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Violette Silve

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SPECIALITE **ÉCOLOGIE ÉVOLUTIVE, FONCTIONNELLE ET DES
COMMUNAUTÉS**

Par Violette SILVE

**Impacts du changement climatique sur la
dérive larvaire de poissons marins :
des frayères aux nurseries côtières**

*Climate change impacts on the larval drift of marine fishes:
from spawning grounds to coastal nurseries*

Sous la direction de : Henrique CABRAL & Hilaire DROUINEAU

Soutenue le 08/12/2023

Membres du jury :

Mme BRIND'AMOUR Anik	Chargée de recherche	IFREMER	Rapporteur
M. LETT Christophe	Directeur de recherche	MARBEC	Rapporteur
Mme GUIZIEN Katell	Directrice de recherche	CNRS	Examinatrice
Mme NEVOUX Marie	Chargée de recherche	INRAE	Examinatrice
M. CABRAL Henrique	Directeur de recherche	INRAE	Directeur de thèse
M. DROUINEAU Hilaire	Ingénieur de recherche	INRAE	Co-directeur de thèse

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Site de Gazinet Cestas, Centre INRAE Nouvelle-Aquitaine,

50 Avenue de Verdun

33612 CESTAS Cedex-France

TITRE : Impacts du changement climatique sur la dérive larvaire de poissons marins : des frayères aux nurseries côtières

RESUME :

Le changement climatique se traduit par de multiples modifications dans l'environnement marin, notamment des altérations de l'hydrodynamique et l'augmentation des températures. De nombreuses espèces de poissons marins dits « estuariens-opportunistes » présentent une période de dérive larvaire passive entre leurs zones de ponte (souvent sur le plateau continental) et leurs zones de nurseries pour les juvéniles (estuaires ou zones côtières). Le changement climatique pourrait avoir un impact significatif sur le succès des individus à atteindre ces nurseries (dit "succès de recrutement"). La taille des larves, ainsi que leur grande dispersion rendent les études *in situ* difficiles et la modélisation biophysique l'outil privilégié pour étudier ce stade de vie. Comprendre et prédire l'évolution de ces populations dans un océan en changement passe par comprendre les processus en jeu et prendre conscience des avantages et des inconvénients que l'usage de ces modèles induisent. Pour ce faire, nous avons utilisé MARS3D, un modèle hydrodynamique développé à l'IFREMER, couplé à un module de déplacement de particules Lagrangien reproduisant la croissance et le comportement des larves. Nous nous sommes basés sur des espèces bien documentées, utilisées en tant qu'archétypes biologiques.

En raison de la complexité de ces modèles et de l'incertitude des paramètres utilisés, la première étape fut d'évaluer la sensibilité du modèle. Nous avons montré que l'hydrodynamique locale et la variabilité interannuelle façonnaient le plus le succès de recrutement, bien plus que les paramètres biologiques ou les caractéristiques des espèces. Les valeurs renseignées pour la tolérance à la température prenaient de l'importance aux limites des aires de répartition des espèces, montrant ainsi comment la température peut modifier les distributions spatiales.

Cela nous a conduit à nous interroger sur les conséquences potentielles que les changements dans l'hydrodynamique locale pourraient avoir dans les années à venir. Plus précisément, nous nous sommes demandés si la localisation des frayères permettant un succès de recrutement fort était stable malgré des conditions environnementales contrastées. Nous n'avons trouvé aucun changement dans l'emplacement des frayères les plus efficaces, bien que leur efficacité relative variait considérablement d'une année sur l'autre. D'un point de vue évolutif, cela suggérerait que la sélection naturelle pourrait privilégier les mécanismes d'homing.

Après cette étape, nous nous sommes demandés si les habitats d'intérêt (frayères et nurseries) identifiés dans la littérature étaient des zones permettant un meilleur recrutement des larves par

rapport à des zones théoriques (basés sur des gammes de profondeur). Nous avons montré que ce n'était pas le cas. Ainsi, cela impliquerait que l'hydrodynamique et le comportement des larves ne suffiraient pas à expliquer seuls l'emplacement observé des frayères et nourriceries.

Plusieurs effets du changement climatique sur la dérive larvaire ont été mis en évidence durant cette thèse, notamment le rôle de la température sur la distribution des larves de poissons, l'impact limité sur l'emplacement des frayères, et le plus grand succès de recrutement au cours d'années caractérisées par un indice NAO et une température élevée. Toutefois, ce travail repose sur une approche théorique, posant la question des choix dans l'échelle spatiale utilisée et dans le degré de précision mis dans la modélisation. Le manque de données limite les moyens de validation, ce qui entrave l'application directe des sorties de modèles dans des cas concrets. Nous recommandons que les futures recherches s'intéressent à l'acquisition de données *in situ*. Les méthodes indirectes (comme la génétique ou la géochimie des otolithes) peuvent ouvrir une voie dans le futur pour une meilleure calibration et validation des modèles.

Mots clés : Poissons, Estuaire, Recrutement, Modélisation, Changement climatique

TITLE: Climate change impacts on the larval drift of marine fishes: from spawning grounds to coastal nurseries

ABSTRACT:

Climate change is leading to a number of changes in the marine environment, including altered hydrodynamics and higher temperatures. Many species of marine fish known as "estuarine-opportunists" exhibit a period of passive larval drift between their spawning grounds (often on the continental shelf) and their nursery grounds used by juveniles (estuaries or coastal areas). Climate change may have a significant impact on the recruitment success (measured by the proportion of individuals reaching nurseries). The size and dispersion of larvae in the ocean make in-situ studies difficult to implement. Therefore, biophysical modelling emerges as the most widely used tool for studying this phase of the life cycle. By using a 3D hydrodynamic model coupled with an individual-based model that simulates larval growth and behaviour, it becomes possible to assess how environmental factors can affect recruitment success by influencing the survival, dispersion, and connectivity of eggs and larvae. Understanding and predicting the evolution of these populations in a changing ocean requires an understanding of the processes involved and an awareness of the advantages and disadvantages of using these models. To achieve this, we employed MARS3D, a model developed by IFREMER, coupled with a Lagrangian particle tracking module reproducing the growth and behaviour of larvae. We used well-documented species of high fisheries importance as biological archetypes.

Due to the complexity of these models and the uncertainty of parameters, the first step was to assess the model sensitivity. Our findings demonstrated that local hydrodynamics and inter-annual variability had the most significant influence on recruitment success, far more than biological parameters or species characteristics. The values assigned to temperature tolerance became particularly relevant at the species distribution boundaries, illustrating how temperature can modify spatial distributions of larvae.

This led us to wonder about the potential consequences that changes in local hydrodynamics could have in the coming years. More precisely, we wondered if the spawning areas allowing for the highest recruitment rate remain in the same places across years showing contrasting environmental conditions. Our analysis showed no changes in the location of the most effective spawning areas even though their relative effectiveness vary greatly between years. From an evolutionary perspective, this suggests that natural selection may favour the emergence of mechanisms that promote strong homing behaviour.

After this step, we questioned whether the habitats of interest (spawning and nursery areas) identified in the literature indeed facilitated better larval recruitment compared to theoretical spawning and nursery zones (based on depth ranges). Our findings indicated that this was not the case. This suggests that hydrodynamics and larval behaviour alone may not suffice to fully explain the observed placement of spawning and nursery areas.

Several effects of climate change were highlighted during this thesis, including the role of temperature on fish distribution, limited impact on the location of spawning areas, and the highest recruitment success during years characterized by a high NAO index and temperatures. However, this work is based on a theoretical approach, raising the question of the choices made in terms of the spatial scale used and the degree of precision applied to the modelling. The lack of data hinders the direct applicability of simulation outputs in concrete cases. We recommend that future research focus on the acquisition of in situ data. Indirect methods (such as the genetics and geochemistry of otoliths) may open up a way forward for better calibration and validation.

Keywords: Fishes, Estuaries, Recruitment, Modelling, Climate change

RESUME SUBSTANTIEL

Le changement climatique fait référence à la modification globale du climat au fil du temps. Les activités anthropiques ont perturbé l'équilibre naturel du système climatique, entraînant des changements rapides et généralisés dans l'atmosphère, l'hydrosphère et la biosphère. Outre la perte d'habitats, la pollution et la surexploitation, le changement climatique est un facteur qui contribue à la sixième extinction de masse en cours. Mieux comprendre le fonctionnement des populations et leurs réponses face à ce changement est un enjeu majeur pour mieux prédire les risques d'effondrement ou les possibles adaptations. Le changement climatique se traduit notamment par de multiples modifications dans l'environnement marin, comme des altérations de l'hydrodynamique et l'augmentation des températures. Or, de nombreuses espèces de poissons présentent une période de dérive larvaire passive, parfois assez longue, entre leurs zones de ponte et leurs nourriceries. C'est notamment le cas des poissons marins dits « estuariens-opportunistes » qui se reproduisent souvent sur le plateau continental et utilisent les estuaires ou les zones côtières comme nourriceries pour les jeunes stades. Durant cette phase de dérive, les œufs deviennent des larves, se développent, gagnant petit à petit plus de capacité d'orientation et de mobilité, jusqu'à pouvoir s'installer dans des zones de nourriceries appropriées. Cette phase est celle permettant la plus grande dispersion au cours du cycle de vie de ces espèces. Dû à la forte sensibilité à la température des œufs-larves mais également à la prédation et à la grande proportion d'individus qui ne parviennent pas jusqu'aux nourriceries, cette phase coïncide également avec les taux de mortalité les plus élevés. Etant donné que cette dérive est largement influencée par les conditions environnementales, on suppose que le changement climatique pourrait avoir un impact significatif sur le succès des individus à atteindre des nourriceries, ce qu'on appellera « succès de recrutement » par la suite. En effet, la durée de la phase larvaire, la période de ponte, les courants et le taux de mortalité ne sont que quelques exemples des modifications attendues avec les changements climatiques. La combinaison de toutes ces modifications pourrait avoir une grande influence sur les patterns de connectivité existants entre frayères et nourriceries.

Cette phase larvaire étant critique dans le cycle de vie des espèces et contribuant aux renouvellements des populations, il est crucial de mieux comprendre les effets du changement climatiques pour prévoir comment ceux-ci pourraient affecter la dynamique des populations. Cependant l'étudier n'est pas une tâche facile. En effet, dû à leur petite taille, et leur grande dispersion dans l'océan il est ardu de mener des études sur le terrain, et impossible de mener ces dernières à une large échelle. C'est pourquoi la modélisation couplée hydrodynamique/biologique s'est rapidement révélée être un outil privilégié afin d'essayer de comprendre les mécanismes impliqués dans la dispersion des larves de poissons. Ces modèles sont constitués de deux composantes. La première composante est un modèle trois-dimensionnels calculant l'hydrodynamique dans la zone voulue, en prenant en compte l'intensité du vent, les précipitations, les écoulements de rivières, et peut estimer différents paramètres physico-chimiques comme la température, la salinité ou le pH. La deuxième composante est un modèle individu centré, permettant de simuler le déplacement Lagrangien de particules au sein des courants marins calculés par le modèle hydrodynamique. Il permet de prendre en compte la croissance, la mortalité ainsi que le comportement des larves. Tout au long de cette thèse, nous avons utilisé le modèle

MARS3D, un modèle hydrodynamique développé à l'IFREMER, couplé à un module de déplacement de particules Lagrangien.

Cette thèse a pour but d'étudier les impacts des changements climatiques sur la dérive des larves de poissons marins « estuariens-opportunistes » à travers l'utilisation de modèle biophysiques. Plus précisément, l'objectif est d'essayer de comprendre les potentiels effets du changement climatique sur le succès de recrutement et la connectivité, tout en mettant en évidence les avantages et les inconvénients liés à l'utilisation de ces modèles. Les trois chapitres traitent des thèmes suivants : (1) la sensibilité du modèle aux paramètres liés aux traits d'histoire de vie et aux paramètres externes, (2) la stabilité de la localisation des frayères dites « favorables » entre des années montrant des conditions environnementales contrastées et (3) la comparaison de l'efficacité en terme de succès de recrutement entre des habitats d'intérêt identifiés et d'autres théoriques.

Le **Chapitre 1** a pour objectif d'évaluer la sensibilité du modèle utilisé. Les modèles biophysiques sont des modèles complexes qui nécessitent de nombreux paramètres, dont beaucoup sont incertains. Dès lors, une analyse de sensibilité paraît une étape préliminaire nécessaire pour mieux appréhender les paramètres clés des modèles et évaluer les incertitudes des sorties liées à une méconnaissance sur les paramètres d'entrée. Afin d'obtenir une vision holistique, l'étude s'est concentrée sur cinq espèces de poissons estuariens-opportunistes bien documentés, avec un fort intérêt halieutique. Le choix de ce panel d'espèces vise à établir des archétypes écologiques montrant des stratégies de reproduction et de traits d'histoire de vie contrastés (la sole commune *Solea solea*, la sole sénégalaise *Solea senegalensis*, la plie commune *Pleuronectes platessa*, le flet commun *Platichthys flesus* et le bar européen *Dicentrarchus labrax*). La zone d'étude englobait tout le Nord-Ouest de l'Europe occidentale, créant ainsi cinq sous-régions : la côte ibérique, le Golfe de Gascogne, la Manche, la mer du Nord et la mer Celtique. Nous avons sélectionné cinq facteurs intrinsèques : la profondeur des frayères, la période de frai, la migration verticale nyctémérale (i.e. s'opérant lors de cycles journaliers), le taux de croissance, la mortalité journalière, et la gamme de tolérance à la température. Migration verticale mise à part qui s'est vue traitée en présence/absence, chacun de ces paramètres s'est vu attribué une valeur haute et une valeur basse suivant une gamme de variation de 10% autour des valeurs standards issues de la littérature. Deux paramètres extrinsèques sont venus se rajouter, étant les années (cinq années choisies comme ayant des conditions environnementales contrastées) et les régions (cinq régions décrites précédemment). L'analyse de sensibilité a montré que la tolérance thermique des espèces était l'un des principaux facteurs influençant les estimations du recrutement, ce qui suggère qu'il s'agit d'un paramètre essentiel, en particulier lors de la modélisation du succès du recrutement des espèces à la limite de leur aire de répartition. D'autre part, d'autres paramètres tels que la migration verticale nyctémérale, qui sont souvent abordés dans ces exercices de simulation de dérive larvaire, se sont avérés avoir une influence plus limitée pour une analyse à une échelle spatiale aussi grande. Dans l'ensemble, lors de l'étude de la dérive larvaire à grande échelle, l'hydrodynamique locale et les variations interannuelles ont la plus grande influence sur la dérive larvaire.

Cela nous a conduit à nous interroger sur les conséquences potentielles que les changements dans l'hydrodynamique locale pourraient avoir dans les années à venir, et plus précisément sur la localisation des frayères. En effet, les espèces de poissons estuariens-opportunistes ont développé des stratégies évolutives afin d'améliorer le succès de recrutement de leur progéniture, y compris la sélection de frayères appropriées. Cependant, l'augmentation de la température due au changement climatique peut entraîner des changements dans l'hydrodynamique, des dérives larvaires plus courtes et une reproduction plus précoce, et par conséquent l'emplacement des frayères les plus appropriées pourrait changer. Dans le **Chapitre 2**, nous cherchons à savoir si la localisation des frayères les plus favorables (permettant de plus grands succès de recrutement) est stable dans le temps, et si des différences peuvent être trouvées entre des années contrastées environnementalement. Plus précisément, nous nous demandons si les frayères permettant les taux de recrutement les plus élevés restent aux mêmes endroits d'une année sur l'autre, favorisant alors l'émergence de stratégie type homing où les individus adultes se reproduiraient toujours au même endroit afin d'assurer une meilleure survie de la progéniture, ou bien si les frayères favorables se déplacent favorisant ainsi l'émergence de stratégies de sélection de frayères plus adaptatives en fonction de signaux externes. Pour ce faire, la zone d'étude a été réduite à trois sous-régions (le Golfe de Gascogne, la Manche et la mer Celtique) et à trois espèces (la sole commune, le flet commun et le bar européen). Nous avons travaillé sur 21 années, de 1999 à 2019. Les années ont été caractérisées selon des paramètres environnementaux : deux indices de pression atmosphérique (l'oscillation Nord Atlantique - NAO et le pattern Atlantique Est - EA), et pour chaque région la température de la mer en surface et les précipitations. L'utilisation d'une analyse en composantes principales et d'une classification ascendante hiérarchique nous a permis de séparer nos 21 années en trois groupes possédant des conditions environnementales jugées similaires. Un groupe dit d'années « chaudes » caractérisées par une température et un indice NAO fort ($n = 8$), un groupe d'années dites « froides » à l'opposé avec une température et un indice NAO faible ($n = 8$), et pour finir un groupe d'années dites « sèches » montrant de particulièrement faibles précipitations ($n = 5$). Pour chacune de ces années, nous avons modélisé la dispersion de larves lâchées sur l'entièreté des frayères théoriques, jusqu'à leur recrutement dans les nourriceries. Nous avons récupéré pour chaque particule son emplacement de départ, et des informations sur son succès de recrutement et la durée de sa dérive larvaire si en effet elle avait bien recruté. Un lissage basé sur un kernel binaire a été utilisé afin d'obtenir une estimation de la probabilité de succès de recrutement sur l'ensemble de la frayère théorique, permettant d'obtenir pour chaque espèce et chaque année une carte montrant les probabilités de succès de recrutement selon l'endroit de ponte. Afin de délimiter les frayères dites « favorables », nous avons réalisé une analyse de hot-spot (Getis-Ord G_i^*). Cela nous a permis d'obtenir pour chaque espèce et année une carte binaire montrant en chaque point si la zone de frai est « favorable » ou non. En empilant ces cartes binaires au sein de chaque groupe d'années, nous avons obtenu pour chaque groupe d'années une carte montrant la récurrence des frayères « favorables ». Nous avons ensuite pu les comparer en utilisant l'indice D de Schoener, permettant de quantifier la similarité entre des cartes. Dans un premier temps, notre modèle montre un recrutement moyen différent selon les conditions environnementales : plus fort lors d'années « chaudes » et plus faible lors d'années « froides ». C'est un résultat classique en modélisation de dérive larvaire, expliqué par le fait qu'une température élevée

accélère le développement des particules, les faisant recruter en nourriceries plus rapidement. Ainsi, les larves sont exposées moins longtemps à la mortalité journalière appliquée dans le modèle. Cependant, même si le recrutement moyen possède une forte variabilité inter-annuelle, ce n'est pas le cas de la localisation des principales frayères. En effet, notre modèle ne montre aucun changement dans l'emplacement des frayères les plus favorables malgré des conditions environnementales contrastées. Cela pourrait suggérer que la sélection naturelle pourrait privilégier l'émergence d'homing fort. Par « homing » nous entendons la visite répétée des individus matures sur les mêmes sites de ponte, et non pas l'utilisation de frayères possédant des caractéristiques abiotiques similaires.

