logit functions are the standard options in a binomial regression, ensuring that predicted values lie between 0 and 1 since we analysed proportions, and that predicted values close to zero have variances close to zero), without accounting for the number of particles (accounting for the number of particles would arbitrarily modify the power of the statistical tests; White et al., 2014). For each species and zone, the initial model was built with all variables and second-order interactions. Then, we iteratively removed the variable (or second-order interaction) with the highest p .

Table 2
Variation range for parameters used in the sensitivity analysis for our five species of interest.

	Developmental rate		Vertical migration		Global mortality (day ⁻¹)	
	High	Low	High	Low	High	Low
All species	m _i >0.9	m _i >1.1	Presence	Absence	0.099	0.081

	Spawning ground bathymetry (m)		Spawning season (spawning events)		Temperature tolerance (°C)	
	High	Low	High	Low	High	Low
<i>S. solea</i>	33-99	27-81	13/01, 11/02, 13/03, 12/04, 12/05	20/12, 18/01, 17/02, 19/03, 18/04	>9.6 ; 17.6<	>7.9 ; 14.4<
<i>S. senegalensis</i>	33-99	27-81	19/02, 05/04, 20/05, 04/07, 18/08	14/01, 28/02, 14/04, 29/05, 13/07	>13.2	>10.8
<i>P. flesus</i>	22-55	18-45	16/02, 25/03, 01/05, 07/06, 15/07	17/01, 23/02, 01/04, 08/05, 15/06	>8.8 ; 16.5<	>7.2 ; 13.5<
<i>P. platessa</i>	22-44	18-36	19/12, 02/02, 19/03, 03/05, 18/06	13/11, 28/12, 11/02, 28/03, 13/05	>2.2 ; 13.2<	>1.8 ; 10.8<
<i>D. labrax</i>	55-99	45-81	13/01, 11/02, 13/03, 12/04, 12/05	20/12, 18/01, 17/02, 19/03, 18/04	>9.9 ; 18.7<	>8.1 ; 15.3<

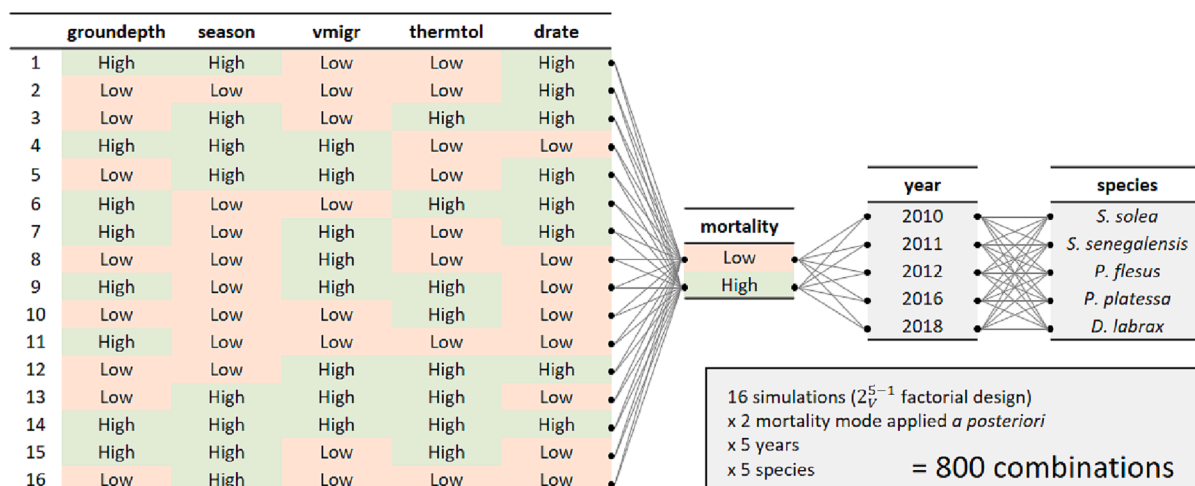


Fig. 3. Simulation design used for the sensitivity analysis. “Grounddepth” stands for the bathymetry of the spawning ground, “season” for the spawning season, “vmigr” for the vertical migration, “thermtol” for the tolerance to temperature, “drate” for the developmental rate and “mortality” for the global mortality rate.

value (from χ^2 tests) till all remaining variables were significant (i.e. all p.values < 0.05). The explained deviances were used to assess for the impact of every model parameter on the outputs.

3. Results

On overall, parameters importance differ according to the species and area considered. The inter-annual variability seems to be the most important factor driving recruitment success (Fig. 4, Table 4). On the other hand, vertical migration has a minor role in the total variability, whatever the species. The developmental rate and the global mortality have the same impact on recruitment, which seems logical as both play on the larval drift duration. In fact, the growth rate allows the particle to recruit more or less quickly, while the daily mortality rate makes the

particle’s ‘value’ higher or lower at the time of recruitment. Most particles recruited at approximately 20 days of age, predominantly prior to the completion of their larval stage duration (Fig. S.1.).

Regarding the influence of parameters on recruitment success, *D. labrax* shown a very similar profile to *S. solea*. For both of them, whether a particle survived or not was mainly due to year conditions. Due to an early spawning period in the model, as we move northwards the spawning period (noted as “season” in the figures) and temperature tolerance become more and more important in explaining recruitment success. Compared to those two, *S. senegalensis* seemed affected by year-to-year variations in the lower latitude regions (Iberian Coast), and more by the depth of the spawning grounds when going upward. In the North Sea, for the few particles that managed to survive, the depth defining the spawning areas was of great importance for *S. senegalensis* (24% of

Table 3
Modelling assumptions, further discussed in the discussion section.

Parameter	Definition	Assumption
vmigr	Nycthemeral vertical migration	Did not include tidal migration, considered as irrelevant at our study scale.
season	Spawning period window used	Five spawning events were considered to bring enough information to cover the whole spawning period. They were set consistent across all geographical regions.
thermtol	When meeting a temperature outside of its temperature tolerance range, the particles instantly died	Did not consider adaptation.
mortality	Daily mortality to limit the overestimation of long-drifts	The daily mortality was set as the same for all developmental stages and across the whole study area. We did not account for any post-settlement mortality.
PLD _{max}	Maximum larval drift duration, set at 70 days	We considered that most particles recruit before (Fig. S.1), and that the few ones that could have recruited after would not have changed the results much because of the daily mortality rate.
Recruitment success	The particle successfully reached nursery grounds while being still alive and at least in its FFL stage, and can continue its life cycle	A first-feeding larvae was considered developed enough to remain in a nursery ground once it reached it

explained variance). This is consistent with a species at the margin of its distribution area, as only in very specific locations the recruitment success could be achieved. Also in the North Sea, the depth of the spawning grounds also appeared to influence recruitment success for the cold water species *P. platessa* (12% of explained variance), which spawns there naturally on the contrary to *S. senegalensis*. As for in lower latitudes for *P. platessa*, in the Bay of Biscay several parameters related to temperature conditions (year & the mortality due to temperature tolerance) came out as important. Apart from these two notable points, the other parameters of interest in the plaice models did not exceed 8% explained variance.

The main differences between *S. solea* and *P. flesus* in the way they were modelled was their spawning areas and their spawning period, with *P. flesus* laying eggs closer to the coasts and *S. solea* spawning eggs earlier. With the generalized linear models, it seemed like *P. flesus* was less sensitive to the mortality due to temperature, and to the vertical migration.

4. Discussion

Larval drift simulation model are important tools to explore the influence of environmental conditions on present or future fish recruitment success. However, given the limited knowledge on fish larval biology and the complex of both the hydrodynamic and IBM models, lot of uncertainties undermine the results. In this context, this study presents a comprehensive sensitivity analysis to quantify the relative importance of most commonly reported sources of uncertainty (Swearer et al., 2019).

4.1. Approach

In this article, we used a large-scale approach, which of course impairs the realism of each modelled species. However, such a large scale allowed us to compare sensitivity of recruitment estimates in very contrasted oceanographic conditions and to study the influence of large

scale factors, such as latitude effects (Vinagre et al., 2008). Similarly, we used simple species archetypes that allowed us to compare important traits of spawning behaviour despite the limited literature on the ecology of fishes at first life stages. Of course, such archetypes do not aim to precisely mimic the species, as would be required in a predictive modelling exercise. However, using contrasted archetypes enabled us to better understand which factors influence the recruitment depending on species characteristics.

This “archetype approach” was also used for the parametrization of the sensitivity analysis. Depending on species, some processes are more well known than others. As such, species by species, the uncertainty surrounding parameters values are not similar. However, this is variable within species and within parameters, so we chose to use a common 10% range of uncertainty around parameters, a standard range frequently used in sensitivity analysis (Xu and Gertner, 2008) to standardize and facilitate comparisons. Of course, if focusing on a specific species and region, it would be worthwhile adapting the range of uncertainty to the available knowledge on the parameter.

By doing so, we do not take into account local adaptations that species may display to enhance recruitment success in specific environmental conditions. This includes local adaptation in spawning ground selection to improve the larval drift transport or in spawning dates to ensure that offspring develop in suitable thermal conditions, and any kind of adaptations to environmental variability (Yamahira and Conover, 2002). As such, our analysis should not be seen as a precise exploration of the effect of a factor on a specific species in a specific region, but rather as a general exploration of the impact of several parameters on more general archetypes.

Another limitation of this large spatial scale and multispecies approach is that the number of particles per species and year should be limited because of memory limitations. Here, we use “only” 30.000 particles per species and year, which might be smaller than in other simulations and it might be interesting in the future to include the number of particles as a parameter of the sensitivity simulation, as well as more frequent releases (as in Monroy et al., 2017). Despite these limitations, since our sensitivity analysis was carried out on multiple years and given that the experimental design ensures the orthogonality between years and other parameters, this partly mitigates the potentially limited number of particles in each single year.

To carry out the sensitivity analysis, we built orthogonal simulation design to quantify the influence of different source of uncertainties. While orthogonal experimental design have been largely applied to explore the sensitivity of complex ecological models, they have rarely been applied to larval drift models, for which one-factor-at-a-time strategies have generally been used (Lacroix et al., 2013; Tanner et al., 2017). A fractional factorial simulation design was used to decrease the number of simulations while preserving the orthogonality of factors, ensuring independency of parameters. It should be noted that we used a complete factorial design for the mortality parameter, as such, the orthogonal fractional design for most parameters was “nested” into a complete factorial design for mortality. This strategy was selected because the effect of mortality was run a posteriori on simulations and as such did not require running extra time-consuming simulations. Nesting a fractional factorial design within a complete factorial design preserves the orthogonality of all factors, and as such did not affect the estimation of the parameters of the fractional design, while improving the estimation of the effect of mortality (reducing the standard-error) without any extra-simulation costs. Orthogonal design allows for the simultaneous quantification of the main effects (as in a one-factor-at-a-time strategy), and of their first-order interactions, while limiting the number of simulations to carry out (Faivre et al., 2013). Here, results show that main effects were largely dominant. For example, it can be seen that many factors interact with year and spawning season. As such, the effects of those parameters differ depending on the yearly environmental conditions. Consequently, simulating larval drift over multiple years appear require to get a reliable average pattern. In order to comprehend this