Suite à cela, nous nous demandons dans le **Chapitre 3** si les frayères permettant le plus grand succès de recrutement selon notre modèle correspondent à des frayères documentées dans la littérature. Nous nous intéressons également à la distance de dispersion parcourue, en nous demandant s'il y a des différences notables dans la localisation des frayères permettant beaucoup de dispersion, et celles qui permettent de la rétention dans les nourriceries les plus proches. Pour ce faire, nous nous sommes concentrés sur la sole commune *Solea solea* et le bar européen *Dicentrarchus labrax* dans le Golfe de Gascogne, qui présentaient des données facilement accessibles sur la localisation de leurs habitats dans cette zone. Nous avons divisé la zone d'étude par latitude, en nous basant sur les rectangles statistiques de l'ICES. En utilisant les mêmes sorties de MARS3D que pour le chapitre précédent sur 21 années, nous avons pu regarder les proportions de larves recrutées dans des nourriceries documentées qui provenaient de frayères théoriques ou bien documentées. Nos résultats montrent que la distance de dispersion semble en grande partie être liée à la distance aux nourriceries disponibles. Les frayères documentées ne semblent pas permettre un succès de recrutement particulièrement plus grand que les frayères théoriques, et les nourriceries documentées ne reçoivent pas plus de larves que les nourriceries théoriques. Cela semble bien indiquer que le potentiel succès de recrutement de la progéniture, incluant l'hydrodynamique et le comportement larvaire, ne suffisent pas à expliquer l'emplacement observé des frayères. Cela nous amène également à nous poser des questions sur les choix de modélisation que nous avons fait, comme l'absence de migration tidale ou de mécanismes d'orientation.

En conclusion, plusieurs effets du changement climatique sur la dérive larvaire sont mis en évidence dans cette thèse, notamment le rôle de la température sur la distribution des larves de poissons, l'impact limité sur l'emplacement des frayères dites « favorables », et le plus grand succès de recrutement au cours d'années caractérisées par un indice NAO et une température élevée. Toutefois, ce travail repose sur une approche théorique, posant la question des choix dans l'échelle spatiale utilisée et dans le degré de précision mis dans la modélisation. Le manque de données limite les moyens de validation, ce qui entrave l'application directe des sorties de modèles dans des cas concrets. L'émergence de nouvelles techniques pourrait conduire vers de nouvelles opportunités en matière de validation. Les méthodes indirectes (comme la génétique ou la géochimie des otolithes) peuvent ouvrir une voie dans le futur pour une meilleure calibration et validation des modèles.

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GENERAL INTRODUCTION

1. Marine Estuarine-Opportunists fish species

1.1. Life-cycle

Marine estuarine-opportunists (MEO) are fish species that undergo ontogenic habitat shifts during their life cycle, each habitat serving a specific purpose in completing the distinct needs of their life stages (Fig.1). They are defined as species that regularly enter estuaries, primarily during their juvenile phase, but they can also use coastal waters as alternative nursery grounds (Potter *et al.*, 2015).

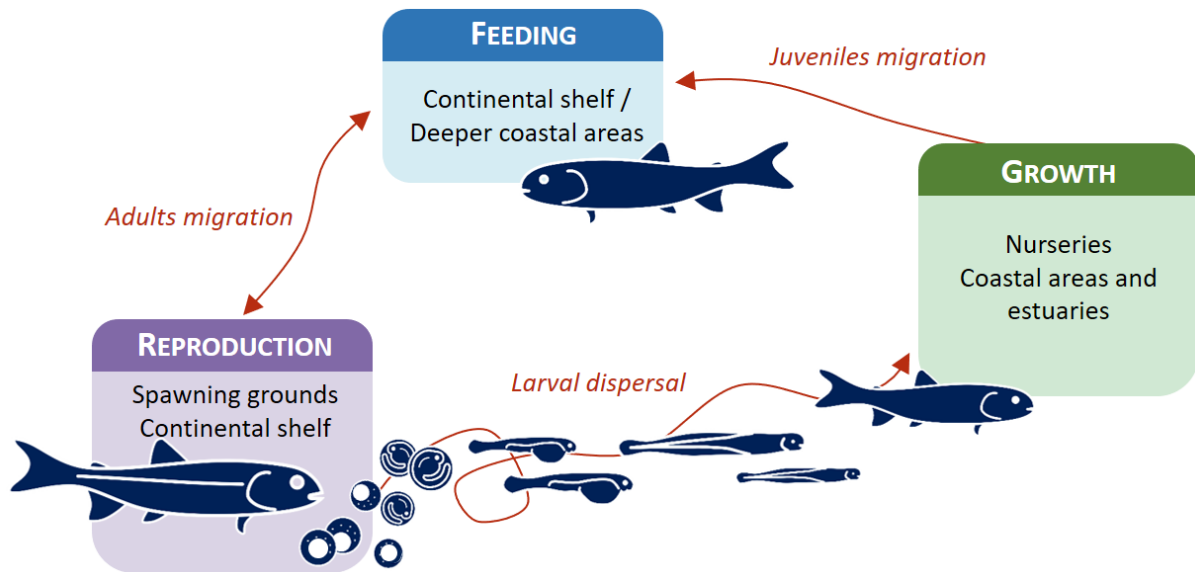


Figure 1. Life cycle of Marine-Estuarine Opportunists fish species. Adapted from Potter *et al.* 2015.

In fact, most of MEOs spawn offshore on the continental shelf. Each female releases a substantial number of eggs, typically several hundreds of thousands (Devauchelle *et al.*, 1987; Devauchelle and Coves, 1988), depending on species, size, age, and environmental factors (Sardi *et al.*, 2023). This large amount of offspring is due to their reproductive strategy, which involves the production of a large number of eggs in order to increase the chances of survival for at least some of the offspring (Singh, 2019). These eggs drift along ocean currents, undergoing several life stages before eventually successfully reach an estuary or a shallow marine nearshore zones (Nodo *et al.*, 2023; Veale *et al.*, 2015). These environments are ideal for juvenile development, offering abundant food availability, optimal growth conditions, and low predation risks (Duffy-Anderson *et al.*, 2015). Within these regions, which serve as nursery grounds for juveniles, individuals remain for a variable duration often ranging from one to two years, depending on the species, before migrating to adults' feeding grounds in deeper coastal areas or offshore on the continental shelf. Once they reach maturity, they can go reproduce on spawning grounds to lay eggs periodically throughout the spawning period, potentially doing so multiple times over their lifetimes.

In fisheries science, “recruitment” is a term used to define the proportion of individuals attaining a life stage suitable for exploitation (*i.e.* reaching the legal size to be potentially harvested, Camp *et al.*, 2020): this would refer to the amount of individuals reaching adult feeding grounds on Fig.1. Nonetheless, for the duration of this study and henceforth, the term "recruitment success" will exclusively refer to the percentage of larvae that have successfully reached and settled in nursery areas, which is another possible use of this term (Boehlert and Mundy, 1988).

1.2. Larval stage: a key stage to infer on whole populations

The most common situation in these species is that eggs are released and fertilized in open water. The larva develops progressively inside the egg, before hatching after a few days, attached to the yolk-sac. This yolk-sac larva has its mouth and gut closed. As the yolk resorbs, the larva starts external feeding thus being called a “first-feeding larva”, generally starting feeding on rotifers (Martinez and Bolker, 2003). For some species, like flatfish, this is when a clear metamorphosis happens, with a rotation of the eye and a shift in the orientation of the body so that larvae come to lie on one side. All these stages are precisely described in Barnabe *et al.*, 1976, Blaxter, 1969, Martinez and Bolker, 2003 or Schreiber, 2013 and can be partially seen in Fig.2.

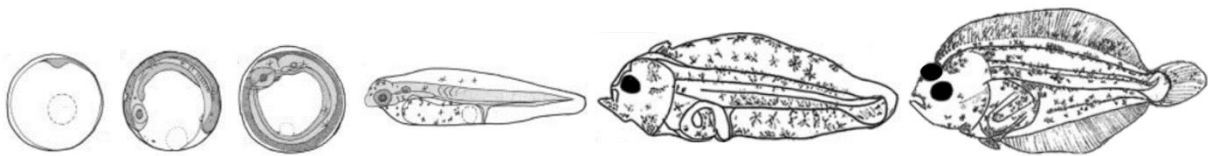


Figure 2. Larval stages of *Paralichthys dentatus* taken from Martinez and Bolker (2003). The first three pictures are eggs stages. The fourth picture is a yolk-sac larva, recognizable by its head still attached to the yolk-sac. Comes after the first-feeding larva with its operational mouth and finally the metamorphosing larvae which has undergone its eye migration.

The pelagic larval duration (PLD), which refers to the total duration of larval development during the pelagic planktonic phase, varies depending on the species, and more specifically on the egg size, on the maternal genetics and on the temperature experienced by the individual (Fox *et al.*, 2003; O’Connor *et al.*, 2007). It can last from days to months, and the PLD does not necessarily correlate with the distance covered between the spawning and nursery grounds (*i.e.* dispersal distance, Shanks, 2009).

Throughout the developmental stages of these MEO fishes, starting from the first-feeding larval stage, both mobility and speed increase as the organism grows (Clark *et al.*, 2005; Osse and Van Den Boogaart, 1997). This adaptation facilitates food foraging and enables the organism to swim towards

areas of lower salinity, bringing it closer to river plumes (Bos and Thiel, 2006). Furthermore, it allows individuals to undergo vertical migrations (Grioche *et al.*, 2000; Lagardère *et al.*, 1999). In fact, for many species during the initial stages, individuals predominantly inhabit the upper water column due to the buoyancy conferred by the yolk-sac (Yin and Blaxter, 1987). Once it has resorb, and the larva has to feed externally, fins become more developed allowing for vertical swimming behaviour, which helps improve individuals' survival and recruitment success (Teodósio *et al.*, 2016). In fact, first-feeding larvae can demonstrate diel (or nycthemeral) vertical migration patterns, moving up the water column at night for feeding and moving down during daylight hours to mitigate predation risk (Grioche *et al.*, 2000; Lagardère *et al.*, 1999). In the later stages, larvae can undertake tidal vertical migrations, going up during high tide to progress further in the river plumes, and descending when the tide is low to remain at the same place (Bos *et al.*, 1995; Grioche *et al.*, 2000; Lagardère *et al.*, 1999). Overall, vertical migrations are known as being a key behaviour for larval fishes, enabling the selection of advantageous currents, and increasing recruitment success (Beraud *et al.*, 2018; Fox *et al.*, 2006; Zölck *et al.*, 2015). However, this behaviour is difficult to observe and consequently poorly known for most species (not for all species, not in all populations, not for the same stages...), and frequently debated (Bolle *et al.*, 2009).

Studying larval stage is important as it can provide insights on whole populations (Sardi *et al.*, 2021). In fact, Howell and Baynes (2004) highlighted that external factors affecting larval development bear consequences during later life stages. Compared to these stages, individuals when they are in their larval stage experience the highest dispersal potential (Cowen and Sponaugle, 2009), but also the highest natural mortality rates (Le Pape and Bonhommeau, 2015) and the highest sensitivity to environmental stressors (Hutchinson *et al.*, 1998). Indeed, the larval stage is the one for which the mortality is the highest (May, 1974). Le Pape and Bonhommeau (2015) estimated recruitment success to be around 1:100,000. Several reasons have been advanced in literature, the most famous one being the "Critical Period hypothesis" enunciated by Hjort in 1914, which has sparked extensive discussion since (Houde, 2008; Le Pape and Bonhommeau, 2015; May, 1974; Sifa and Mathias, 1987 to only cite a few). The critical period hypothesis posits that the increased mortality observed in the larval phase is a result of insufficient food availability when the larva changes from endogenous to exogenous feeding. In fact, food availability is one of the most limiting factor for larvae (Yamashita *et al.*, 2001). However, it is postulated that hydrodynamic conditions might also hinder larvae feeding performances, a phenomenon called "hydrodynamic starvation" (China *et al.*, 2017; China and Holzman, 2014; Holzman *et al.*, 2015). Other parameters widely infer on larvae mortality, such as the

encounter with lethal temperature, predation, or loss in hydrodynamic currents (Cowen and Sponaugle, 2009; Eme *et al.*, 2015; Houde, 2008; Mueller, 2018).

1.3. Balancing connectivity and mortality in larval dispersion

Among all the life stages of MEO fishes, the pelagic larval stage contributes the most to dispersion of individuals towards potentially distant habitats (Cowen and Sponaugle, 2009). This dispersion promotes genetic diversity, and the interconnections of sub-fractions of populations, potentially contributing to the emergence of meta-population rather than independent populations. This mechanism not only mitigates potential drift effects and inbreeding depression in small populations but also facilitates the colonization of new habitats, and can mitigate the risk of some habitats becoming temporarily or definitively unavailable (Kerr *et al.*, 2010; Ronce, 2007). However, even though long-distance dispersal confers all these benefits at the population level, it also comes with risks. In fact, as mentioned earlier, larval drift is associated with a high mortality rate, due to starvation, predation, encounter with lethal temperatures or with the risk of not reaching suitable nursery grounds. As a result, a longer drift associated with longer distance increases the risk of mortality. This balance between a shorter larval drift distance ensuring high recruitment success, and a longer larval drift that might be associated with heightened mortality is known as the retention/dispersion trade-off (Jones *et al.*, 2009; Shima and Swearer, 2009; Stephenson *et al.*, 2015). Spawning timing and location (Bailey *et al.*, 2005; Huret *et al.*, 2010) or even the eggs density (Pacariz *et al.*, 2014) can promote a good retention towards close nursery grounds, or dispersion far from the spawning grounds. The interest of the retention/dispersion at the individual level comes down to this famous expression: Is it better to put all your eggs in one basket, or have fewer eggs but in several different baskets? The idea is to diversify your options to minimize risks and avoid losing everything in case of failure. This is directly linked to the portfolio concept, used in economy to describe the practice of diversifying investments to minimize capital losses risks (Byers *et al.*, 2015). Here, in ecology, this portfolio concept can be transcribed as the diversity in the individuals way to ensure for offspring survival thus sustaining the whole population, but also as the diversity of available habitats (Schindler *et al.*, 2015). In fact, numerous species, among which highly exploited ones, are highly dependent on coastal and/or estuarine nurseries (Lellis-Dibble *et al.*, 2008). Therefore, these populations are highly reliant on habitats connectivity and on the diversity of available and suitable nurseries for juveniles.

Dispersion or retention, the success of recruitment heavily depends on effective larval transport, which is influenced by the hydrodynamic conditions (changing annually) and the reproductive behaviour of

individuals. This behaviour is shaped by adaptive processes and can either be stable from year to year or, conversely, be driven by environmental cues.

2. Climate change

2.1. Overview

Climate change refers to global change of climate over time. Anthropogenic activities have disrupted the natural balance of the climate system leading to widespread and rapid changes in the atmosphere, hydrosphere and biosphere (Calvin *et al.*, 2023). The totality of these disruptions initiated by humans mark the transition from Holocene to a new era called Anthropocene (Crutzen, 2006). The increase in global temperature (Callendar, 1938) has gradually become a growing concern leading to the creation of the Intergovernmental Panel on Climate Change (IPCC) in 1988. In addition to habitat loss, pollution, and over-harvesting, climate change constitutes a factor contributing to the ongoing sixth mass extinction (Ceballos *et al.*, 2015). Warming temperatures result in both geographical and temporal shifts in wild populations (Burrows *et al.*, 2011). The latter is known as phenological shift, *i.e.* the seasonal timing of history events, and impacts numerous plant and animal species (Scranton and Amarasekare, 2017; Visser and Both, 2005). The need to understand population dynamics in order to forecast whether it is at a risk of collapse or is able to adapt to environmental changes has become more critical than ever (Cerini *et al.*, 2023).

2.2. Its effects on larval drift

By affecting many abiotic factors such as temperature and pH, but also by modifying hydrodynamic conditions, climate change is expected to have drastic consequences on the entire larval drift, recruitment success and population connectivity.

2.2.1. *Altered abiotic factors: climate change impacts on the marine environment*

The high atmospheric CO₂ emissions cause a cascading effect on the ocean (Calvin *et al.*, 2023). This is primarily due to the greenhouse effect, wherein the rise in atmospheric and oceanic temperatures instigates significant alterations across the entirety of the oceanic system. These alterations encompass changes in hydrodynamic currents, stratification patterns, weather patterns (both frequency and intensity), turbidity, salinity and pH levels (Bashevkin *et al.*, 2020; Sen Gupta and McNeil, 2012, Fig.3).

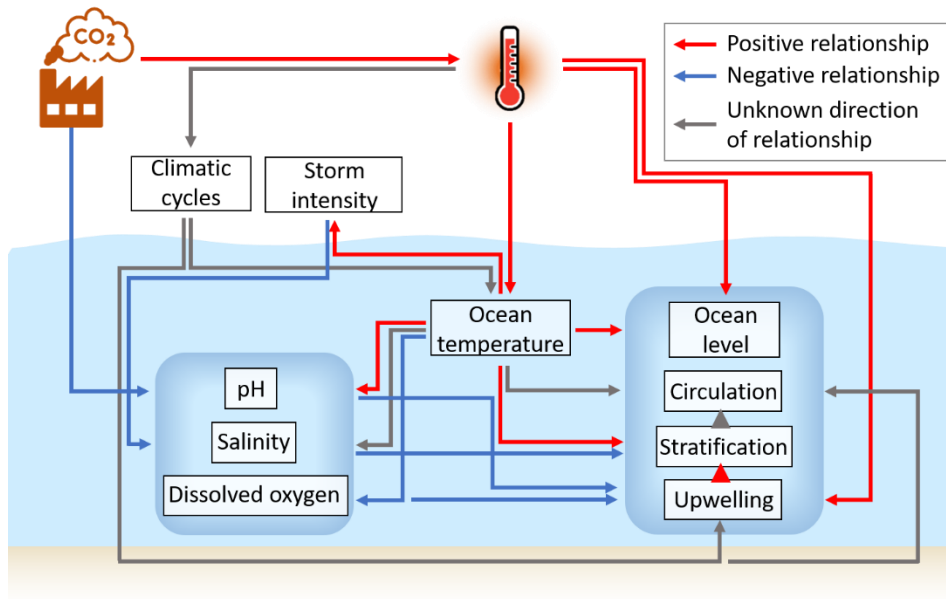


Figure 3. Important effects of climate change on the ocean, adapted from Bashevkin *et al.* 2020. Arrows show the cascading effect caused by a higher concentration of greenhouse gases in the atmosphere.

For passive drifters, changes in currents have huge implications (Gennip *et al.*, 2017). Several major circulation patterns are known to be modified by climate change. For instance, the Atlantic Meridional Overturning Circulation (AMOC), a crucial oceanic current that transports warm waters towards the Northern Atlantic, has been gradually deteriorating (Boers, 2021; Boulton *et al.*, 2014; Thornalley *et al.*, 2018). The North Atlantic Oscillation (NAO) index has also shown a different pattern in recent years (Delworth *et al.*, 2016; Gillett *et al.*, 2003). The NAO index quantifies an atmospheric pressure anomaly over the North Atlantic Ocean, and informs on the general conditions in weather and water circulation extending from eastern North America to western and central Europe (Hurrell and Deser, 2010). Strong positive phases of the NAO are associated with warmer years and stronger currents (Barnston and Livezey, 1987). These positive phases have been more frequent in the recent years (Gillett *et al.*, 2003), though to be actively participating in the northern atmosphere warming (Delworth *et al.*, 2016).

2.2.2. Modified biotic traits: climate change impacts on larvae

MEO fish larvae are highly sensitive to changes in temperature. In fact, the early life stages are among the most temperature-sensitive phases for fish (Dahlke *et al.*, 2020). Even small variations can have significant effects on their development, growth, and survival (Eme *et al.*, 2015; Mueller, 2018). The comprehensive review conducted by Alix *et al.* in 2020 regarding the impact of elevated temperatures on teleost reproductive biology indicates a decrease in egg quality associated with a higher deformity rate. This is coupled with reduced fertilization rates, lower survival and hatching rates. Depending on

the species, there is also evidence of an earlier spawning season, as spawning timing can be influenced by external factors such as temperature thresholds or photoperiods (Devauchelle and Coves, 1988; Fincham *et al.*, 2013; Oliveira *et al.*, 2009). Additionally, the study observes variations in the duration of the spawning season, which can either lengthen or shorten depending on the species considered. Moreover, elevated temperature accelerates individual growth rates, thereby reducing the duration of the larval stage, shortening the larval drift (Houde, 1989; Keller *et al.*, 2020; Teal *et al.*, 2008). As mentioned previously, higher temperatures can also induce early spawning. Therefore, with all these pieces of information, with warming temperatures ones might expect an earlier spawning with a shorter larval drift. However, some studies indicate that the opposite is occurring. Indeed, with earlier spawning, larvae on average develop in cooler water temperatures, which leads to an extended larval drift (Lacroix *et al.*, 2018). Phenological shifts are particularly important, as a shift in the spawning period can also lead to a mismatch between prey and predator abundance (Cushing, 1990; Keller *et al.*, 2020). In fact, ichthyoplankton communities are mainly influenced by temperature (Guerreiro *et al.*, 2021). Thus, an excessively advanced spawning period can result in most fish larvae searching for food when no preys are available, leading to high mortality (Daewel *et al.*, 2011). Studies have also examined the interactions between elevated temperatures and reduced food supply, revealing that these two factors interact, suggesting a prolonged larval duration in the upcoming years (Allan *et al.*, 2022; McLeod *et al.*, 2013). Therefore, a change in global temperature can have multifaceted repercussions on the spawning and larval development of marine fish, and the interactions among the alterations brought about by this temperature change make predictions more challenging.

2.2.3. *Changes in environmental conditions and larval characteristics leading to modifications in connectivity*

Because of changes in abiotic conditions, northwards shifts in species distributions have been observed or predicted to remain in their optimal thermal niches (Cheung *et al.*, 2012; García Molinos *et al.*, 2017; Lima *et al.*, 2022; Poloczanska *et al.*, 2013; Santiago *et al.*, 2016). These biogeographical shifts, along with the previously discussed phenological shifts, and the altered biotic and abiotic factors affecting larval drift, are highly likely to impact local and global connectivity dynamics (Lacroix *et al.*, 2018). Indeed, as specific spawning locations, timing and current conditions play a crucial role to transport larvae to particular nurseries (Hinckley *et al.*, 2001), alterations to these parameters can impede the drift towards some nurseries. Some nurseries themselves might become temporarily unavailable or unsuitable because of hydrological conditions (Alp and Pichon, 2020; Van der Veer *et al.*, 2022), or even permanently unsuitable due to rapid warming rates (Scanes *et al.*, 2020). Alternatively, these

changes can also lead to new trophic interactions (Nicolle *et al.*, 2022). As such, it has increased the importance of discerning populations that serve as sources, those that function as sinks, and those that are connected through larval exchange. In this shifting habitat mosaic where migration routes are compromised, the flexibility of species traits in response to a changing environment is a critical factor driving their adaptive capacities (Vary *et al.*, 2023). Whether through physiological, geographical, or temporal adjustments, animal species have the capacity to adapt when confronted with a changing environment. This raises the question of how rapidly these species can adapt, given the rate at which climate change is unfolding (Hughes, 2000).

3. Exploring the toolbox: how to study fish larval drift

3.1. Diverse methodological approaches

Studying larval drift in ocean currents is a complex task (Levin, 2006). First, because larvae are minuscule, produced in large number and suffer from high mortality rate. Moreover, identifying them at the species level can be quite challenging. Due to their size, it is not possible to attach tracking devices to individuals, as can be done in later developmental stages to study spawning site locations and site fidelity phenomena (Dando, 2011; Pawson *et al.*, 2007). Apart from fishes, some particular larvae are possible to track *in situ*, like ascidians larvae which are relatively large (~5mm ; Olson and McPherson, 1987) and settle only a few meters away from their parents colony after a few minutes (Davis and Butler, 1989). For fish however, because of the impossibility to follow them directly, laboratory experiments were undertaken to understand larvae development and behaviour (Dionísio *et al.*, 2012; Oliveira *et al.*, 2009; Ryland, 1966; Ryland and Nichols, 1975; Solemdal, 1967). However, studies in controlled environments alone cannot provide definitive conclusions about population dynamics. As such, indirect empirical methods are particularly valuable. In those methods, we can cite the use of stable isotope marking (Almany *et al.*, 2007), eggs surveys (van der Land, 1991), otolith studies (Allen *et al.*, 2008), genetic approaches (Christie *et al.*, 2010; Hoffman *et al.*, 2012) and even the use of drifters (Vendrami *et al.*, 2021).

The cons of most of these methods are that they largely focus on successfully recruited larvae (or at least, on larvae that have survived until the observation), thus, they can offer insights into the larvae's origins and arrival point, they don't provide insights on what happened in between. In addition, these methods perform well on a small scale, but the sampling effort needed to study a larger area would be tremendous. In fact, these approaches only provide empirical evidence of a single event, but fail to estimate the potential dispersal kernel of particles, and the likely dispersal to other locations.

In this context, modelling have proved to be a relevant tool to provide a more holistic overview of the larval drift (Fig.4). Relying on data collected in laboratories and in the field, biophysical models based on individuals are parameterised to model both ocean currents and the growth and behaviour of larvae. One obvious advantage over the described above indirect and direct methods is the study of multiple releases of larvae. These releases repeated through time and space allow for the capturing of recruitment variability, and able to infer on potential dispersal and related connectivity (Cowen and Sponaugle, 2009; Leis *et al.*, 2011).

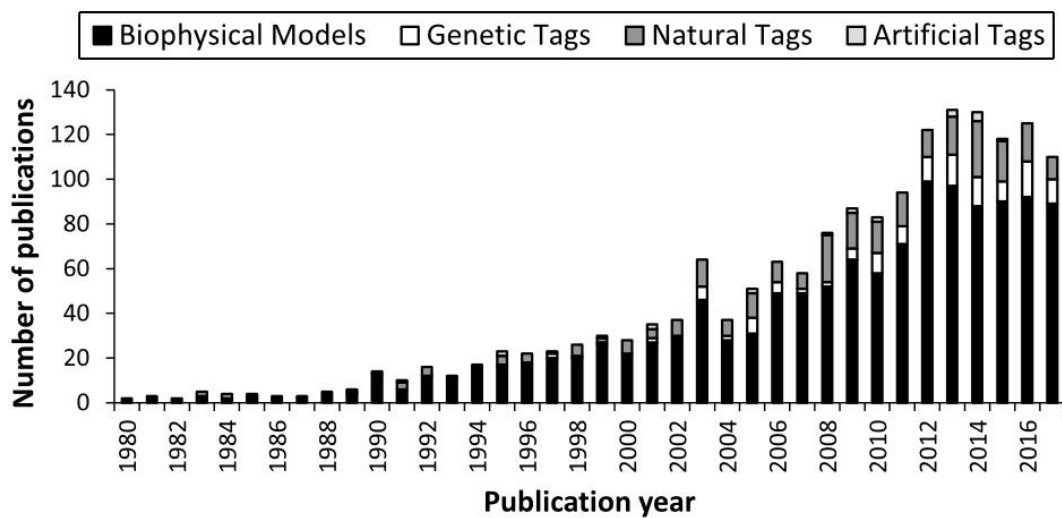


Figure 4. Prevalence of different methodologies used to study larval drift across the years. This figure was taken from Swearer *et al.*, 2019.

3.2. Focus on biophysical modelling

Biophysical models have two components: the hydrodynamic and the particle-tracking model.

The hydrodynamic model calculates the ocean circulation pattern in a certain area, ending in a vector field in which the individual based model is able to run. Some of these hydrodynamic models may also compute temperatures, salinities, and take into account hydrographic features of the coastal zone, which are particularly difficult to model (e.g. breaking waves, upwelling, tides, waves, rivers runoff). Each model and configuration have specific resolution, temporally, horizontally and vertically with a certain number of generalized sigma layers to represent the water column. As such, the choice of the hydrodynamic model to be used must be made depending on the ecological question and the resulting resolution needed to answer it. Hydrodynamic models are numerous as they can be specific to certain regions and scale, but also reflect the diversity of available modelling platforms or the different working groups. Among these 3D models, we can cite the Bryan-Cox-Semtner model, which gave rise

to the Baltic Sea Ice-Ocean Model, the NEMO model (Nucleus for European Modelling of the Ocean) which gave the MFS (Mediterranean Sea Forecasting System), the ROMS model (Regional Ocean Modelling System), the COHERENS model (Coupled Hydrodynamical Ecological model for REgionAl Shelf seas) or also the MARS model (Model for Applications at Regional Scale).

On top, or consequently to the hydrodynamic model, a particle tracking model is used to mimic the larval drift. Additionally to the physical transport in currents in the x, y, z and time structure of the hydrodynamic model, those individual-based models can include key biological traits, thus allowing for species-specific modelling. They allow the computation of the particles density, size, development, swimming behaviour and can do so in accordance with the external conditions computed by the hydrodynamic model. Once again, numerous models exist including for instance LTRANS, CMS or Ichthyop.

Determining to which extent each model can wield to different results is a work in progress (Amemou *et al.*, 2020; Hufnagl *et al.*, 2017). Each model is unique in the sense that it is defined by choices. Modelling involves simplifying reality, which may entail omitting or simplifying certain processes. Therefore, every choice made by a modeller can have consequences and should be thoughtfully considered to fully comprehend the implications on the results.

4. Thesis objectives

The aim of this thesis was to study the impacts of climate change on the drift of Marine Estuarine-Opportunists fish larvae with biophysical models. More specifically, the aim was to try to understand the potential effects of climate change on recruitment success and connectivity, while highlighting the advantages and disadvantages of using these models. The main text is composed of three research papers, each constituting a chapter.

Due to the complexity of biophysical models, the many parameters required and the uncertainty of many of those, a comprehensive sensitivity analysis was a crucial step before drawing conclusions on the effects of environmental drivers. The **first chapter** goal was to assess the relative influence of extrinsic (years and region's hydrodynamic) 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.

Following this chapter, we investigated further the hydrodynamics and inter-annual variability effects on larval drift by addressing the inter-annual variability in the location of spawning grounds. In the **second chapter**, 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.

The favourable spawning areas found in the second chapter through modelling were then confronted to their documented counterparts. The **third chapter** focuses on the differences between the potential habitats, according to species preferences in terms of depth and sediments, compared to habitats identified in the literature, inferred through indirect information. Comparisons were made to detect if documented habitats exhibit distinct patterns of recruitment success and connectivity, as their location may be the result of adaptive process.

Finally, we have examined the knowledge acquired throughout this thesis regarding the overall effects of climate change on fish larvae dispersion. We have also discussed how this knowledge might guide future research in larval drift modelling, by addressing its limitations and potential directions.

Throughout this thesis, we employed MARS3D, a model developed by IFREMER (Lazure and Dumas, 2008 with the same configuration as in Petton *et al.*, 2023), coupled with a Lagrangian particle-tracking module reproducing the growth and behaviour of larvae (Huret *et al.*, 2010). The model was set on a broad study area encompassing the Western Europe (Iberian coast, Bay of Biscay, Celtic Sea, English Channel and North Sea; as in Savina *et al.*, 2016). We used five well-documented species of high fisheries importance (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*). Because of their differences in life-history traits, they were used as ecological archetypes to infer and extrapolate results to a wider diversity of species. The study area's size and the number of ecological archetypes modelled decreased progressively throughout the chapters to better align with issues that were more specific, or when species-specific information were not available. MARS3D outputs were then transferred to R version 4.0.3 (R Core Team, 2020) to conduct statistical analysis.

CHAPTER 1: 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 fish 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.

Keywords larval drift models, sensitivity analysis, fish larvae, life history, oceanography, climatic changes

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 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 appears 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 (Trembl *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 (Faivre *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 Tab.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 Petton *et al.* (2023) in the same study area as 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 2.5 km horizontal resolution with 30 vertical generalized sigma layers. We used a time step of about 2 minutes 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).

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 (Tab.1, Fig.5). 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, 1,200 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.6 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*.

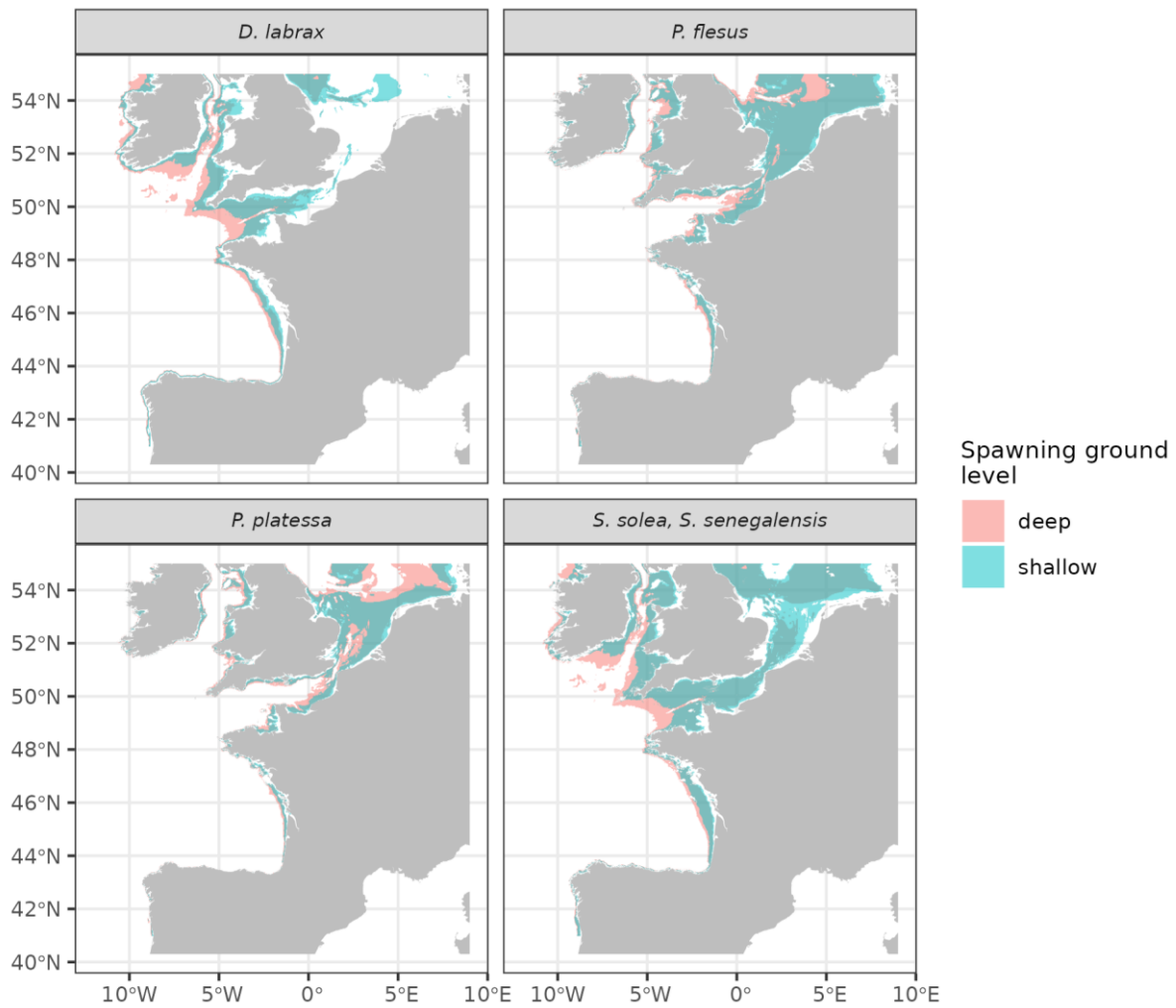


Figure 5. Location of spawning areas considered in the modelling. Spawning areas were computed based on the species preferential spawning areas depths and bottom sediments (Tab.1). The bathymetry was extracted from MARS3D, and sediments originated from EMODnet Geology project seabed substrates map, 2019. The high and low modalities had this depth range respectively increased by 10% or reduced by 10% (Tab.2).

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 metamorphosing 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 Tab.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 temperature dependent maturation level ($m_i(t)$) into a length, we postulated that stage transition occur at constant length (Tab.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 (Tab.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 20m deep; Fig.6) (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 Tab.1, and set with 70 days as a maximum).

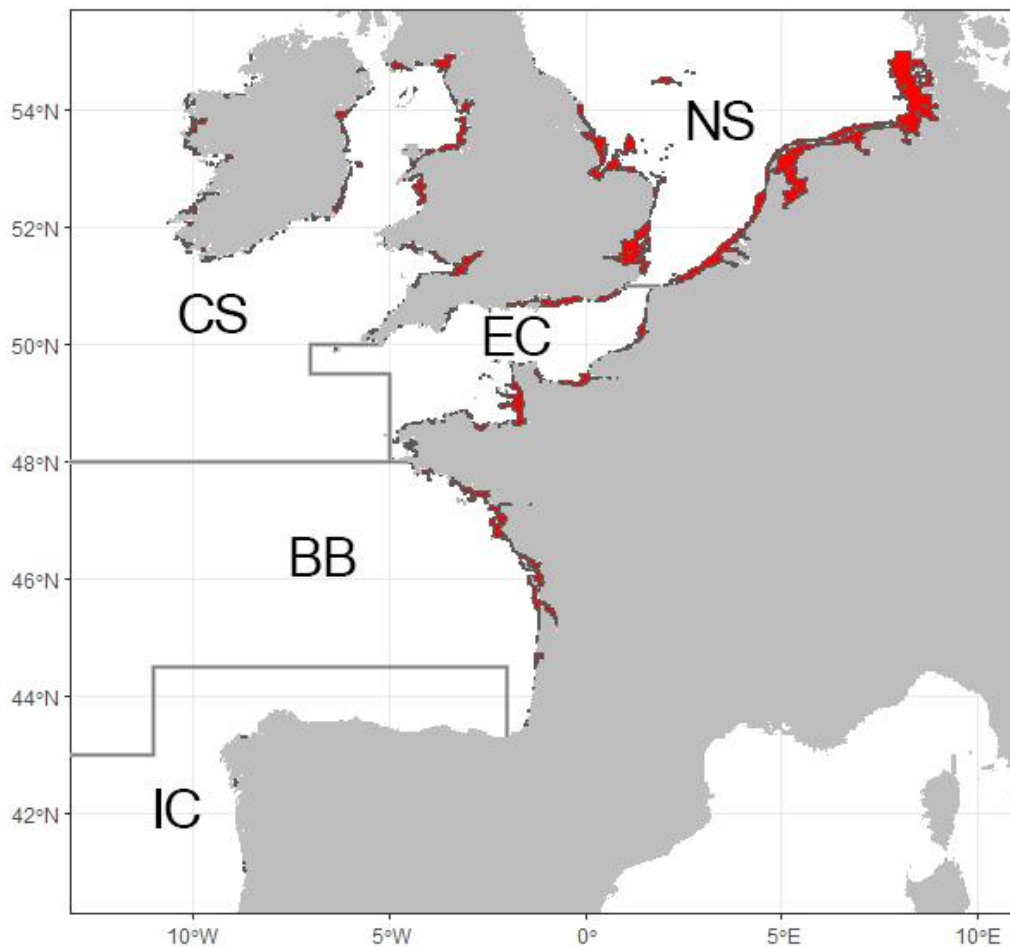


Figure 6. Sub-areas and nursery location considered in the modelling. All species shared common nursery areas (depth<20m, bathymetry extracted from MARS3D). The study area was divided into five sub-areas, following the ICES statistical rectangles: the Iberian coast (IC), the Bay of Biscay (BB), the Celtic Sea (CS), the English Channel (EC) and the North Sea (NS).