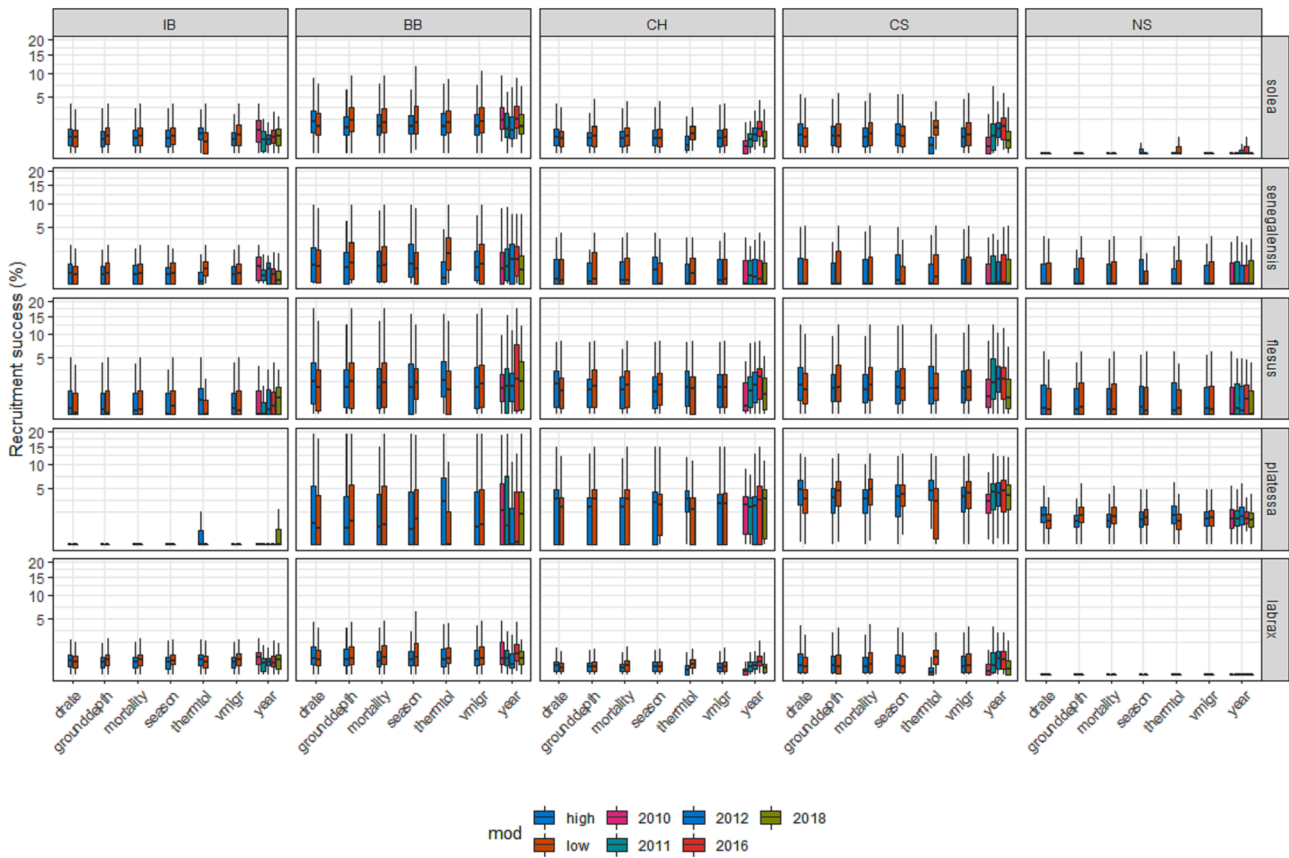


Fig. 4. Recruitment success according to parameters modalities within each spawning area for each species (IB: Iberian coast, BB: Bay of Biscay; CH: English Channel; CS: Celtic Sea; NS: North Sea). “Drate” stands for the developmental rate, “grounddepth” for the bathymetry of the spawning ground, “mortality” for the global mortality rate, “season” for the spawning season, “thermtol” for the tolerance to temperature, “vmigr” for the vertical migration and “year” for the five years tested: 2010, 2011, 2012, 2016 and 2018.

Table 4

Deviances explained (%) by the different parameters in the GLM. The p-values can be found in [table S1](#). Only significant variables were kept in final models ($p < 0.05$). An empty cell indicates that the variable was not statistically explaining positive recruitment values. “Grounddepth” stands for the bathymetry of the spawning ground, “season” for the spawning season, “vmigr” for the vertical migration, “thermtol” for the tolerance to temperature, “drate” for the developmental rate, “mortality” for the global mortality rate, and “year” for the five years tested: 2010, 2011, 2012, 2016 and 2018.

	<i>S. solea</i>					<i>S. senegalensis</i>					<i>P. flesus</i>					<i>P. platessa</i>					<i>D. labrax</i>				
	IB	BB	CH	CS	NS	IB	BB	CH	CS	NS	IB	BB	CH	CS	NS	IB	BB	CH	CS	NS	IB	BB	CH	CS	NS
grounddepth	1	4	4		5	5	5	19	16	24	1	3	6	3	6		3	6	4	12	1	1	2	3	
season	1	5	2		12	1	3	4	1	4		1	1				0	2			1	6	3		7
vmigr	8	5	1	5		2	4			4	1			1				0	2		3	3	2		
thermtol	2		8	17	8	5	10	1			1			3	11		12	3	3	8			5	16	16
drate		1	1	1		0					2	3	2	2	2		3	8	6	7	2	2	2	3	2
year	16	3	25	18	4	18		3	6	4	14	11	10	8			13	10	4		6	4	28	15	12
mortality	2	2	2	3	3	1	1	2	2	2	2	2	2	2	2		2	7	7	6	3	2	3	4	4
grounddepth:season								1																	
grounddepth:temp																					1				1
grounddepth:year																									8
season:thermtol	0					0								1			1	1	3		1				
season:drate																									2
season:year	2		1	2	8	4		4	2	2	5	9					3				6		1	2	19
vmigr:year																					2				
thermtol:year	2	2				2	4	2			6	2	2	1	4		3	5							4

inter-annual variability in recruitment, various approaches have been proposed in the existing literature including the exploration of indices associated with local hydrodynamics (Hidalgo et al., 2019) and employing models simulating more frequent particle releases over extended timeframes (Monroy et al., 2017).