- *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 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.

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	Dambrine <i>et al.</i> , 2021; Koutsikopoulos <i>et al.</i> , 1989; Skerritt, 2010; Tanner <i>et al.</i> , 2017; Wegner <i>et al.</i> , 2003	
Spawning period	January-April	February-July	February-June	December-May	January-April	Amara <i>et al.</i> , 1994; Dambrine, 2020; Devauchelle <i>et al.</i> , 1987; Imsland <i>et al.</i> , 2003; Rijnsdorp, 1997; Skerritt, 2010	
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	Koutsikopoulos and Lacroix, 1992; Pickett and Pawson, 1994; Yin and Blaxter, 1987	
Stage duration D	Egg	$\alpha = 274.64$; $\beta = 1.5739$		$\alpha = 12.65$; $\beta = 0.33$	$\alpha = 114.18$; $\beta = 0.95$	$\alpha = 6.47$; $\beta = -0.129$	Barbut <i>et al.</i> , 2019; Beraud <i>et al.</i> , 2018
	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	Bedoui, 1995; Dinis <i>et al.</i> , 1999; Fernández-Díaz <i>et al.</i> , 2001; Fonds, 1979; Munk and Nielsen, 2005; Skerritt, 2010
	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	

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 (Tab.2) for parameters values set based on literature (Tab.1).

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

	Developmental rate		Spawning ground bathymetry (m)		Vertical migration		Spawning season (spawning events)		Temperature tolerance (°C)		Global mortality (day ⁻¹)	
	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low
<i>S. solea</i>	m>0.9	m>1.1	33-99	27-81	Presence	Absence	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<	0.099	0.081
<i>S. senegalensis</i>							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>							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>							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>							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<		

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.7). 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.7).

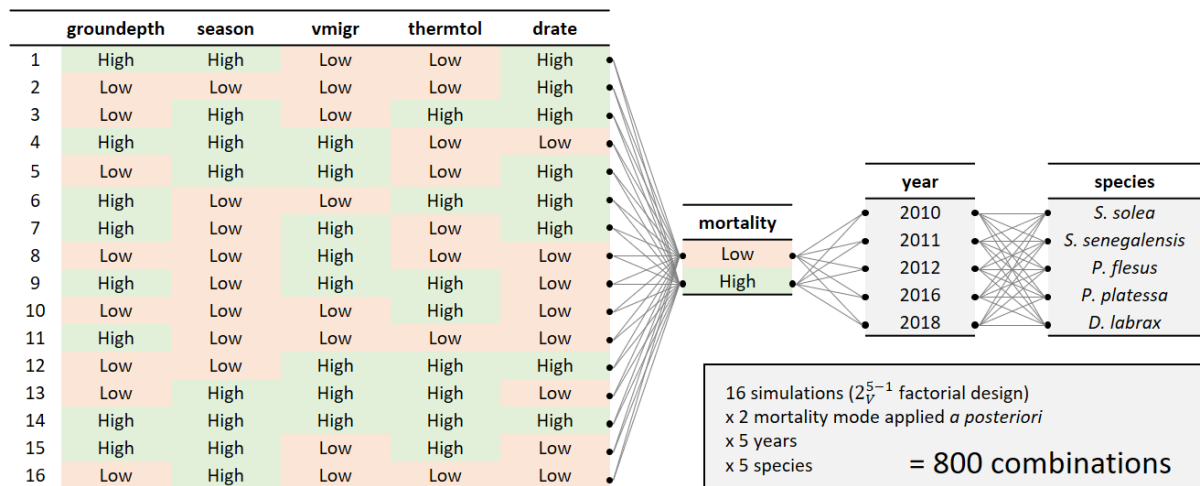


Figure 7. Simulation design used for the sensitivity analysis. “Grounddepth” stands for the bathymetry of the spawning ground, “season” for the spawning season, “vmigr” for the vertical migration, “thermtol” for the tolerance to temperature, “drate” for the developmental rate and “mortality” for the global mortality rate.

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

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

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.value (from χ^2 tests) until 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.8, Tab.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.).

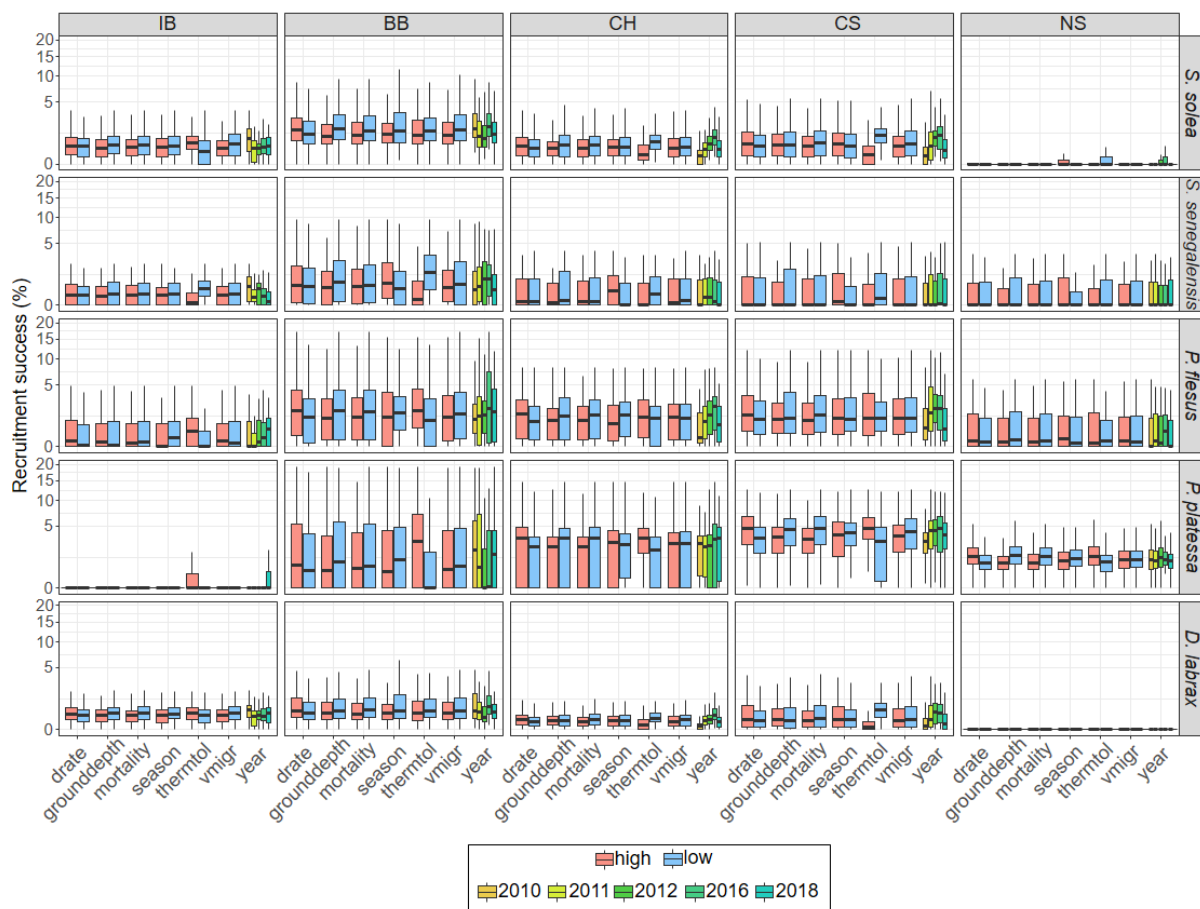


Figure 8. Recruitment success according to parameters modalities within each spawning area for each species (IB: Iberian coast, BB: Bay of Biscay; CH: English Channel; CS: Celtic Sea; NS: North Sea). “Drate” stands for the developmental rate, “grounddepth” for the bathymetry of the spawning ground, “mortality” 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.

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 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.

Table 4. Deviances explained (%) by the different parameters in the GLM. The p-values can be found in Tab.S.1. 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

4. Discussion

Larval drift simulation models 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 complexity of both the hydrodynamic and IBM models, a 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 (Favre *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 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 leaded 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 nycthemeral 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 nycthemeral 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.8, 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.

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.

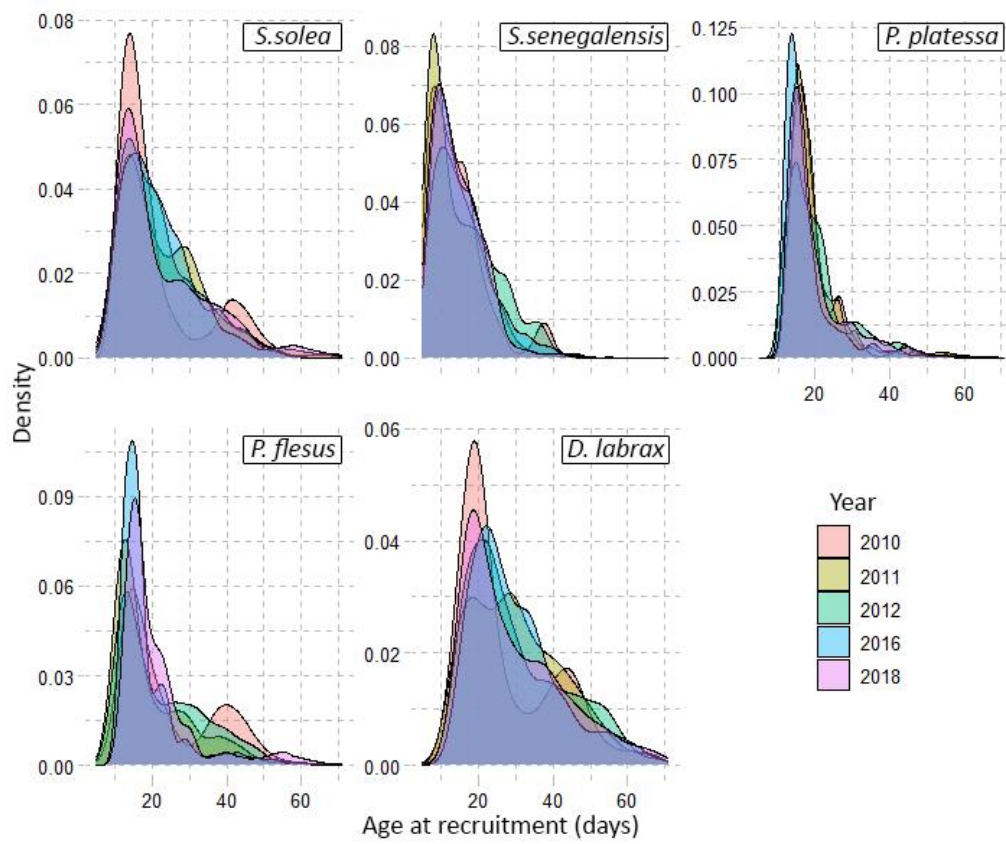


Figure S.1. Age at recruitment for recruited particles.

Table S.1. P-values used to decide which parameter to keep in GLM. P<0.05 were kept.

	<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	1.9E-04	4.6E-09	3.1E-11	1.1E-01	2.5E-04		1.3E-10	4.0E-10	5.9E-31	7.7E-22	1.4E-31		1.5E-02	2.3E-08	7.8E-13	8.6E-08	3.6E-09		2.5E-07	1.9E-15	7.5E-12	2.3E-31		9.0E-05	5.7E-03	5.7E-05	2.1E-01	3.2E-01		
season	1.7E-03	4.1E-11	7.7E-07	7.6E-01	4.7E-08		5.9E-03	3.0E-06	3.1E-07	1.2E-02	4.5E-06		1.9E-01	2.7E-03	7.3E-03	5.7E-01	3.2E-01		4.6E-02	5.1E-07	2.5E-01	2.1E-01		4.4E-03	2.7E-13	3.5E-07	2.3E-01	2.1E-06		
vmigr	1.1E-19	2.1E-10	1.3E-04	4.4E-13	3.7E-01		2.2E-04	1.6E-08	1.5E-01	1.6E-01	3.9E-06		6.4E-03	2.4E-01	7.0E-01	3.1E-02	1.6E-01		6.7E-01	2.7E-02	1.0E-05	6.3E-02		5.1E-08	1.1E-06	2.3E-06	4.8E-07	3.3E-01		
thermtol	2.5E-06	5.8E-02	5.3E-23	5.5E-41	4.6E-06		1.0E-11	8.7E-19	4.5E-02	7.7E-01	9.1E-01		4.2E-02	8.7E-01	6.4E-01	2.5E-06	3.6E-15		1.0E-23	3.5E-08	6.4E-11	3.0E-21		4.0E-01	9.2E-02	3.5E-12	5.8E-33	1.9E-13		
drate	3.7E-01	1.1E-03	1.7E-04	1.3E-04	5.9E-01		3.6E-02	7.8E-01	5.8E-01	4.4E-01	3.7E-01		2.2E-03	2.3E-07	1.9E-05	1.6E-04	3.5E-04		1.2E-06	1.3E-19	3.4E-18	9.3E-20		8.5E-05	4.5E-05	1.9E-05	2.7E-07	6.8E-03		
year	4.7E-35	3.5E-06	1.6E-62	3.2E-39	2.1E-02		3.5E-33	4.3E-01	2.5E-04	1.7E-06	6.2E-05		1.1E-16	4.5E-20	4.2E-18	1.1E-13	1.4E-01		2.2E-22	3.9E-23	3.3E-11	1.0E-02		1.0E-11	1.3E-06	2.7E-57	1.7E-27	9.4E-08		
mortality	6.4E-06	2.7E-05	6.2E-07	9.7E-08	1.0E-02		8.6E-04	9.1E-03	6.1E-04	8.6E-04	6.0E-04		1.1E-03	2.3E-05	2.1E-06	8.7E-06	4.0E-04		8.7E-06	2.4E-18	3.2E-21	2.5E-16		8.9E-09	6.0E-06	6.1E-08	1.4E-08	2.2E-04		
grounddepth:season	6.0E-01	6.2E-01	7.2E-01	6.8E-01	1.0E-01		2.7E-01	9.5E-01	4.2E-02	8.0E-01	7.8E-01		6.9E-01	8.3E-01	5.1E-01	9.0E-01	5.7E-01		7.1E-01	8.7E-01	9.3E-01	7.8E-01		2.1E-01	8.8E-01	4.8E-01	4.6E-01	6.2E-02		
grounddepth:vmigr	4.6E-01	5.7E-01	4.8E-01	5.8E-01	6.4E-01		6.4E-01	5.9E-01	8.7E-01	8.3E-01	3.4E-01		7.7E-01	4.4E-01	4.1E-01	4.6E-01	7.1E-01		6.5E-01	7.1E-01	6.0E-01	3.6E-01		8.4E-01	7.9E-01	2.6E-01	3.0E-01	5.5E-02		
grounddepth:thermtol	3.6E-01	7.5E-01	5.9E-01	7.7E-01	1.7E-01		6.7E-01	2.8E-01	9.5E-01	4.2E-01	1.4E-01		9.7E-01	7.5E-01	7.2E-01	3.5E-01	8.1E-01		1.8E-01	6.5E-01	6.3E-01	5.0E-01		1.1E-02	9.1E-01	8.9E-01	9.3E-01	4.8E-02		
grounddepth:drate	5.1E-01	2.8E-01	3.5E-01	9.5E-01	8.4E-01		4.3E-01	4.1E-01	8.7E-01	3.7E-01	1.0E-01		7.9E-01	6.9E-01	6.1E-01	7.5E-01	6.0E-01		4.1E-01	5.5E-01	5.1E-01	6.6E-01		3.8E-01	7.6E-01	7.5E-01	6.7E-01	2.6E-01		
grounddepth:year	2.7E-01	9.2E-01	9.6E-01	8.8E-01	2.5E-01		9.1E-02	9.8E-01	9.4E-01	6.7E-01	5.9E-01		9.8E-01	8.7E-01	9.4E-01	9.1E-01	9.8E-01		6.0E-01	9.9E-01	9.1E-01	9.3E-01		1.2E-01	9.5E-01	8.2E-01	9.5E-01	3.6E-05		
grounddepth:mortality	8.9E-01	9.2E-01	8.6E-01	9.3E-01	8.8E-01		9.2E-01	9.2E-01	8.9E-01	9.1E-01	7.7E-01		9.7E-01	9.7E-01	9.0E-01	9.2E-01	9.2E-01		9.9E-01	9.6E-01	9.6E-01	8.9E-01		8.9E-01	9.6E-01	9.2E-01	9.5E-01	9.6E-01		
season:vmigr	3.4E-01	5.3E-01	1.7E-01	9.0E-01	7.1E-01		8.2E-01	5.5E-01	1.4E-01	8.2E-01	6.3E-01		6.3E-01	8.5E-01	9.0E-01	9.9E-01	5.8E-01		7.3E-01	9.9E-01	6.3E-01	6.5E-01		6.0E-01	5.2E-01	7.9E-01	9.2E-01	3.7E-01		
season:thermtol	4.0E-02	1.4E-01	8.4E-01	4.5E-01	8.6E-02		4.0E-02	2.4E-01	5.8E-01	2.1E-01	4.8E-01		7.0E-01	2.9E-01	8.0E-01	7.3E-01	5.5E-03		9.5E-02	1.5E-03	1.4E-04	5.2E-07		2.4E-03	7.4E-01	3.9E-01	1.6E-01	6.7E-02		
season:drate	6.6E-01	8.9E-01	8.8E-01	6.2E-01	9.6E-01		4.4E-01	8.9E-01	7.9E-01	7.3E-01	6.6E-01		8.7E-01	1.3E-01	8.4E-01	9.9E-01	7.0E-01		6.4E-01	9.8E-01	4.7E-01	7.5E-01		8.7E-01	5.2E-01	6.2E-01	1.0E-01	1.8E-02		
season:year	2.1E-03	6.3E-02	3.8E-02	1.4E-04	1.5E-03		1.4E-06	2.4E-01	6.0E-06	1.2E-02	5.9E-02		1.9E-05	2.3E-16	1.2E-01	4.7E-01	8.4E-01		1.5E-04	6.2E-01	4.7E-01	1.1E-01		4.5E-12	1.4E-01	3.5E-02	3.0E-03	1.5E-13		
season:mortality	9.2E-01	9.5E-01	9.4E-01	9.7E-01	9.5E-01		9.6E-01	8.7E-01	9.8E-01	9.9E-01	9.0E-01		9.8E-01	8.2E-01	9.7E-01	9.7E-01	9.9E-01		9.7E-01	1.0E+00	9.2E-01	8.8E-01		9.8E-01	8.6E-01	8.3E-01	9.9E-01	9.4E-01		
vmigr:thermtol	4.9E-01	6.0E-01	6.8E-01	8.1E-01	9.1E-01		8.2E-01	6.8E-01	6.5E-01	8.0E-01	8.5E-01		9.3E-01	6.7E-01	6.5E-01	9.2E-01	9.8E-01		8.0E-01	7.1E-01	8.1E-01	4.8E-01		8.7E-01	9.7E-01	8.4E-01	7.4E-01	9.3E-01		
vmigr:drate	5.0E-01	9.5E-01	8.7E-01	8.2E-01	8.0E-01		6.7E-01	8.1E-01	9.2E-01	8.6E-01	4.3E-01		9.1E-01	7.5E-01	6.8E-01	4.8E-01	9.9E-01		7.3E-01	9.3E-01	5.1E-01	9.2E-01		7.1E-01	5.9E-01	6.9E-01	9.8E-01	7.5E-01		
vmigr:year	4.1E-01	5.1E-01	6.2E-01	4.4E-01	9.4E-01		1.1E-01	9.7E-01	9.0E-01	9.2E-01	8.7E-01		2.7E-01	8.2E-01	8.4E-01	8.6E-01	1.0E+00		9.4E-01	7.2E-01	9.5E-01	1.0E+00		1.9E-04	1.3E-01	9.6E-01	9.1E-01	1.6E-01		
vmigr:mortality	8.9E-01	8.5E-01	9.5E-01	8.7E-01	9.9E-01		9.0E-01	8.8E-01	9.7E-01	9.7E-01	9.9E-01		9.0E-01	9.3E-01	9.9E-01	9.4E-01	9.9E-01		9.7E-01	9.6E-01	8.5E-01	9.8E-01		8.5E-01	9.3E-01	9.8E-01	9.2E-01	9.8E-01		
thermtol:drate	8.9E-01	7.8E-01	9.3E-01	5.0E-01	7.8E-01		4.7E-01	8.4E-01	4.5E-01	3.3E-01	8.0E-01		3.9E-01	3.7E-01	8.9E-01	9.2E-01	7.8E-01		4.4E-01	9.1E-01	6.2E-01	7.9E-01		4.4E-01	8.0E-01	9.7E-01	9.6E-01	7.0E-01		
thermtol:year	1.9E-04	3.7E-02	4.3E-01	8.4E-01	9.4E-01		9.4E-04	7.7E-05	6.1E-03	6.4E-02	3.9E-02		4.4E-07	7.0E-04	3.0E-04	1.4E-02	8.2E-03		3.4E-05	2.3E-10	7.2E-02	2.7E-01		1.8E-01	1.3E-01	6.9E-01	3.0E-01	1.1E-03		
thermtol:mortality	9.7E-01	9.2E-01	7.6E-01	7.5E-01	9.1E-01		8.5E-01	8.4E-01	9.0E-01	8.9E-01	8.6E-01		9.9E-01	7.8E-01	6.1E-01	7.1E-01	7.6E-01		9.5E-01	7.6E-01	7.1E-01	6.4E-01		1.0E+00	9.1E-01	7.3E-01	7.3E-01	8.5E-01		
drate:year	8.5E-01	1.0E+00	8.4E-01	8.6E-01	7.6E-01		8.4E-01	9.9E-01	9.5E-01	8.9E-01	9.8E-01		1.0E+00	7.0E-01	9.9E-01	9.8E-01	9.5E-01		6.6E-01	1.0E+00	8.8E-01	8.4E-01		7.3E-01	9.6E-01	9.2E-01	8.7E-01	8.7E-01		
drate:mortality	8.3E-01	8.2E-01	7.9E-01	7.7E-01	8.7E-01		8.6E-01	8.8E-01	8.1E-01	8.1E-01	8.5E-01		8.0E-01	7.7E-01	7.5E-01	7.8E-01	8.1E-01		7.6E-01	5.5E-01	5.2E-01	5.5E-01		7.4E-01	7.7E-01	7.0E-01	6.9E-01	8.4E-01		
year:mortality	9.9E-01	1.0E+00	1.0E+00	1.0E+00	1.0E+00		1.0E+00	1.0E+00	1.0E+00	1.0E+00	1.0E+00		1.0E+00	1.0E+00	1.0E+00	1.0E+00	1.0E+00		1.0E+00	1.0E+00	1.0E+00	1.0E+00		9.8E-01	1.0E+00	1.0E+00	1.0E+00	1.0E+00		