Strictly speaking, this paper does not directly focus on studying climate change. Instead, our research examines the relative significance of changes in parameters that affect larvae recruitment. We conducted a sensitivity analysis, considering various parameters that are influenced by climate change, such as spawning period, larval duration, and mortality. By identifying the parameter that exerts the greatest influence on larval recruitment, we can infer on the recruitment stability in the upcoming years, and the relative sensitivity of different species to upcoming changes.

4.2. Sensitivity of recruitment estimates to parameters

Overall, the impact of two-way interactions on recruitment success was found to be limited. Only a small number of interactions were statistically significant, with the most influential ones being the interactions involving the yearly conditions with thermal tolerance and spawning season. This finding is reasonable considering that we did not calibrate biological parameters for each region, and our spawning period did not align with a specific temperature threshold (Sims et al., 2004; Vinagre et al., 2008). Consequently, under certain annual conditions, recruitment success was influenced by a specific combination of spawning timing and temperature tolerance. However, these two-way interactions were not as crucial as the main effects of the parameters.

Among biological parameters, the temperature tolerance appear to be one of the most influential parameter influencing recruitment success. While this is especially true for species that are at the edge of their distribution areas (e.g. *S. senegalensis* in the Bay of Biscay, *P. platessa* in the Bay of Biscay Cabral et al., 2021 & van Keeken et al., 2007), it also appears as holding much influence on *S. solea* and *D. labrax* in northern areas. For these two species, this can be explained by the fact that their spawning periods were the most wintery in the modelling, which led them to spawn in water that was sometimes too cold especially in high latitudes. As such, great care should be granted on setting thermal tolerant and it might be valuable to refine the model using optimal curve rather than simple thresholds as in our study. While literature exists for some species, generally arising from controlled experiments (Mora and Ospina, 2001) and often for species which are grown in aquaculture (Fonds, 1979), data are scarce for other species such as *S. senegalensis* or *P. flesus*. Even in data-rich situation, thermal tolerance is likely to vary among regions for a given species because of local adaptation (Nati et al., 2021). As such, it is highly recommended to use data originating from the studied region when available.

The fact that the thermal tolerance of species is one of the leading factors especially when modelling species recruitment success at the edge of their distribution range is a result echoing with climate change. The thermal niches of species are expected to undergo changes because of both species' thermal adaptation and the influence of climate velocities (Kleisner et al., 2017; Pinsky et al., 2013). Hence, it is imperative to ascertain species-specific, realistic lethal temperatures for fish larvae to achieve precise predictions and anticipations regarding the future distribution of fish populations, while considering the individual species' temperature tolerance range and adaptation mechanisms (Pinsky et al., 2021).

Interestingly, variations due to yearly conditions (year factor) seem to be the most influential, especially for the common sole and the seabass (the two species that are not at the edge of their distribution areas). As such, it is crucial to analyse multiple years to account for this variability when exploring connectivity matrices among spawning and nursery grounds. Similarly, recruitment varies more among geographic regions than among range of parameters value. The classification of the most effective spawning areas by recruitment success are very consistent

among years for each archetype, suggesting that the inter-annual variations are less important than the zones specific features. This is consistent with Savina et al., 2010 findings, in which hydrodynamic variability was the leading factor. Overall, these results suggest that if the aim of the modelling study is to compare inter-annual variations in recruitment success or to compare overall success among large regions, the effects of those environmental conditions is indeed likely to be higher than uncertainty on biological parameters.

Several parameters had a slightly more limited influence on the results: daily instantaneous mortality rate, developmental rate and the nyctemeral vertical migration. As such, misspecifications of parameters values are not likely to affect the results of the model. Regarding our developmental rate, considering that the maximum PLD possible was already set fixed for all species, its effect was only to make recruitment possible earlier or later in the particles drift according to their developmental stage. It is worth mentioning that we have considered a simplistic growth model. It would be interesting to extend the analysis with more complex but more biologically realistic model such as Dynamic Energy Budget Models (Sardi et al., 2023). Such DEB models might also allow accounting for the effect of food availability on growth (and starvation), and as such to have a more comprehensive overview of the cumulative effects of temperature and food on recruitment success. This was not possible in the exercise since data was not available for all our archetypes.

Regarding mortality rate, we assumed a constant mortality rate through time. In such a situation, increasing or decreasing the mortality rate just multiplies or divides the probability to survive until settlement, so that comparisons among areas or periods are not affected (at least until the development duration remains is not too affected). Of course, here we do not account for variations in mortality due to other factors such as predation (Cowan et al., 1996; Paradis et al., 1996). Neither do we take into account a differential mortality depending on the developmental stage (as expressed in Hjort's "Critical period" theory Houde, 2008, see also Arevalo et al., 2023 for review). In such situation, complementary analysis would be required. However, the results would be more influenced by the variations of the quantity of predators (which are generally an external forcing factor) rather than of the parametrization of the basal natural mortality rate. Regarding, migration behaviour, Beraud et al., 2018 and North et al., 2009 showed that it can have an influence, but rather due to tidal migration during the latest stage of larval development (e.g. tidal migration i.e. in Beraud et al., 2018 or horizontal swimming towards lower salinities Bos and Thiel, 2006). Fish larvae undergo nyctemeral vertical migration to descend during the day to avoid predators and ascend at night to feed on abundant surface plankton, optimizing their survival and feeding opportunities (Gibson et al., 2016). As such, while nyctemeral migration behaviour is often mentioned as an important parameter, it is not likely to be one of the most important influential parameter when studying the spatial distribution of recruitment at such a large spatial scale, even if not considered at all. However, at a finer scale, it might be worthwhile to take vertical migrations into account, especially the tidal one as Fox et al., 2006 demonstrated. A potential avenue for future research could involve quantifying this tidal migration in comparison to other migration patterns as the diel one (as was began in Beraud et al., 2018). To sum it up, these two factors (daily mortality rate and diel vertical migration) critically depend on external forcing (e.g. quantity of predators for mortality, tidal currents and river discharge for migratory behaviour). While it might be worthwhile using more complex models and fine parametrization for local scale studies, this seems impossible at larger scale as literature on those processes is often more limited.

Overall results show that, while recruitment levels is different among archetypes, the patterns in terms of sensitivity to key parameters is rather consistent among them. This is even more the case for sole and seabass, which had very similar spawning strategies in the model. This indicates the most sensitive parameters are likely similar for many species. However, on Fig. 4, we observe that the width of the boxplots

are larger than inter-archetypes differences. This suggests that, even with limited variations of parameters values, not accounting for parameters uncertainty can modify the ecological conclusions we draw from a modelling exercise.

5. Conclusion

The sensitivity analysis highlights that because of the great influence of yearly conditions, it is highly recommended to simulate over multiple year when exploring the connectivity among spawning and nursery areas. Comparing different areas, the most driving parameter remains the regional hydrodynamics, shaping recruitment patterns. In addition, thermal tolerance is a key factor influencing simulation results. As such, great care should be taken when setting this parameter, and especially when extrapolating from data from close species or regions. Future research aiming to predict how climate change would influence species distributions should focus on estimating those temperature thresholds more accurately by considering acclimation, adaptation, and variations among different life stages. Other parameters are of smaller importance and are not likely to modify the spatial and temporal large scale parameters, as diel vertical migrations which does not hold much influence on recruitment on our large scale. However, differences among species may be hindered by uncertainty in parameters. *In vivo* studies would be welcomed to strengthen the foundations on which larval drift models rely.

CRedit authorship contribution statement

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

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2023.103102>.

References

- Almany, G.R., Berumen, M.L., Thorrold, S.R., Planes, S., Jones, G.P., 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316, 742–744 <https://doi.org/10/c8dvp9>.
- Amara, R., Desauinay, Y., Lagardere, F., 1994. Seasonal variation in growth of larval sole *Solea solea* (L.) and consequences on the success of larval immigration. *Neth. J. Sea Res.* 32, 287–298 <https://doi.org/10/cxxdpj>.