From the sensitivity analysis, to the exploration of the spawning ground location stability

Throughout this first chapter, the large-scale sensitivity analysis has revealed that local hydrodynamics and inter-annual variations have the most significant influence on larval drift, far more than species-specific biological traits. However, it is interesting to explore whether other species share similar life-history traits than the five archetypes we used, in order to know whether our results are likely to be valid for other species. In this context, I have supervised Théo Schnebelin, a L3 student who carried out an internship in order to constitute groups of MEO species according to their life history traits. He conducted an extensive literature review on 28 MEO fish species, and made groups thanks to an HCPC (Hierarchical Clustering on Principal Components) based on a PCA. Our five archetype species ended up in the same group of species, opposed to groups characterized by more spring or even summer (e.g. *M. Meluccius* or *S. sprattus*) or winter species, which are cold-tolerant and capable of spawning on rocky substrates (e.g. *C. harengus* or *M. merlangus*). Theo Schenebelin's internship report can be found in the supplementary materials at the end of this thesis.

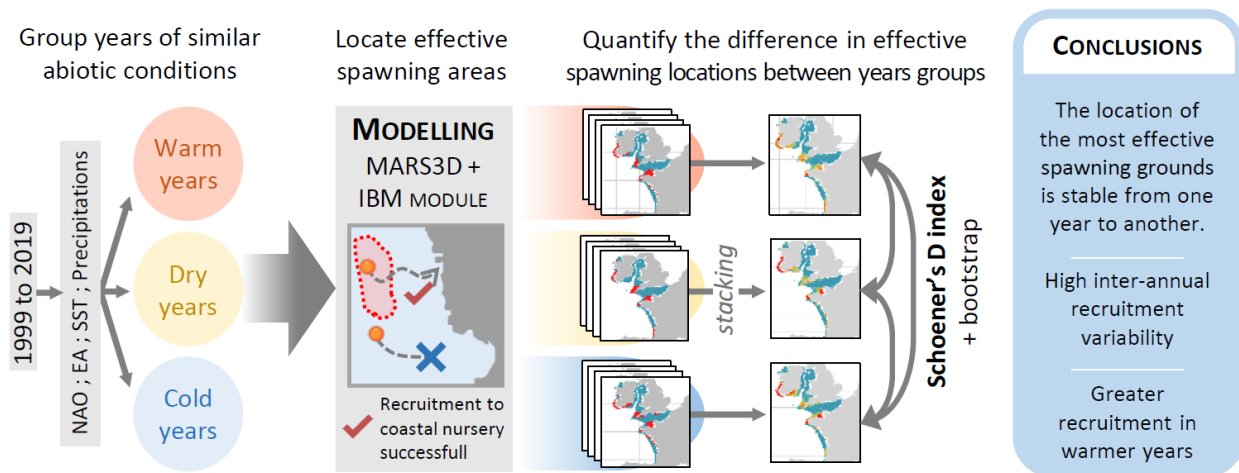
We know that changes in hydrodynamics between years contribute to variable recruitment success (Vaz *et al.*, 2023). Climate change, and the increased temperature associated to it, can result in shifts in hydrodynamics (Gillett *et al.*, 2003), shorter larval drifts (Houde, 1989; Keller *et al.*, 2020), and earlier reproduction (Fincham *et al.*, 2013) thus greatly modifying larval drift recruitment success and connectivity (Lacroix *et al.*, 2018). This raises the question about the need for species to adapt their spawning behaviour to adapt with environmental changes. Natural selection is thought to have shaped many spawning strategies to improve the recruitment success of offspring, including the choice of appropriate spawning grounds (Bailey *et al.*, 2005). Because of climate change, larvae may experience different conditions that would affect their drift, thus it may change the suitability of usual spawning grounds. As such, in the next chapter, we explore whether the location of the most “favourable” spawning areas are sensitive to change between environmentally contrasted annual conditions.

CHAPTER 2: Stability of spawning grounds location: potential impact of climate change

Violette Silve, Henrique Cabral, Martin Huret, Hilaire Drouineau

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.

Keywords Larval drift models, fish larvae, spawning grounds, climatic changes, hydrodynamics

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 centre 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 prey (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 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. 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; Tremblay *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 (Trembl *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 (Pinsky *et al.*, 2013 suggest that marine taxa are able to track geographic shifts of isotherms over time to adapt their occupied niche). 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) might have 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 snapshots 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 there in). 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 *Platychthis 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 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. 9.d). 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 to 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 (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 2.5km horizontally, and 40 generalized sigma layers in the vertical with a time-step of approximately 2 minutes.

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 (Tab.5). Based on the information contained in Table 5, seabass experience a longer larval drift, with spawning occurring in deeper waters.

The individual-based model relies on a Lagrangian module for particle transport (Huret *et al.*, 2010) and takes into account multiple 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 Tab.5. 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 Tab.5):

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

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 descended to 40m depth 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.

Table 5. 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	30-90m deep soft sediments	20-50m deep soft sediments	50-90m deep	Dambrine <i>et al.</i> , 2021; Skerritt, 2010; Tanner <i>et al.</i> , 2017
Spawning period	December-May	February-June	December-April	Amara <i>et al.</i> , 1994; Billard and Monod, 1997; Eastwood <i>et al.</i> , 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	$\alpha = 274.64$; $\beta = 1.5739$	$\alpha = 12.65$; $\beta = 0.33$	$\alpha = 6.47$; $\beta = -0.129$
	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
	YSL	3.00	2.50	3.50
	FFL	4.25	4.00	5.50
	ML	12.00	8.50	11.00

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 (Tab.5). 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 d^{-1} in Horwood, 1993 for soles and 0.048 d^{-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:

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

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

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

$$= \frac{30 * 0.04}{\frac{50 + 70}{2}} = 0.02 d^{-1}$$

2.2.5. Spawning releases

For each species, spawning areas and spawning periods were determined based on literature (Tab.5, Fig.9).

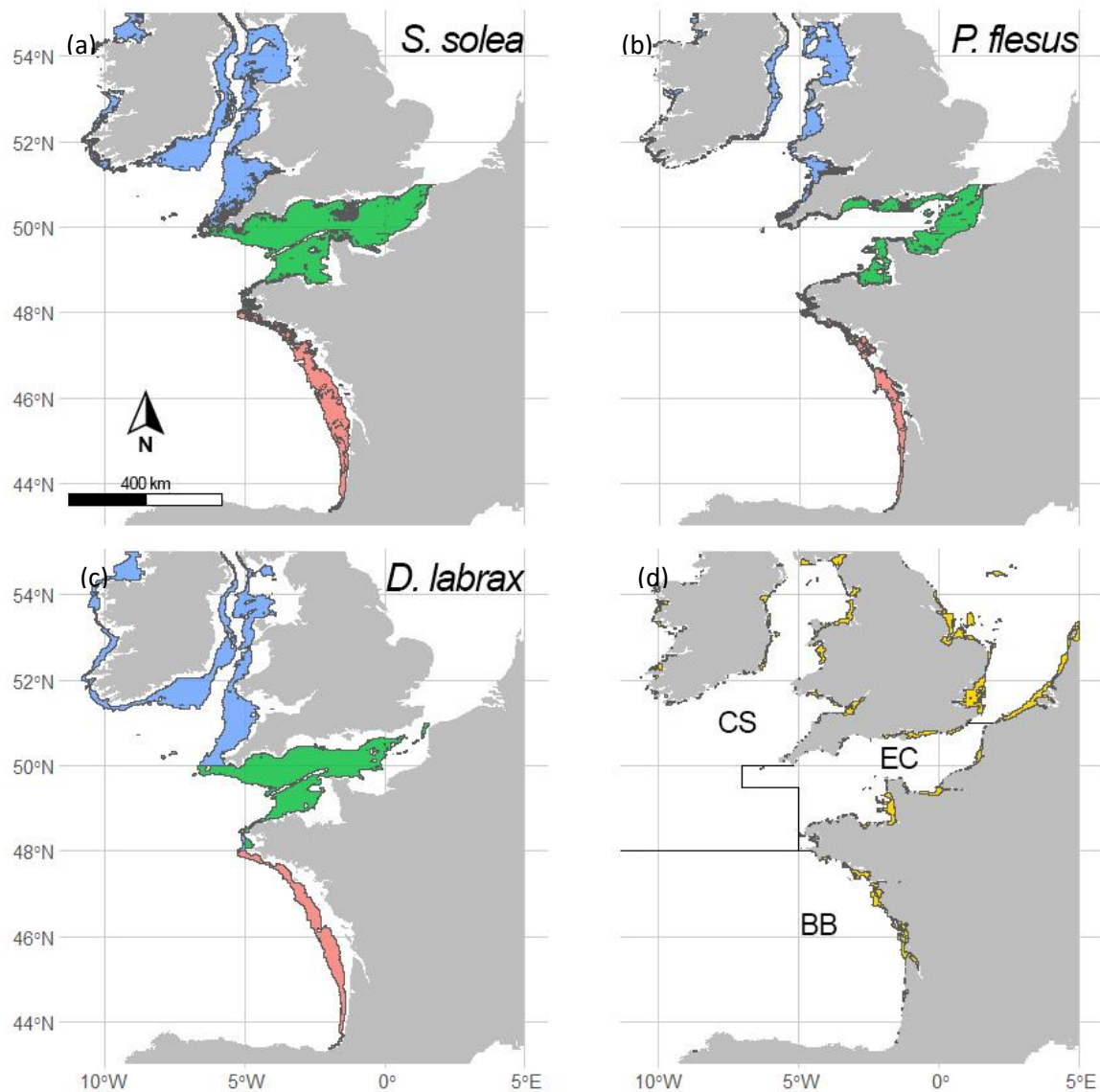


Figure 9. Spawning (a, b and c, according to species) and nursery areas (d, for all species; coastal areas with less than 20m depth) considered in the modelling for the three species. Sub-regions are symbolised by different colours: red for the Bay of Biscay, green for the English Channel and blue for the Celtic Sea.

We assumed an extended spawning period for simplicity encompassing all the possible spawning dates found in the literature across the whole study area (Tab.5). For many species, spawning events are triggered by specific temperature or photoperiod thresholds (Devauchelle 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 (3,500 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 20m 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 5km 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 summarised in Fig.10.

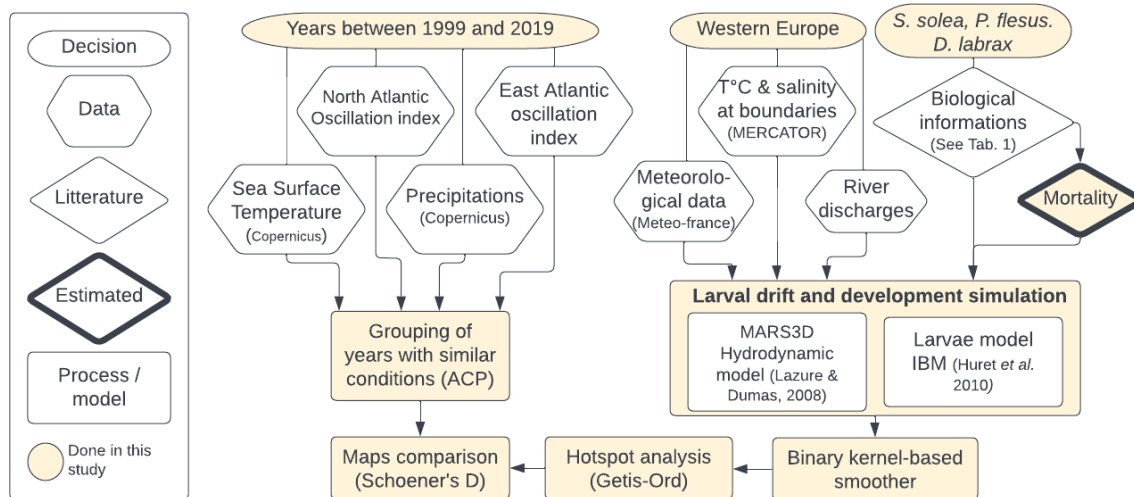


Figure 10. Flowchart of the methods used to assess the stability of potential spawning areas ensuring a good recruitment success among years with contrasted environmental conditions.

3. Results

Annual recruitment rate means and trends were different according to species and sub-regions (Fig.11). 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. 11). 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. 11).

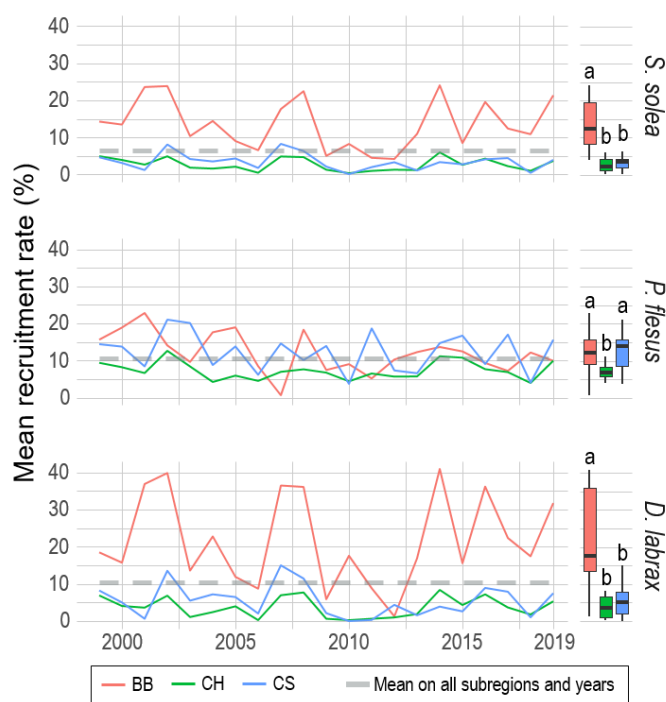


Figure 11. Average recruitment rate through the years for the three species of interest (*Solea solea*, *Platichthys flesus*, *Dicentrarchus labrax*), for each sub-region (BB - Bay of Biscay ; CH – English Channel ; CS – Celtic Sea). The grey dotted lines represent the recruitment mean for each species, 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).

The PCA performed to evaluate environmental conditions for the different years of the 1999-2019 time-series revealed three different groups (Fig.S.2). The first group is mainly characterised by low SST and 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.12).

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.13). Globally, there is a 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.11). 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.

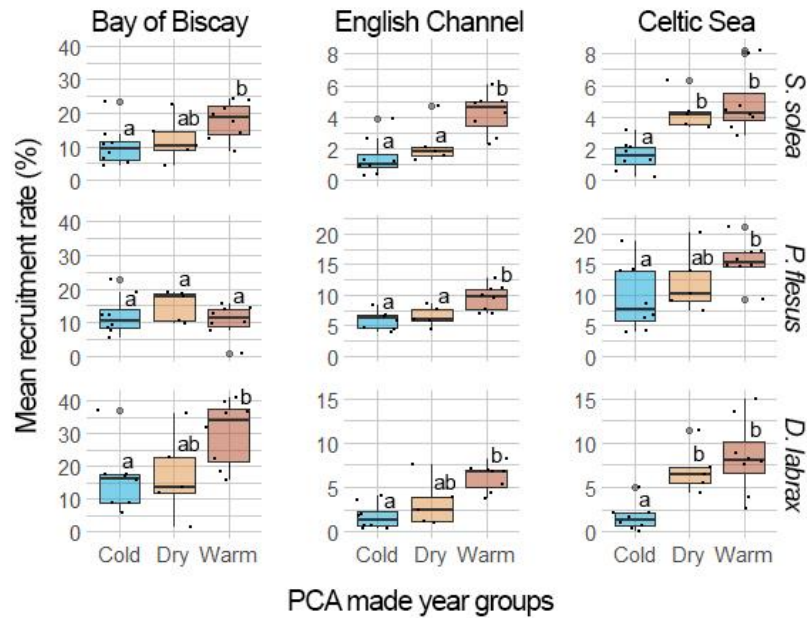


Figure 12. Average recruitment rate for each group of environmentally contrasting years (that resulted from the PCA) within each sub-region and for each species (*Solea solea*, *Platichthys flesus*, *Dicentrarchus labrax*). Each point represents a year. Letters correspond to Kruskal-Wallis tests ($p < 0.05$).

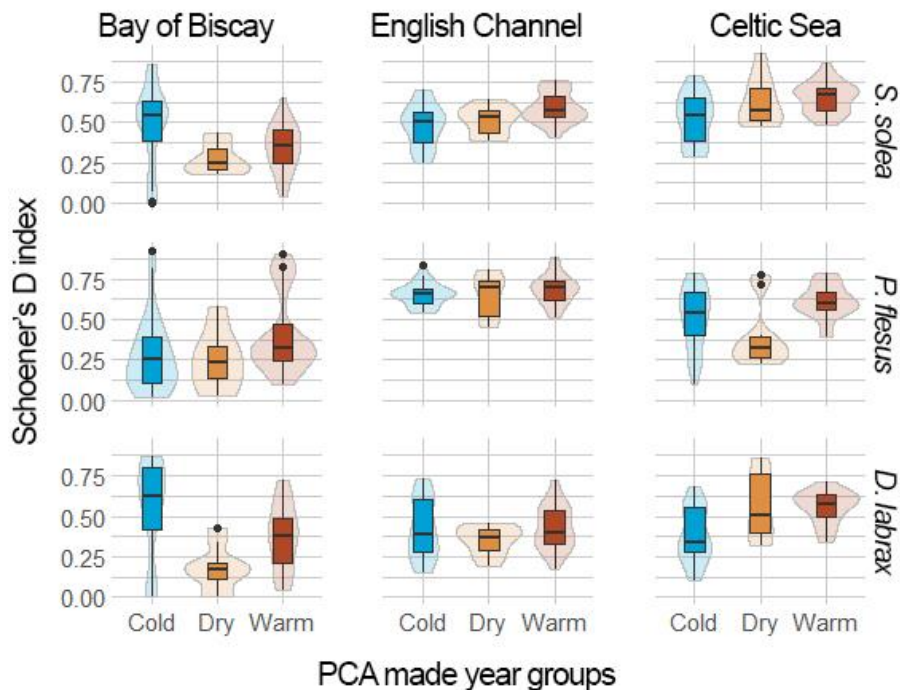


Figure 13. Differences in the location of favourable spawning areas between two years belonging to the same group of environmentally contrasting years (Cold, Dry or Warm year groups). Differences were assessed using the Schoener's D index (1 = maps are the same, 0 = maps are entirely different). The number of observations being the number of possible combinations without repetitions, for both the Cold and Warm year groups $n = 28$ and for the Dry year group $n = 10$.

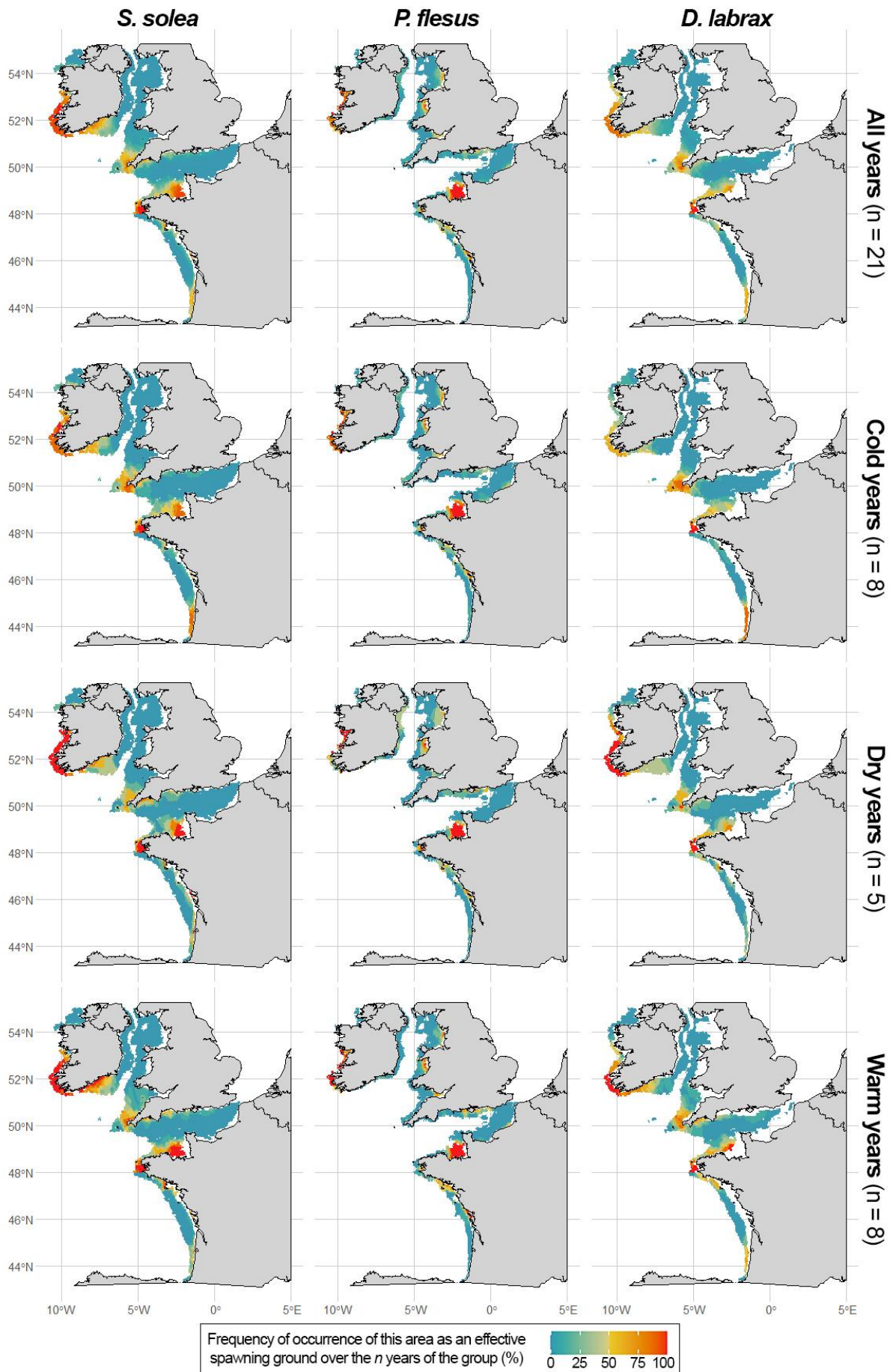


Figure 14. Frequency maps showing the most suitable spawning locations estimated by our model for the three species and for each year group individually.

The location of the most favourable spawning areas are shown for all years combined and for each years group in Fig. 14. 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.15). 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}).

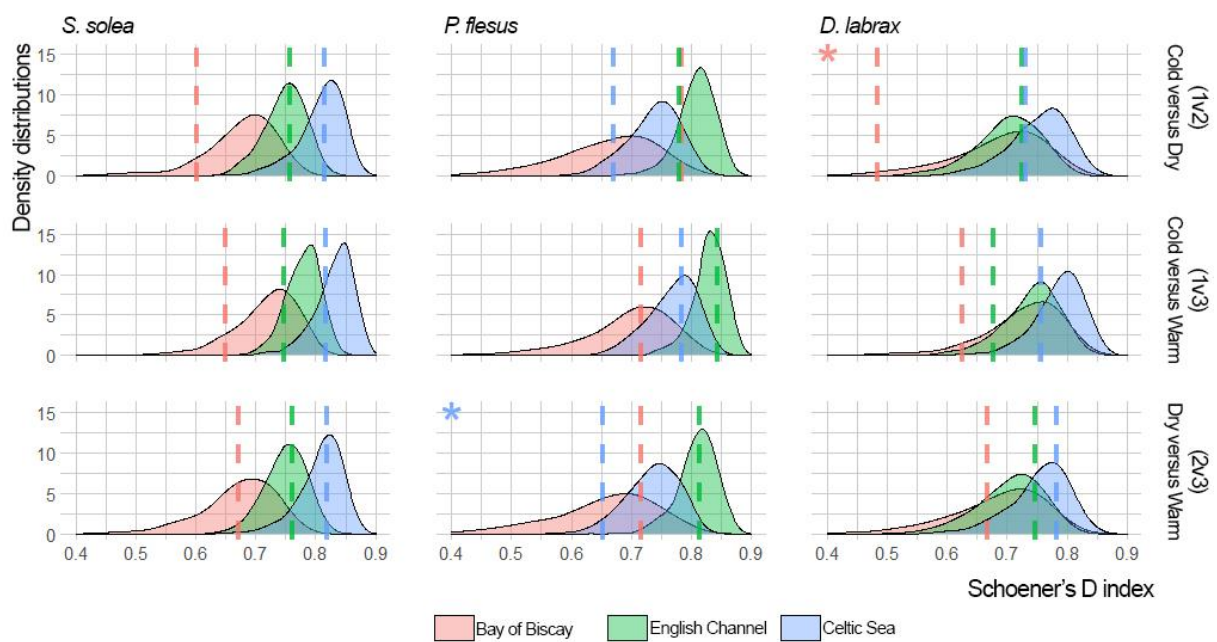


Figure 15. Differences between the effective spawning ground frequency maps of environmentally defined year groups for the three species (*Solea solea*, *Platichthys flesus*, *Dicentrarchus labrax*). Differences were assessed using the Schoener's D index (1 = maps are the same, 0 = maps are entirely 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.

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 characterized 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. This hypothesis was tested *a posteriori*, and figures in the supplementary materials (Fig.S.3).

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. Other 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 (>50m deep) such as cod *Gadus morhua* (Cohen *et al.*, 1990), mackerel *Scombrus scombrus* (Priede *et al.*, 1995) or red mullet *Mullus barbatus* (Gücü and BiNgel, 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 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 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.

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.

Supplementary material

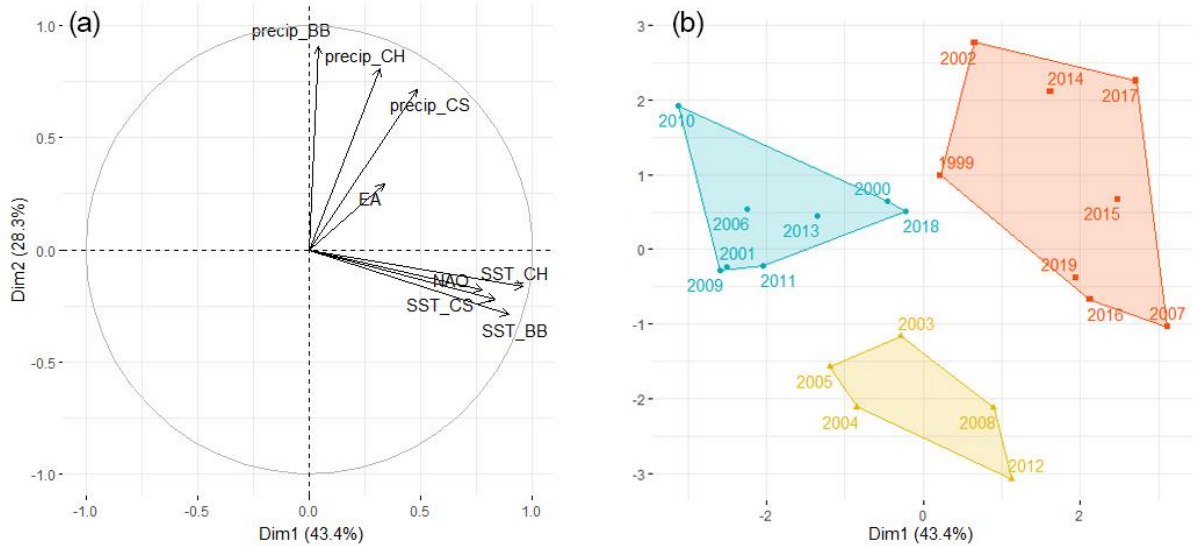


Figure S.2 PCA plots. a) Variable correlation plots, with “precip” being the precipitations in the Bay of Biscay (BB), English Channel (CH) and Celtic Sea (CS); “SST” the sea surface temperature and NAO and EA the atmospheric pressure index. b) Individuals (years) are regrouped by the HCPC in three clusters. The so-called “Cold” years are in blue, “Warm” in red and “Dry” in yellow.

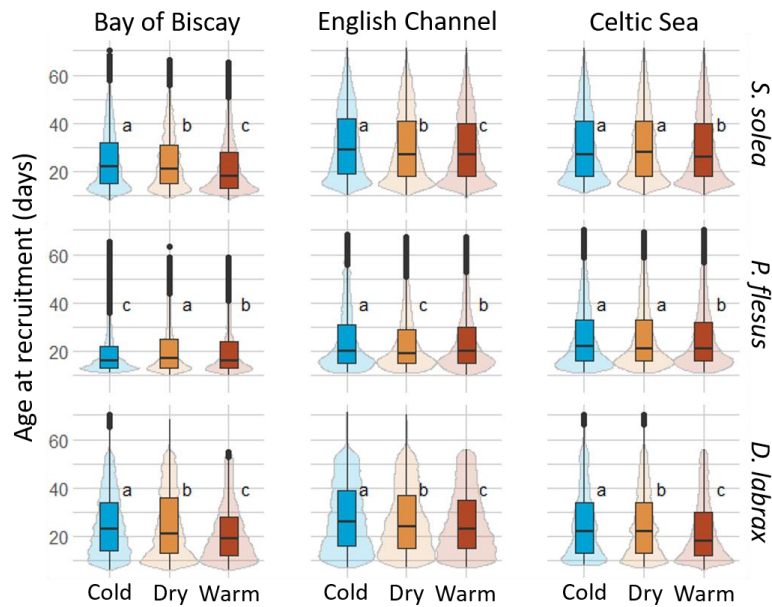


Figure S.3 Age at recruitment for successfully recruited larvae. Letters correspond to Kruskal-Wallis tests ($p < 0.05$).

The hypothesis stating that the modelled recruitment success is higher in warm years because of an earlier arrival in nurseries is validated here.

Transitioning from the exploration of spawning grounds stability to the investigation of their defining parameters

In the second chapter, we saw that the location of the most suitable spawning grounds were stable through time, even across environmentally contrasted years. However, until now, we have used spawning and nursery areas determined based on species depth and sediment preferences. This was required to apply our large spatial scale and multi-species approach since knowledge on local spawning and nursery areas is not always available. In fact, given that the precise locations of spawning and nursery grounds are not always known, theoretical grounds based on preferences are often used instead of documented locations (Cabral *et al.*, 2021; Rochette *et al.*, 2012; Savina *et al.*, 2016; Silve *et al.*, 2023, in prep.). However, these 'optimal' spawning grounds we identified differed from those documented in the literature (Alglave *et al.*, 2022; Armstrong, 2001; Dambrine *et al.*, 2021), those latter being more spatially restricted. As such, it is interesting to explore whether particles released in those “documented” spawning grounds and bound for recruiting in those “documented” nursery grounds display specific features, especially in terms of dispersion (*i.e.* distance travelled between spawning and recruitment areas) or retention (stable recruitment in adjacent areas). In the following chapter, we compared larval drift resulting from spawning and/or recruiting in documented grounds, as opposed to theoretical grounds. We focused on whether documented spawning and/or nursery grounds exhibit distinctive patterns of recruitment success and connectivity.

**CHAPTER 3: Retention/dispersion trade-offs of
recruitment success among spawning and nursery
areas: any evidence of an adaptive response to
hydrological conditions?**

Abstract

Dispersal is a key mechanism in wildlife populations ensuring gene flows between different areas, enhancing population resilience, and enabling the colonization of new habitats. For Marine Estuarine-Opportunists fish species (MEO), this dispersal mostly occurs during the early life stages through larval drift that takes place between spawning and nursery grounds. However, while long dispersal favours the colonisation of distant new habitats, it also increases the risk of not reaching favourable nursery areas. This is referred as the retention-dispersion trade-off in the recruitment success. This study sought to explore whether the documented habitats (spawning and nursery grounds) in the literature exhibit distinct patterns of recruitment success and connectivity, when compared with theoretical ones defined according to species ecological preferendum. As doing so, this study aims to understand whether hydrodynamics and larval behaviour are the main parameters explaining the localization of these crucial areas. To investigate this, we focused on the common sole, *Solea solea*, and the European sea bass, *Dicentrarchus labrax*, in the Bay of Biscay, as readily accessible data were available for the location of their habitats in this area. We divided the study area by latitude, using the ICES statistical rectangles as a basis. Using a hydrodynamic model (MARS3D) coupled with an individual-based model, we simulated the drift of larvae over the span of 21 years. Then, we examined the proportions of recruited larvae in documented nurseries originating from either theoretical or well-documented spawning grounds. Our findings indicate that larval dispersal distance appears to be largely associated with the proximity to available nurseries. Documented grounds do not appear to yield significantly higher recruitment success than theoretical ones. This strongly suggests that the potential recruitment success of offspring, including hydrodynamics and larval behaviour, does not explain the observed locations of spawning grounds on its own. It also raises questions about the modelling choices we made, such as the absence of tidal migration or orientation mechanisms

Keywords

Larval drift models, fish larvae, Biscay, retention, dispersion

1. Introduction

Dispersal is a key mechanism in wildlife populations ensuring gene flows between different groups, enhancing ecological resilience, and enabling the colonization of new habitats and as such potential adaptive distribution shifts (Kerr *et al.*, 2010; Ronce, 2007). As most fish species, marine-estuarine opportunists (MEO) fish species undergo a larval drift in early life pelagic phase, from spawning zones located on the continental shelf, where mature adults lay eggs, to coastal and/or estuarine nursery habitats (Houde, 2008). This drift represents a critical phase enabling extensive long-distance dispersion; but is however associated with high mortalities. Therefore, it plays a main role in the viability of species, in their renewal, but also in the connectivity among distant populations or habitats. Nurseries are areas ensuring good conditions for a rapid juvenile growth and survival, generally because of both abundance of quality prey, and limited predation risk (Cabral *et al.*, 2022 and references therein). Several processes affect the proportion of larvae successfully reaching these nurseries (called “recruitment success” in the rest of the chapter). As larvae develop during their drift, their mobility increases progressively (Clark *et al.*, 2005). Vertical migrations in the water column, coupled with orientation mechanisms tied to salinity detection (Bos and Thiel, 2006), are several examples of processes enabling individuals to maximize their recruiting chances (Beraud *et al.*, 2018) by selecting the most appropriate current or avoiding predation risks.

Beyond behavioural mechanisms of larvae, recruitment heavily relies on passive dispersal, and as such, environmental conditions are key factors. Indeed, local hydrodynamic conditions emerge as particularly important when assessing the influence of various factors on recruitment (Silve *et al.*, 2023). In this context, the selection of spawning area locations often results from adaptations to local conditions to optimize recruitment success (Bailey *et al.*, 2005; Mullon *et al.*, 2002).