- Arevalo, E., Cabral, H.N., Villeneuve, B., Possémé, C., Lepage, M., 2023. Fish larvae dynamics in temperate estuaries: a review on processes, patterns and factors that determine recruitment. *Fish and Fisheries* n/a 24 (3), 466–487.
- Barbut, L., Groot Crego, C., Delerue-Ricard, S., Vandamme, S., Volckaert, F.A.M., Lacroix, G., 2019. How larval traits of six flatfish species impact connectivity. *Limnol Oceanogr.* 64, 1150–1171 <https://doi.org/10/gm424s>.
- Barnston, A.G., Livezey, R.E., 1987. Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. *Mon. Weather Rev.* 115, 1083–1126 <https://doi.org/10/b3rxww>.
- Bedoui, R., 1995. Rearing of *Solea senegalensis* (Kaup, 1958) in Tunisia. *Cahier Options Méditerranée* 16, 31–39.
- Beraud, C., van der Molen, J., Armstrong, M., Hunter, E., Fonseca, L., Hyder, K., 2018. The influence of oceanographic conditions and larval behaviour on settlement success—the European sea bass *Dicentrarchus labrax* (L.). *ICES J. Mar. Sci.* 75, 455–470 <https://doi.org/10/gm424g>.
- Bos, A.R., Thiel, R., 2006. Influence of salinity on the migration of postlarval and juvenile flounder *Pleuronectes flesus* L. in a gradient experiment. *J. Fish Biol.* 68, 1411–1420 <https://doi.org/10/bxn52n>.
- Cabral, H.N., Borja, A., Fonseca, V.F., Harrison, T.D., Teichert, N., Lepage, M., Leal, M.C., 2022. The role of estuaries and coastal areas as nurseries for fish: concepts, methodological challenges and future perspectives. In: Humphreys, J., Little, S. (Eds.), *Challenges in Estuarine and Coastal Science*. Pelagic Publishing, pp. 223–238. <https://doi.org/10.1002/9781119705345.ch6>.
- Cabral, H., Drouineau, H., Teles-Machado, A., Pierre, M., Lepage, M., Lobry, J., Reis-Santos, P., Tanner, S.E., 2021. Contrasting impacts of climate change on connectivity and larval recruitment to estuarine nursery areas. *Prog. Oceanogr.* 196, 102608 <https://doi.org/10/gpb9gx>.
- Champalbert, G., Koutsikopoulos, C., 1995. Behaviour, transport and recruitment of bay of biscay sole (*Solea Solea*): laboratory and field studies. *J. Mar. Biol. Ass.* 75, 93–108 <https://doi.org/10/b3c8bm>.
- Cowan, J.H., Houde, E.D., Rose, K.A., 1996. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. *ICES J. Mar. Sci.* 53, 23–37. <https://doi.org/10.1006/jmsc.1996.0003>.
- Dambrine, C., Woillez, M., Huret, M., de Pontual, H., 2021. Characterising essential fish habitat using spatio-temporal analysis of fishery data: a case study of the european seabass spawning areas. *Fish. Oceanogr.* 30, 413–428. <https://doi.org/10.1111/fog.12527>.
- Dambrine, C., 2020. Caractérisation et connectivité des Habitats Ecologiques Essentiels des stades adulte et juvénile du bar européen.
- Devauchelle, N., Alexandre, J.C., Le Corre, N., Letty, Y., 1987. Spawning of sole (*Solea solea*) in captivity. *Aquaculture* 66, 125–147 <https://doi.org/10/cpqxgn>.
- Dinis, M.T., Ribeiro, L., Soares, F., Sarasquete, C., 1999. A review on the cultivation potential of *Solea senegalensis* in Spain and in Portugal. *Aquaculture* 176, 27–38 <https://doi.org/10/ck8zt4>.
- Dubois, M., Rossi, V., Ser-Giacomi, E., Arnaud-Haond, S., López, C., Hernández-García, E., 2016. Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems. *Glob. Ecol. Biogeogr.* 25, 503–515. <https://doi.org/10.1111/geb.12431>.
- Dupuis, H., Michel, N., Sottolichio, A., 2006. Wave climate evolution in the Bay of Biscay over two decades. *J. Mar. Syst.* 63, 105–114. <https://doi.org/10.1016/j.jmarsys.2006.05.009>.
- EMODnet Geology project, 2019. Seabed Substrates.
- Faivre, R., Iooss, B., Mahévas, S., Makowski, D., 2013. Analyse de sensibilité et exploration de modèles, Quae. Ed. Versailles, France.
- Fernández-Díaz, C., Yýfera, M., Cañavate, J.P., Moyano, F.J., Alarcón, F.J., Díaz, M., 2001. Growth and physiological changes during metamorphosis of Senegal sole reared in the laboratory. *J. Fish Biol.* 58, 1086–1097 <https://doi.org/10/bhxnwv>.
- Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F., Huse, G., 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Mar. Ecol. Prog. Ser.* 347, 195–205 <https://doi.org/10/dbk8v5>.
- Fonds, M., 1979. Laboratory observations on the influence of temperature and salinity on development of the eggs and growth of the larvae of *Solea solea* (Pisces). *Mar. Ecol. Prog. Ser.* 1, 91–99.
- Fox, C.J., Mccloughrie, P., Young, E.F., Nash, R.D.M., 2006. The importance of individual behaviour for successful settlement of juvenile plaice (*Pleuronectes platessa* L.): a modelling and field study in the eastern Irish Sea. *Fish. Oceanogr.* 15, 301–313 <https://doi.org/10/d8z4kk>.
- Gibson, R.N., Atkinson, R.J., Gordon, J.D., 2016. Zooplankton diel vertical migration—a review of proximate control. *Oceanogr. Mar. Biol.* 47, 77–110.
- Hidalgo, M., Rossi, V., Monroy, P., Ser-Giacomi, E., Hernández-García, E., Guijarro, B., Massutí, E., Alemany, F., Jadaud, A., Perez, J.L., Reglero, P., 2019. Accounting for ocean connectivity and hydroclimate in fish recruitment fluctuations within transboundary metapopulations. *Ecol. Appl.* 29, e01913.
- Houde, E.D., 2008. Emerging from Hjort’s Shadow. *J. Northw. Atl. Fish. Sci.* 41, 53–70 <https://doi.org/10/b9b3wd>.
- Hufnagl, M., Payne, M., Lacroix, G., Bolle, L.J., Daewel, U., Dickey-Collas, M., Gerkema, T., Huret, M., Janssen, F., Kreuz, M., Pätzsch, J., Pohlmann, T., Ruardij, P., Schrum, C., Skogen, M.D., Tiessen, M.C.H., Petitgas, P., van Beek, J.K.L., van der Veer, H.W., Callies, U., 2017. Variation that can be expected when using particle tracking models in connectivity studies. *J. Sea Res., St. North Sea Coastal Syst.* 127, 133–149. <https://doi.org/10.1016/j.seares.2017.04.009>.
- Huret, M., Petitgas, P., Woillez, M., 2010. Dispersal kernels and their drivers captured with a hydrodynamic model and spatial indices: a case study on anchovy (*Engraulis encrasicolus*) early life stages in the Bay of Biscay. *Prog. Oceanogr.* 87, 6–17 <https://doi.org/10/fjjvrn>.

- Hurrell, J.W., Van Loon, H., 1997. Decadal variations in climate associated with the north atlantic oscillation. *Clim. Change* 36, 301–326. <https://doi.org/10.1023/A:1005314315270>.
- Imsland, A.K., Foss, A., Conceição, L.E.C., Dinis, M.T., Delbare, D., Schram, E., Kamstra, A., Rema, P., White, P., 2003. A review of the culture potential of *Solea solea* and *S. senegalensis*. *Rev. Fish Biol. Fish.* 13, 379–408 <https://doi.org/10/bxgw8m>.
- Kleinsner, K.M., Fogarty, M.J., McGee, S., Hare, J.A., Moret, S., Perretti, C.T., Saba, V.S., 2017. Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. *Prog. Oceanogr.* 153, 24–36. <https://doi.org/10.1016/j.pocean.2017.04.001>.
- Kough, A.S., Paris, C.B., 2015. The influence of spawning periodicity on population connectivity. *Coral Reefs* 34, 753–757 <https://doi.org/10/f7m9qz>.
- Koutsikopoulos, C., Desaunay, Y., Dorel, D., Marchand, J., 1989. The role of coastal areas in the life history of sole (*Solea solea* L.) in the Bay of Biscay. *Scientia Marina (Barcelona)*.
- Koutsikopoulos, C., Lacroix, N., 1992. Distribution and abundance of sole (*Solea solea* L.) eggs and larvae in the Bay of Biscay between 1986 and 1989. *Neth. J. Sea Res.* 29, 81–91 <https://doi.org/10/bfbb42>.
- Lacroix, G., Maes, G.E., Bolle, L.J., Volckaert, F.A.M., 2013. Modelling dispersal dynamics of the early life stages of a marine flatfish (*Solea solea* L.). *J. Sea Res.* 84, 13–25 <https://doi.org/10/f5jst2>.
- Lazure, P., Dumas, F., 2008. An external–internal mode coupling for a 3D hydrodynamical model for applications at regional scale (MARS). *Adv. Water Resour.* 31, 233–250 <https://doi.org/10/bxnqdz>.
- Lett, C., Ayata, S.-D., Huret, M., Irsson, J.-O., 2010. Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Prog. Oceanogr.* 87 (1–4), 106–113.
- Michel, S., Treguier, A.-M., Vandermeirsch, F., 2009. Temperature variability in the Bay of Biscay during the past 40 years, from an in situ analysis and a 3D global simulation. *Cont. Shelf Res.* 29 (8), 1070–1087.
- Monroy, P., Rossi, V., Ser-Giacomi, E., López, C., Hernández-García, E., Paris, C., 2017. Sensitivity and robustness of larval connectivity diagnostics obtained from Lagrangian Flow Networks. *ICES J. Mar. Sci.* 74 (6), 1763–1779.
- Mora, C., Ospina, A., 2001. Tolerance to high temperatures and potential impact of sea warming on reef fishes of Gorgona Island (tropical eastern Pacific). *Mar. Biol.* 139, 765–769. <https://doi.org/10.1007/s002270100626>.
- Mullon, C., Cury, P., Penven, P., 2002. Evolutionary individual-based model for the recruitment of anchovy (*Engraulis capensis*) in the southern Benguela. *Can. J. Fish. Aquat. Sci.* 59, 910–922 <https://doi.org/10/dn22qp>.
- Munk, P., Nielsen, J.G., 2005. Eggs and larvae of North Sea fishes. *Biofolia*.
- Nati, J., Svendsen, M., Marras, S., Killen, S., Steffensen, J., McKenzie, D., Domenici, P., 2021. Intraspecific variation in thermal tolerance differs between tropical and temperate fishes. *Sci. Rep.* 11 <https://doi.org/10.1038/s41598-021-00695-8>.
- North, E.W., Gallego, A., Petitgas, P., 2009. Manual of recommended practices for modelling physical – biological interactions during fish early life. *ICES Cooperative Res. Report*.
- Ospina-Alvarez, A., Parada, C., Palomera, I., 2012. Vertical migration effects on the dispersion and recruitment of European anchovy larvae: from spawning to nursery areas. *Ecol. Model.* 231, 65–79 <https://doi.org/10/f3xd6t>.
- Paradis, A.R., Pepin, P., Brown, J.A., 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. *Can. J. Fish. Aquat. Sci.* 53, 1226–1235. <https://doi.org/10.1139/f96-051>.
- Paris, C., Chérubin, L., Cowen, R., 2007. Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar. Ecol. Prog. Ser.* 347, 285–300 <https://doi.org/10/b3zhqx>.
- Petitgas, P., Magri, S., Lazure, P., 2006. One-dimensional biophysical modelling of fish egg vertical distributions in shelf seas. *Fisheries Oceanogr.* 15, 413–428 <https://doi.org/10/d9vhbs>.
- Pickett, G.D., Pawson, M.G., 1994. *Sea Bass: biology*. Springer Science & Business Media.
- Pingree, R., 2005. North atlantic and north sea climate change: curl up, shut down, NAO and ocean colour. *J. Mar. Biol. Ass.* 85, 1301–1315. <https://doi.org/10.1017/S0025315405012488>.
- Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., Levin, S.A., 2013. Marine taxa track local climate velocities. *Science* 341, 1239–1242. <https://doi.org/10.1126/science.1239352>.
- Pinsky, M.L., Fenichel, E., Fogarty, M., Levin, S., McCay, B., St. Martin, K., Selden, R.L., Young, T., 2021. Fish and fisheries in hot water: what is happening and how do we adapt? *Popul. Ecol.* 63 (1), 17–26.
- Randon, M., Réveillac, E., Le Pape, O., 2021. A holistic investigation of tracers at population and individual scales reveals population structure for the common sole of the Eastern English Channel. *Estuar. Coast. Shelf Sci.* 249, 107096 <https://doi.org/10/gpb4xq>.
- Reis-Santos, P., Tanner, S.E., Aboim, M.A., Vasconcelos, R.P., Laroche, J., Charrier, G., Pérez, M., Presa, P., Gillanders, B.M., Cabral, H.N., 2018. Reconciling differences in natural tags to infer demographic and genetic connectivity in marine fish populations. *Sci. Rep.* 8, 10343. <https://doi.org/10.1038/s41598-018-28701-6>.
- Rijnsdorp, A.D., 1997. Changes in reproductive parameters of North Sea plaice and sole between 1960 and 1995.