During larval drift, individuals face multiple sources of mortality (*e.g.* starvation, predation, lethal environmental conditions), and thus, the longer the drift the higher the chance of dying (Horwood, 1993). Moreover, a long and distant drift may increase the risk to reach unsuitable spawning grounds. However, in cases of spatially and temporally varying environmental conditions, they may be favourable at the individual scale to increase the chance that at least a portion of the offspring reaches suitable habitats. From another point of view, long drifts may be beneficial at the population level by promoting connectivity between distant habitats. As such there is a trade-off between favouring higher recruitment success at low distance, or lower recruitment success but with higher dispersal, which is usually called the “retention/dispersion trade-off” (Jones *et al.*, 2009; Shima and Swearer, 2009; Stephenson *et al.*, 2015). Several factors may influence retention/dispersion trade-off, namely

spawning area location or spawning timing (Huret *et al.*, 2010). If individuals have the capacity to adapt their strategies according to environmental conditions, this may enhance the stability at the population scale by buffering environmental variability (Schindler *et al.*, 2015; Thorson *et al.*, 2018)

Since species generally spawn in spatially restricted and recurrent spawning areas, we postulated that those selections could be the result of adaptive responses to the dispersion-retention trade-off. For some species, the precise locations of some spawning grounds are known or have been inferred from indirect information. This determination can be achieved through the use of various methods such as fisheries trawl data (Alglave *et al.*, 2022; Dambrine *et al.*, 2021), ichthyoplankton surveys (Fox *et al.*, 2008), habitat suitability evaluation (Zhou *et al.*, 2022) or tagging and tracking mature adults (Richardson *et al.*, 2016). Each method has its advantages and limitations, along with its level of confidence. Moreover, such data is not available in all regions and for all species, and as such, it frequently imposes to use theoretical spawning grounds based on species known preferences instead of documented locations (Cabral *et al.*, 2021; Rochette *et al.*, 2012; Savina *et al.*, 2016; Silve *et al.*, 2023, in prep.). The question arises as to whether these estimated zones can accurately represent the actual areas or if they are overly broad approximations. Indeed, if “real spawning grounds” result from an adaptive response to the dispersion-retention trade-off, they are likely to be only a restricted fraction of the theoretical spawning grounds. In this context, we sought to explore whether the documented spawning grounds in the literature (hereafter called “confirmed” spawning grounds) exhibit distinct patterns of recruitment success and connectivity, when compared with theoretical ones defined according to species ecological preferendum. We firstly examined whether confirmed spawning areas exhibit higher recruitment rates compared to theoretical ones defined according to species ecological preferendum in terms of depth. Then, we focused on nurseries with a similar question: do confirmed nurseries receive more larvae compared to theoretical nurseries? Finally, we explored whether the dispersion levels in confirmed spawning areas differ from those in theoretical counterparts in order to explore the dispersion hypothesis. To do so, we used a Lagrangian particle tracking module embedded in a hydrodynamic model (Lazure and Dumas, 2008) calibrated on two extensively documented fish species in the Bay of Biscay. We simulated larval drift on 21 years, and compared the larvae recruitment success based on the spawning location.

2. Methods

2.1. Modelling larval drift

We used two coupled models: the first one being MARS3D, which models hydrodynamics, and the second one calculates the development and drift of particles mimicking larvae behaviour within the vector field generated by MARS3D. Nycthemeral vertical migration, growth correlated with temperature, daily mortality, and mortality due to lethal temperature were all considered. Particles drifted between theoretical spawning locations (computed based on documented ecological preferendum of spawning ground depths in the literature) and theoretical nursery grounds (<20m depth). Both theoretical areas can be seen in Fig.16. The drift simulations were performed over a span of 21 years, from 1999 to 2019. Here, we exclusively retained the particles that were released within the Bay of Biscay. We focused on the two species with the most abundant literature, namely *S. solea* and *D. labrax* for which data on the location of effective nursery and spawning areas in the Bay of Biscay were available.

2.2. Statistical analyses

2.2.1. Partitioning the study Area based on ICES statistical rectangles and identifying key latitudinal zones

The study area was partitioned according to latitudes, based on ICES (International Council for Exploration of the Sea) statistical rectangles (30' for each, <https://www.ices.dk/data/maps/Pages/ICES-statistical-rectangles.aspx>). This division resulted in the identification of eleven distinct subzones in the Bay of Biscay, labelled from A in the north to K in the South. An extra area was added in the English Channel (CH) to ensure that long drifting particles towards the North are taken into account.

We used the same theoretical areas as in the last chapter (Silve *et al.*, in prep.), which were based on depth and sediments type. We then compared our theoretical spawning areas and nurseries to documented ones (Fig. 16). What we considered in this chapter as being the “confirmed areas” are in fact the theoretical areas delimited by depths, segmented by the latitude of the areas identified in literature. Latitudes corresponding to documented spawning areas seems to be: B, D, E, F, G, H for *S. solea* and E, F, G, H for *D. labrax* (based on Alglave *et al.*, 2022; Dambrine *et al.*, 2021). For nurseries, both species seem to share approximatively the same nursery grounds (Regimbart *et al.*, 2018; Trimoreau *et al.*, 2013), corresponding to areas C, E, F and G.

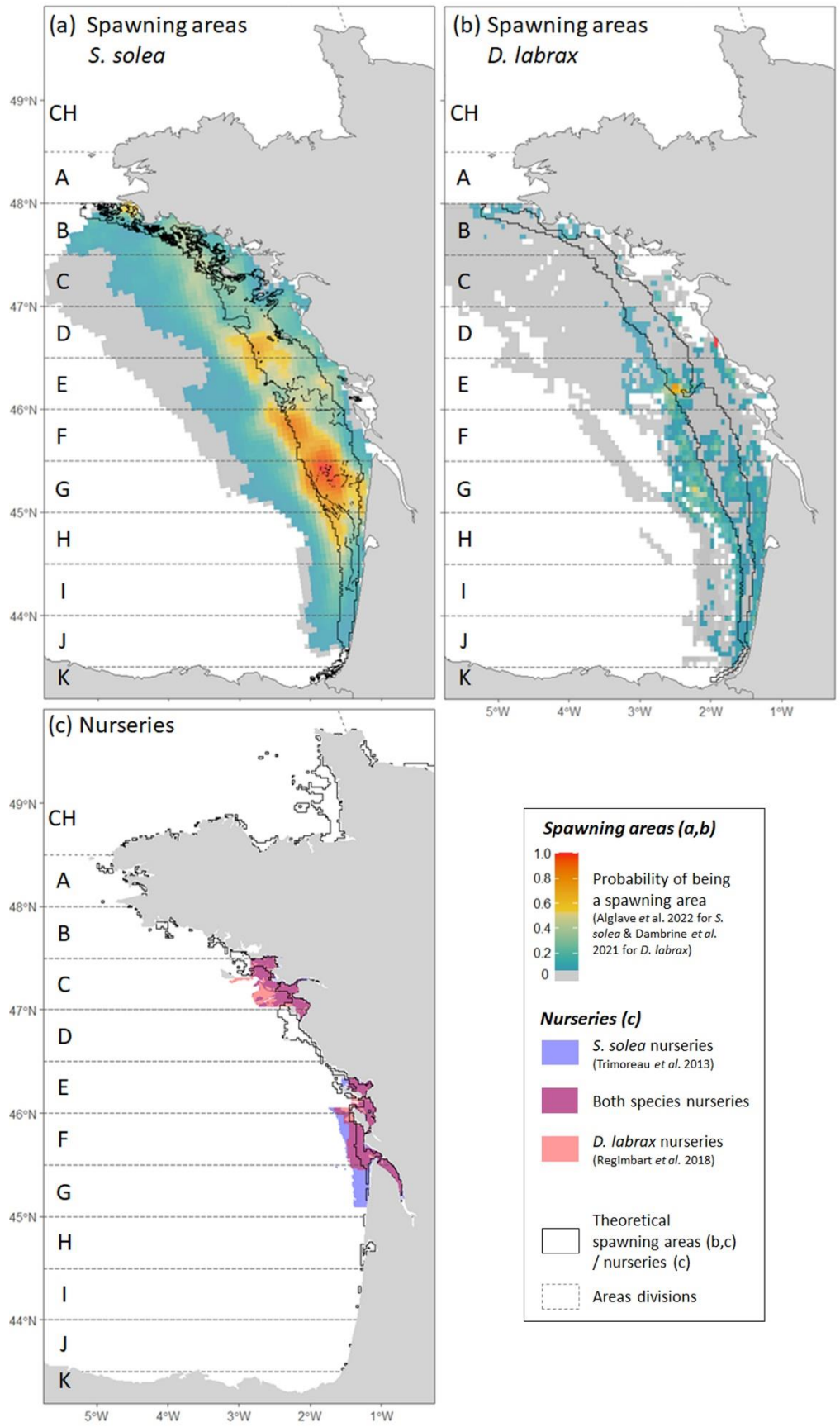


Figure 16. Comparison of known and theoretical areas of interests. (a) Spawning areas of *S. solea*. (b) Spawning areas of *D. labrax*. (c) Nursery areas for both species nurseries.

2.2.2. Connectivity matrices

In total, 52,500 particles/year/species were released in the Bay of Biscay. Since releases were randomized across the entire theoretical spawning area, the distribution of particles varies among different divisions, with more particles spawned in the larger divisions (e.g. E, F, G) compared to the smaller ones (e.g., B, J, or K). To sum up information, we made connectivity matrices as shown in Tab.6, one for each year and species.

Table 6. Connectivity matrix. In the first cells are summarised the number of particles r that came from the spawning division i and arrived at the nursery j . To visualise these divisions in the spawning area and nursery, see Fig.16. As well as the destination of recruited particles, we added the amount of particles that died because of an encounter with lethal temperature, the amount of particles that survived but didn't reach a nursery ground ("lost") and the total number of particles spawned in i .

	1		...	j	<i>Dead by temperature</i>	<i>Lost</i>	<i>Total</i>
1	$r_{1,1}$						
⋮							
i				$r_{i,j}$			

In addition to retaining the amount of recruited particles within the connectivity matrices, for each recruited particle we also calculated the distance between their initial to final points.

To assess the recruitment success across different latitudes of spawning areas, we retained the particles that successfully recruited into confirmed nursery areas (latitudes C, E, F and G). As in previous chapters, a particle was considered as successfully recruited if moving alive into a nursery area and at least at its first-feeding larvae stage. Then, we calculated for each year and each spawning area latitude, the proportion of particles that have successfully recruited into a confirmed nursery.

To evaluate the attractiveness nurseries, we only kept particles originated from confirmed spawning areas latitudes (B, D, E, F, G, H for *S. solea* and E, F, G, H for *D. labrax*) and, for each year, we estimated the proportion of particles arriving in the different theoretical or confirmed nurseries.

Lastly, to visualise the average distance between the release and the settlement point, we extracted the starting and ending locations of recruited larvae and computed the average distance based on the spawning site locations in squares of 5km.

3. Results

Overall, even though the latitudes associated with confirmed spawning areas exhibited a slightly higher recruitment success rate compared to theoretical counterparts, a confirmed spawning area did not necessarily guarantee an enhanced recruitment (Fig.17). Some theoretical spawning areas latitudes also demonstrated high recruitment success rate (e.g. C and I for both species, and D for seabass).

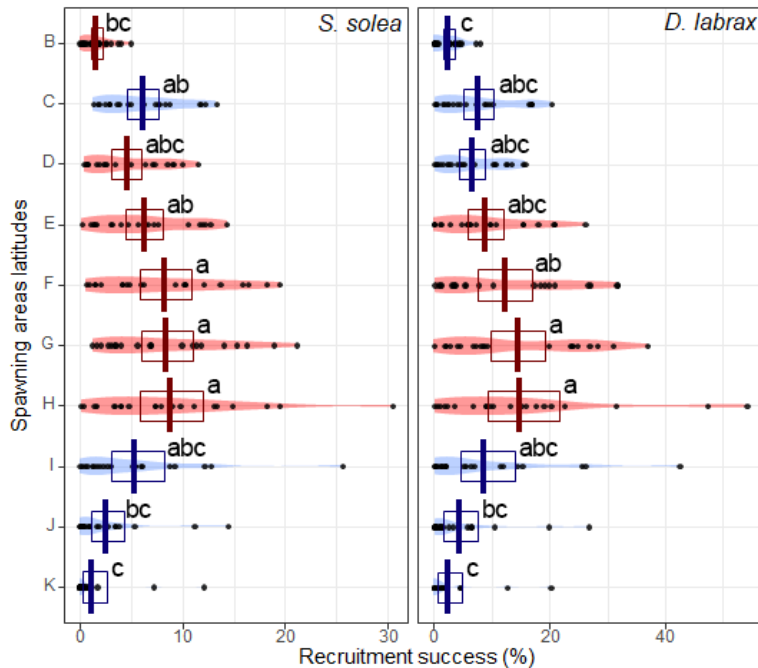


Figure 17. Recruitment success in confirmed nursery areas for each spawning areas latitudes. The latitudes corresponding to confirmed spawning areas are red, while theoretical ones are blue. Each point represents a year. Letters correspond to a Tukey test based on an ANOVA.

For nurseries, the confirmed nurseries did not systematically receive more drifting larvae than theoretical ones (Fig.18). In fact, latitudes corresponding to areas where no real nurseries are documented, also received a large amount of particles (e.g. D and H). Lastly, both species exhibit the same patterns of dispersal distance according to the spawning locations (Fig.19). Apart from the latitude E, all the spawning zones in front of a nursery had a small dispersal distance (~50km), while the ones further from these nurseries had a higher one (e.g. D with a dispersal distance ~100km).

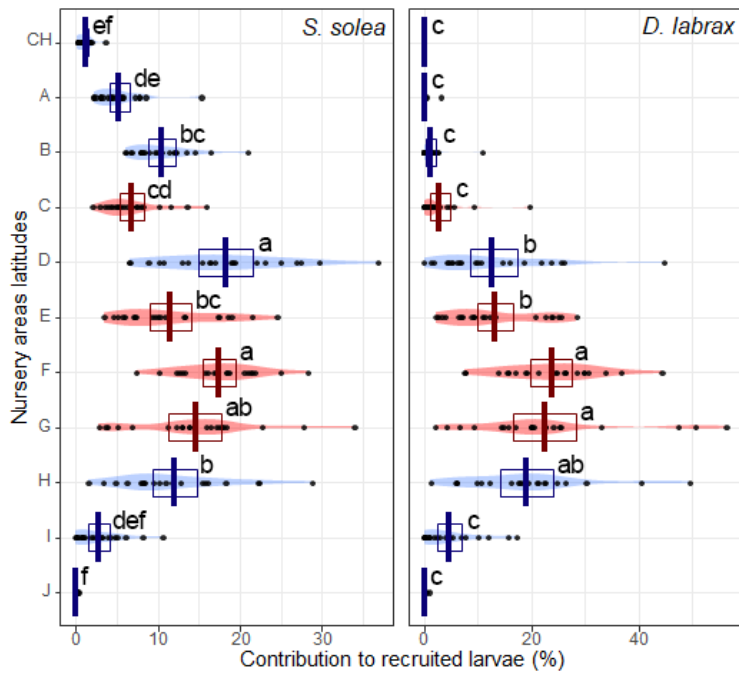


Figure 18. Proportion of larvae coming from confirmed spawning areas that recruited in each nursery. The latitudes corresponding to confirmed nurseries are red, while theoretical ones are blue. Each point represents a year. Letters correspond to a Tukey test based on an ANOVA.

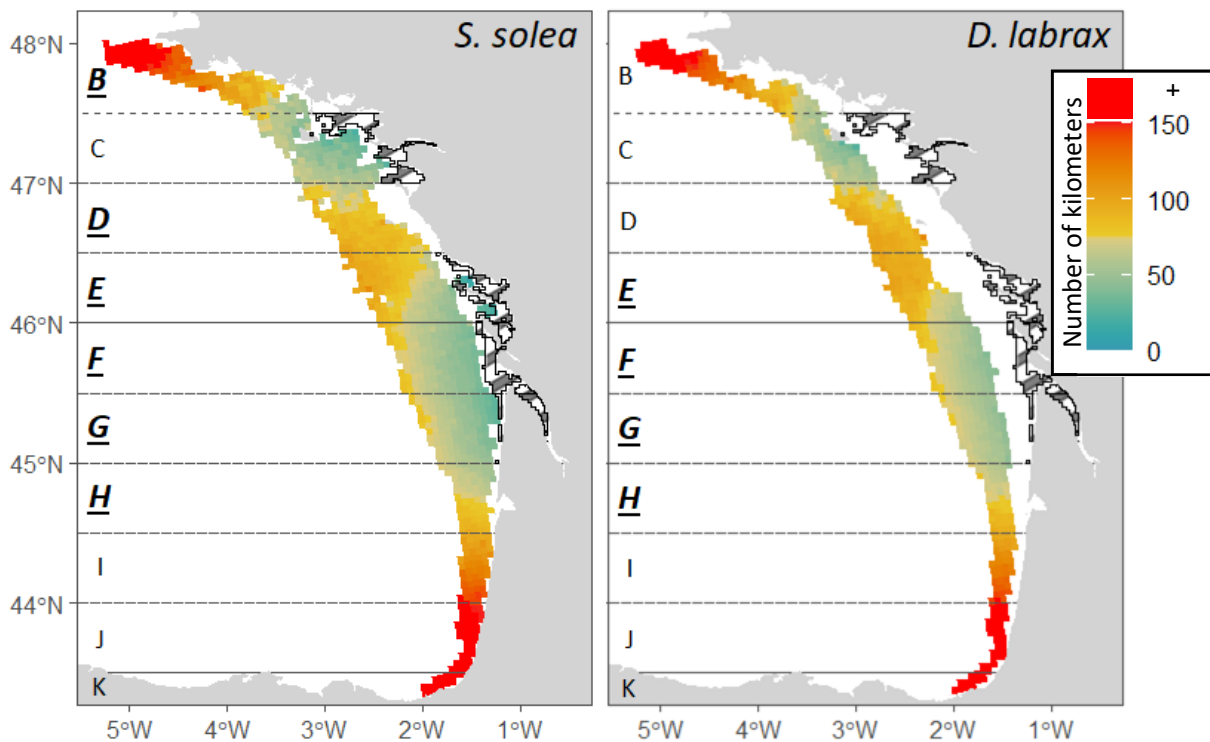


Figure 19. Average distance for recruited larvae from drift start to arrival point in confirmed nurseries according to the spawning location. The confirmed nurseries, in which the particles recruited, are marked as dashed polygons.

4. Discussion

Our approach allowed us to explore connectivity among habitats and to compare the suitability of confirmed habitats compared to theoretical ones in terms of retention and dispersion.

The recruitment success was not systematically higher when spawning in the latitudes of confirmed spawning locations, compared to the other potential spawning latitudes which could also lead to high recruitment success. This outcome can be attributed to multiple factors. Firstly, the recruitment success can not be enough to infer whether a spawning area is effectively used in reality or not. As we said earlier through the retention/dispersion trade-off, high recruitment rate can also be a sign of spawning area allowing for good retention. Secondly, what we used in the modelling were the latitudes corresponding to these identified spawning grounds rather than the spawning grounds themselves, which according to literature were located further west. It would be interesting to focus more precisely on those zones by releasing specifically particles in those areas. However, the zones are quite small, estimated on a limited number of years and as such, the actual spawning locations used by fishes may not be accurately identified. Moreover, these areas were primarily derived from fisheries sampling efforts (Dambrine *et al.*, 2021), which could introduce preferential sampling bias. However, Alglave *et al.* (2022) developed a model to take preferential sampling into account, so the impact of such a bias might be weaker or even non-existent for *D. labrax*. Moreover, while those approaches are likely to detect the areas with highest concentrations of spawning adults, they might not be well suited to detect coarser spawning grounds. It is interesting to observe that spawning grounds documented on the literature (Fig.16) are located close to the margin of the continental shelf. Spawning close to the continental shelf margin might have other adaptive advantages not accounted for in our model, such as more limited predation risk (Shropshire *et al.*, 2022) or this margin makes it easier to locate spawning grounds. Not taking into account adult feeding during spawning and locations favourable to larval survival also led to a mismatch between model predictions and observations concerning spawning grounds for Allain *et al.* (2007). Thus, they revealed that spawning grounds locations may result from a compromise between locations favourable to adult feeding during spawning and locations favourable to larval survival.