- Rochette, S., Huret, M., Rivot, E., Le Pape, O., 2012. Coupling hydrodynamic and individual-based models to simulate long-term larval supply to coastal nursery areas: modelling larval supply to coastal nurseries. *Fish. Oceanogr.* 21, 229–242 <https://doi.org/10/gm423n>.
- Romero-Torres, M., Acosta, A., Tremil, E.A., 2017. The regional structure of spawning phenology and the potential consequences for connectivity of coral assemblages across the Eastern Tropical Pacific. *ICES J. Mar. Sci.* 74, 613–624 <https://doi.org/10/gm424d>.
- Sardi, A.E., Moreira, J.M., Omingo, L., Cousin, X., Bégout, M.-L., Machado, M., Marn, N., 2023. Simulating the effects of temperature and food availability on true soles (*Solea spp.*) early-life history traits: a tool for understanding fish recruitment in future climate change scenarios. *Fishes* 8 (2), 68.
- Savina, M., Lacroix, G., Ruddick, K., 2010. Modelling the transport of common sole larvae in the southern North Sea: influence of hydrodynamics and larval vertical movements. *Journal of marine systems, contributions from advances in marine ecosystem modelling research II 23–26 June 2008*. Plymouth, UK 81, 86–98. <https://doi.org/10.1016/j.jmarsys.2009.12.008>.
- Savina, M., Lunghi, M., Archambault, B., Baulier, L., Huret, M., Le Pape, O., 2016. Sole larval supply to coastal nurseries: interannual variability and connectivity at interregional and interpopulation scales. *J. Sea Res.* 111, 1–10 <https://doi.org/10/f8sjbm>.
- Simons, R.D., Siegel, D.A., Brown, K.S., 2013. Model sensitivity and robustness in the estimation of larval transport: a study of particle tracking parameters. *J. Mar. Syst.* 119–120, 19–29 <https://doi.org/10/gbc5b4>.
- Sims, D.W., Wearmouth, V.J., Genner, M.J., Southward, A.J., Hawkins, S.J., 2004. Low-temperature-driven early spawning migration of a temperate marine fish. *J. Anim. Ecol.* 73, 333–341 <https://doi.org/10/d325md>.
- Skerritt, D.J., 2010. A review of the European flounder *Platichthys flesus* - Biology, Life History and Trends. Population 13.
- Solemdal, P., 1967. The effect of salinity on buoyancy, size and development of flounder eggs. *ICES J. Mar. Sci.* 29, 431–442 <https://doi.org/10/gm423g>.
- Strathmann, R.R., Hughes, T.P., Kuris, A.M., Lindeman, K.C., Morgan, S.G., Pandolfi, J. M., Warner, R.R., 2002. Evolution of local recruitment and its consequences for marine populations. *Bull. Mar. Sci.* 70, 377–396.
- Swearer, S.E., Tremil, E.A., Shima, J.S., 2019. A review of biophysical models of marine larval dispersal. *Oceanogr. Mar. Biol.* <https://doi.org/10/gm4248>.
- Tanner, S.E., Reis-Santos, P., Cabral, H.N., 2016. Otolith chemistry in stock delineation: a brief overview, current challenges and future prospects. *Fish. Res.* 173, 206–213. <https://doi.org/10.1016/j.fishres.2015.07.019>.
- Tanner, S.E., Teles-Machado, A., Martinho, F., Peliz, Á., Cabral, H.N., 2017. Modelling larval dispersal dynamics of common sole (*Solea solea*) along the western Iberian coast. *Prog. Oceanogr.* 156, 78–90 <https://doi.org/10/gb295v>.
- Tremil, E.A., Ford, J.R., Black, K.P., Swearer, S.E., 2015. Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. *Mov. Ecol.* 3, 17 <https://doi.org/10/gm4237>.
- van de Wolfshaar, K.E., Barbut, L., Lacroix, G., Hidalgo, M., 2022. From spawning to first-year recruitment: the fate of juvenile sole growth and survival under future climate conditions in the North Sea. *ICES J. Mar. Sci.* 79 (2), 495–505.
- van Keeken, O.A., van Hoppe, M., Grift, R.E., Rijnsdorp, A.D., 2007. Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries management. *J. Sea Res.* 57 (2–3), 187–197.
- Vinagre, C., Amara, R., Maia, A., Cabral, H.N., 2008. Latitudinal comparison of spawning season and growth of 0-group sole, *Solea solea* (L.). *Estuar. Coast. Shelf Sci.* 78, 521–528 <https://doi.org/10/cctm69>.
- Walker, N.D., Boyd, R., Watson, J., Kotz, M., Radford, Z., Readdy, L., Sibly, R., Roy, S., Hyder, K., 2020. A spatially explicit individual-based model to support management of commercial and recreational fisheries for European sea bass *Dicentrarchus labrax*. *Ecol. Model.* 431, 109179 <https://doi.org/10/ghs558>.
- Warner, R.R., Cowen, R.K., 2002. Local retention of production in marine populations: evidence, mechanisms, and consequences. *Bull. Mar. Sci.* 70, 6.
- Wegner, G., Damm, U., Purps, M., 2003. Physical influences on the stock dynamics of plaice and sole in the North Sea. *scimar* 67, 219–234 <https://doi.org/10/cqw7vn>.
- White, J.W., Rassweiler, A., Samhoury, J.F., Stier, A.C., White, C., 2014. Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* 123, 385–388 <https://doi.org/10/f52qgr>.
- Xu, C., Gertner, G.Z., 2008. Uncertainty and sensitivity analysis for models with correlated parameters. *Reliab. Eng. Syst. Saf.* 93, 1563–1573. <https://doi.org/10.1016/j.res.2007.06.003>.
- Yamahira, K., Conover, D.O., 2002. Intra- Vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* 83, 1252–1262 <https://doi.org/10.1890>.
- Yin, M.C., Blaxter, J.H.S., 1987. Temperature, salinity tolerance, and buoyancy during early development and starvation of Clyde and North Sea herring, cod, and flounder larvae. *J. Exp. Mar. Biol. Ecol.* 107, 279–290. [https://doi.org/10.1016/0022-0981\(87\)90044-X](https://doi.org/10.1016/0022-0981(87)90044-X).