The quality of a nursery depends on multiple factors that promote growth and survival of juveniles. The preferred nursery habitats also differ according to the species and life stage (Nodo *et al.*, 2023). In this regard, defining an effective nursery solely based on suitable depth, as we have done here with our potential nursery zones, is an oversimplification. In our simulations, the documented nurseries

were not receiving systematically more particles than the potential nurseries that were computed based on depth alone. Two hypothesis can be formulated. First, it is likely that a substantial portion of larvae indeed gets lost in coastal areas that do not correspond to actual nursery grounds in the real life. In fact, the success of larval drift is known to be very low (Gargano *et al.*, 2017; Koeck *et al.*, 2015; Stockhausen *et al.*, 2019), particularly because of this random drift. Moreover, it is likely that, during the last stages of the drift, orientation mechanisms might favour active larval navigation towards suitable nursery grounds. For instance, the orientation to lower salinities: larvae are able to detect and swim towards lower salinities, bringing them closer to river plumes (Bos and Thiel, 2006). It might be interesting in the future to test the influence of such orientation behaviours close to the coast, though literature is rather limited. Lastly, we did not include tidal migration, while multiple studies state that it improves recruitment success (Beraud *et al.*, 2018; Ospina-Álvarez *et al.*, 2012). In our previous sensitivity analysis (first chapter), with the same model, vertical migration was not one of the most influential factor regarding recruitment success in nurseries (Silve *et al.*, 2023). However, in this previous study, we used the whole potential nurseries areas computed based on depth instead of using the actually confirmed nurseries. Moreover, we only tested for nycthemeral vertical migration, and not tidal vertical migration (which might be difficult to implement given the spatial resolution of the model we have used in this study). James *et al.* (2023) found that not considering tidal migration into the model led to largely overestimate dispersion. Furthermore, according to de Graaf *et al.* (2004), adding tidal migration in the modelling enabled larvae to reach different nursery grounds. At the beginning, we assumed that tidal migrations might not play a significant role at the large scale we were investigating. Nevertheless, further investigation using the current setup may be necessary to determine whether tidal migrations could be the key factor contributing to an enhanced recruitment success in the confirmed nurseries.

Concerning the dispersal pattern, we only looked at the distance between the starting point and the recruitment point of recruited larvae that went in latitudes corresponding to confirmed nurseries. The pattern we obtained is quite simple, with a bigger distance travelled by particles spawned far from nurseries, and a smaller one for particles laid closer. It was quite expected that spawning areas located near nurseries would allow for a good retention. Looking at the considered confirmed spawning areas, the ones located in the vicinity of les Sables-d'Olonne (latitudes "D" and "E" in this study) might be the only ones allowing for a greater dispersal compared to the other known confirmed areas which are located in front of confirmed nurseries. Studying a bigger area would be interesting in order to examine for wider dispersal to see if individuals are exchanged between geographically distant regions, and in which conditions these exchanges can take place.

The currents and conditions in the Bay of Biscay vary intra and inter-annually (Costoya *et al.*, 2015; Friocourt *et al.*, 2007). As spawning is expected to happen earlier during warmer years, it might lead to specific pattern as northwards currents are stronger in January-December in the Bay of Biscay (Friocourt *et al.*, 2007). Therefore, it could have been interesting to look at the influence of spawning timing and environmental conditions on the potential dispersal and relative connectivity (Bani *et al.*, 2021). Other works have emphasized this problematic. Álvarez-Noriega *et al.* (2020) have for example found that despite a quicker development rate, tropical fish larvae travelled greater distance during warm years due to stronger currents. Lacroix *et al.* (2018) conducted the same analysis in the North Sea, and earlier spawning made the larvae grow in colder water on average, thus lengthening the pelagic larval duration, also leading to more dispersion. At the contrary, Kendall *et al.* (2013) highlighted that fish populations in coral reef systems might become more and more reliant on self-recruitment as the ocean warms, weakening the dispersal links. A high retention could dramatically alter the capacity of populations to adapt as environmental conditions shift (Bashevkin *et al.*, 2020). Climate change might hinder on connectivity in a variety of different directions, each species reacting differently, making predictions particularly challenging (Bani *et al.*, 2021).

Our simplistic holistic approach does not allow us to draw definitive conclusions. The model we used had a resolution calibrated for a large study area, and thus was not the optimal choice to study precise connectivity patterns in the Bay of Biscay. However, it made it possible to gain insights into the connectivity links and the relative importance of identified habitats of interest. As such, our modelling hinted that identified spawning places may not be linked to higher recruitment rates, and that confirmed nurseries may not attract more larvae than other coastal areas. A more extensive approach, encompassing larger areas (similar to those in the first paper), could prove valuable in fully understanding the connectivity between potential sub-populations. Additionally, for future research, incorporating actual key habitat locations, energy budget models, and orientation-driving mechanisms may yield more reliable predictive outcomes. The achieved outcomes could then potentially be juxtaposed with genetic data obtained in-situ from populations (Barbut *et al.*, 2019; Cuveliers *et al.*, 2012), enhancing the validation of the modelling conclusions.

GENERAL DISCUSSION

While larval drift is likely to play a key role in species adaptive responses to global warming by allowing the colonisation of new habitats, its possible deterioration due to the climate change induces modifications in environmental conditions is a threat for species renewal. Modelling stands as the predominant tool to study this drift allowing to represent hydrodynamics as well as fishes biology and ecology. Its application facilitates a deeper understanding of this sensitive life stage, enables predictions regarding future conditions, and can inform on the future of exploited fish stocks. However, these models are often used on single species, or in particular study areas, preventing a more holistic and comprehensive overview. Using a larval drift model, we explored how modelling could provide insights on ecological questions raised by climate change but also the limits of such tools. Our results contribute to a better understanding of where efforts should be focused in order to infer on MEO fish species reaction to climate change.

Due to the complexity of these models, with parameters subject to uncertainty, the first step was to assess the model sensitivity. Using five species as biological archetypes, and a large area in the North-West of Europe encompassing multiple latitudes, we looked at the influence of eight different biological parameters on recruitment success as well as their two-ways interactions using innovative statistics experimental designs. We showed that local hydrodynamics and inter-annual variability were shaping recruitment success the most, far more than any other species characteristics or biological parameter.

This made us infer on the potential effects that changes in local hydrodynamics could have in coming years. More precisely, we wondered if the spawning areas allowing for the highest recruitment rate remain in the same places across years showing contrasting environmental conditions. Our analysis, based on 21 years showed no changes in the location of the most effective spawning areas even though their relative effectiveness vary greatly between years. From an evolutionary perspective, this would suggest that natural selection might favour the emergence of mechanisms that promote strong homing.

Following this step, we questioned if the area allowing for the highest recruitment success correspond to the ones documented in the literature, and showed that it was not the case. Thus implying that hydrodynamics and larvae behaviour might not be enough alone to explain the emplacement of spawning grounds.

In this discussion, I will come back to the knowledge gained throughout this thesis, how it might guide research on larval drift modelling in the future through a study on its limitations and possible perspectives.

1. Climate change potential effects on fish larvae dispersion

1.1. Temperature shaping larvae distribution

In the first chapter, we saw that lethal temperatures were one of the parameters driving recruitment success for species at the edge of their distribution areas. This result was not surprising: along with breeding adults, the embryonic stages constitute the most sensitive to temperature phases in the life-cycle of these fishes (Dahlke *et al.*, 2020) and are often named “life-cycle bottlenecks”. Dahlke *et al.* (2020) showed that by 2100, depending on the future scenario considered, between 10 to 60% of fish species could be affected by water temperature exceeding their tolerance limit during reproduction and spawning. The temperature conditions under which a species can survive, grow and reproduce is called a thermal niche (Schulte, 2020). This thermal niche can vary according to the life stage as explained earlier, with a narrower thermal niche during the breeding season (Righton *et al.*, 2010). With climate change, fish species might have to move to different habitats in order to remain in their optimal temperature range. In fact, the thermal niches of many fish species have been either observed or estimated to move to higher latitudes (Sandø *et al.*, 2020). This phenomenon is called tropicalization, and has been reported in a wide range of wild life populations (Costa *et al.*, 2014; Osland *et al.*, 2021). In the case of our specific studied species in this thesis (*S. solea*, *S. senegalensis*, *P. flesus*, *P. platessa*, *D. labrax*), they are expected to move northward by a few kilometres (Janc *et al.*, in prep.). For some species like the Allis shad or European flounder, climate change may result in a gain of habitats in higher latitudes, but in lower latitudes European flounder may be at a risk of habitat loss (Navarro *et al.*, 2023).

1.2. A mitigated effect on the function of spawning areas

The studies based on habitat suitability indices consider multiple environmental factors, generally by exploring the statistical correlation between current and past distribution of fishes and some environmental predictors. However, they do not take into account the dispersal of individuals spawned in those potential spawning areas. Larval drift models allow a more mechanistic exploration of the connectivity patterns between the spawning areas to the nurseries, and actually determine what happens to the larvae spawned in those suitable spawning grounds. The location of spawning grounds can result from adaptive processes to improve the survival of offspring (Ciannelli *et al.*, 2015). Climate change being known to influence both the biotic and abiotic parameters of the larval drift (Alix *et al.*, 2020; Bashevkin *et al.*, 2020), the location of the most “efficient” spawning grounds might change resulting in possible maladaptation to climate change. Our model indicates that despite modifications

in hydrodynamics and larvae growth rate induced by environmental conditions, the location of the spawning areas allowing for the highest recruitment rate remain spatially stable (seen in the second chapter). From an evolutionary point of view, this supports that natural selection might favour strong homing. This is consistent with field studies that identified a strong spawning site fidelity in similar species (Exadactylos *et al.*, 2003; Hunter *et al.*, 2003). It also validates Ciannelli *et al.* (2015) statement, saying : “*The set of environmental and topographical conditions that fulfil the constraints on spawning (...) must on average always be present for fish to successfully aggregate and reproduce.*”.

It is important to notice that the areas where released particles had the highest chance of recruiting are not necessarily the spawning areas used by species in real life. For instance, an area showing high recruitment success can also indicate an area allowing for high retention (and thus higher chances of survival). In fact, as there is a daily mortality on larvae, the particles recruiting further away have a smaller value than the ones recruiting faster. When testing this hypothesis, the areas allowing for the highest chances of survival according to our simulations were not areas identified in the literature as being used spawning areas by wild populations (third chapter). This confirms that there are more parameters to take into account in the unconscious choice of spawning area than just the hydrodynamics and larvae behaviour. Overall, it is accepted that the choice of a suitable spawning location is subject to multiple trade-offs operating on ecological and evolutionary constraints (Ciannelli *et al.*, 2015; Jørgensen *et al.*, 2008). In this thesis, we considered the ecological constraints influencing the location of spawning areas (defined as areas allowing for high recruitment success, so to say the faster recruitment), but we did not consider the evolutionary ones.

Overall, the strong site fidelity demonstrated in the second chapter and the absence of evolutionary mechanisms in our modelling can raise questions about the actual adaptability of species to climate change.

1.3. A high variability: searching for the culprit

Throughout the thesis, a high temporal and spatial variability could be seen. The recruitment stochasticity and variability is well known and documented, and is related to the high sensibility of the early stages of life (Huwer *et al.*, 2016; Romagnoni *et al.*, 2020; van der Veer *et al.*, 2014).

In the second chapter, we observed that even though the “most efficient” spawning areas were locally stable across years with contrasting environmental conditions, their relative effectiveness was highly variable among years. The mean recruitment success was indeed far higher in years considered as “warm” (years showing high SST and NAO index), especially when compared with the recruitment success in “cold” years (low SST and NAO index). This inter-annual variability has already been reported

for instance in the Iberian coast for *S. solea*, *S. senegalensis*, *P. flesus* and *D. labrax* (Cabral *et al.*, 2021). The higher recruitment in warmer years can be attributed to a faster growth, enabling a faster settlement (Jørgensen *et al.*, 2008; Lett *et al.*, 2010; Raventos *et al.*, 2021). However, other studies suggest that warm years are associated with earlier spawning (Fincham *et al.*, 2013), and thus eggs and larvae grow in an average colder water, thus having a slow growth and settling in nurseries after a wider dispersion (Lacroix *et al.*, 2018). This is not our case here, even though it might be interesting in the future to model our spawning timing to be triggered by a set threshold temperature.

In order to depict the most influential environmental factors of recruitment success, we made a classification of years based on large scale indicators. However, while overall recruitment vary among clusters, variability remain very high within these clusters. This suggests that some local scale environmental factors, not taken in the classification, might play a role and that the global indicators we have used might not be perfectly-suited to describe the conditions at a lower spatial scale (Le Pape *et al.*, 2003).

2. Larval drift models, a tool relying heavily on the modeller choices

Larval drift modelling is a remarkable tool. However, as other models, it imposes that a multitude of assumptions should be made by the modeller. One must be aware of these choices in order to make the wisest decision aligned with the specific question they aim to address

2.1. At each scale another story to tell

As said earlier, the species studied in this thesis have a higher recruitment rate during warm years, however other species might react in the inverse way. Chen *et al.* (2021) found variability in the ichthyoplankton assemblage between “warm” and “cold” years with different species present depending on environmental conditions, so that the total ichthyoplankton biomass remain rather similar between warm and cold years. The answer may lie in the fact that, at a large scale, biomass remains unaffected, but at a smaller scale, there are contrasting species responses. This stability on a large scale, composed of a high variability at a small scale is one of the concept behind the portfolio phenomenon (Schindler *et al.*, 2015). In fact, biological systems tend to be extremely variable when observed at some small scales but relatively invariant at others (Levin, 1992).

There is no “right scale”, as it all depends on the ecological question. As an example, in the first chapter on our large study scale, we concluded that diel vertical migration had a limited impact on recruitment success, whereas most of the literature, made on smaller study scale, demonstrated the exact opposite

(Beraud *et al.*, 2018; Zölck *et al.*, 2015). Thus, it is important to recognize that a conclusion drawn from a specific study may not be transferable to another region or species. In the context of climate change, there is a growing demand in conducting global modelling to gain a more comprehensive overview (Peck *et al.*, 2018). Large-scale studies are valuable for inferring general patterns, which should be further refined if specific or localized conclusions are desired. Therefore, there is complementarity between the two approaches.

2.2. Complexity arises from the precision

As larval drift is a dispersion involving tiny organisms going on big journeys, there is a huge number of parameters that can affect the drift and the development. For instance, recently it has been discovered that anchovy sexual activity during spawning season could greatly increase turbulence, this biomixing is thought to be comparable to storms (Fernández Castro *et al.*, 2022). In our study, all our individuals are identical clones that encounter various environmental conditions and disperse to various habitats in different years. However, in reality, sexual species share genes but express them differently in distinct contexts. Moreover, there exists inherent inter-individual variability (Cerini *et al.*, 2023). Properties of eggs and larvae, such as size and density, may vary depending on the conditions the mother experienced in the months leading up to spawning (Solemdal, 1967). Additionally, egg density can fluctuate with temperature (Ospina-Álvarez *et al.*, 2012) and this may have a direct effect as differences of density can impact the overall dispersion of the eggs. In fact, research by Pacariz *et al.*, (2014) indicated that eggs spawned in the same location could either be retained or dispersed, depending on their density. Furthermore, the availability of nurseries can be partially, temporarily, or completely lost, leading to a disruption in connectivity (Van der Veer *et al.*, 2022). For instance, certain hydrological conditions combined with tidal water level variation may alter the availability of certain estuaries (Alp and Pichon, 2020). Besides, climate change may increase the amount of microalgae near the coast that are harmful to fish larvae (de Boer *et al.*, 2012; Peperzak, 2003). These examples highlight that trying to mimic larval drift can be tricky, and that as with any models, we had to make a set of simplifying assumptions. In modelling, there is a trade-off to strike between the simplicity of the model, and the realism of the model, which can be referred as the accuracy vs simplicity trade-off (Aragones *et al.*, 2002). Adding too much parameters makes potential errors stack up and can also lead to overfitting. This is also why sensitivity analysis are advised before exploiting a model, in order to understand to which extent the included parameters are influencing the chosen output. This is what we did in Chapter 1. In our case, we were able to order the importance of each of the eight parameters that we selected on the recruitment success. However, it is important to note that we studied the

recruitment success, but it does not inform us on the relative connectivity pattern and the influence of those parameters on it, which would have been a whole different and really interesting problematic. The difficulty of sampling or observing real data is making the modelling all the more challenging as there is a lack of validation data.

2.3. The lack of validation: are we stepping too far from reality?

Models produce estimate of recruitment success and population connectivity which should be validated through the confrontation with empirical data obtained on the field (Swearer *et al.*, 2019). Apart from comparing the models with temperature or salinity dataset, hydrodynamics models output can be validated through the use of passive drifters (Amemou *et al.*, 2020). Even though these validation methods exist, it is important to outline that different models do not necessarily generate the same trajectories (Amemou *et al.*, 2020; Hufnagl *et al.*, 2017). Moreover, the passive drifters stay at the surface and lack any behaviour, as such they are not able to validate more complex aspects of the larval drift.

To validate larvae behaviour, the recruitment success is often used as an indicator. For instance, the tidal vertical migrations have been observed in the late larvae stage for a few species (Bos *et al.*, 1995 on *P. flesus* ; Grioche *et al.*, 2000 on *P. flesus* and *S. solea*; Lagardère *et al.*, 1999 on *S. solea*). In modelling, including a vertical migration can induce a higher recruitment success rates (Beraud *et al.*, 2018; Zölck *et al.*, 2015). Henceforth, it is accepted that tidal migrations may happen for all species (Swearer *et al.*, 2019). Without questioning the existence of tidal migrations which have been observed on the field, I would like to emphasize that due to the difficulty of observing larvae on the field, modellers may have to make assumptions or generalizations. Models are often constructed based on previous models. As such, they may be built upon a stack of assumptions considered true without having been empirically validated. Even though we can wonder whether models are stepping too far from reality, validation methods over long-trends recruitment have shown potential. The modelled larval recruitment can be compared to observed larvae recruitment (Daewel *et al.*, 2015), or compared with observed juvenile distribution (Huwer *et al.*, 2016), each wielding promising results.

3. Retrospective and perspective

3.1. Looking backwards: What could have been done differently?

Looking backwards, the model could have also encompassed several other processes, such as predation, feeding, orientation, tidal vertical migrations, or a more detailed spawning period. We will go through each of those points in the following lines.

Our modelling included two mortality types, among which a daily mortality accounting for predation, and staying constant every day. However, predation risk changes with the particle's size and can be variable in space (Akimova *et al.*, 2016; McManus and Woodson, 2012). DEB models can help take this mortality into account, as they model the energy allocation, and thus the growth and development (van de Wolfshaar *et al.*, 2021). As interesting as it may be to incorporate this aspect, mortality rates remain subject to significant uncertainty, primarily stemming from the challenge of accurate estimation. Feeding is another aspect that would have been interesting to integrate into the model. Starvation is one of the main mortality sources, higher when larvae transition from endogenous to exogenous feeding and is also variable in space (Di Pane *et al.*, 2021). The trade-off between the predation risk and the feeding can determine the location of the actual spawning locations (Shropshire *et al.*, 2022).

Throughout this thesis, we have assumed that our particles lacked active behaviours to more efficiently reach the nurseries. Indeed, there is evidence that larvae can orient themselves toward lower salinities (Berenshtein *et al.*, 2022), and that tidal vertical migration could greatly assist the late stages in approaching the coast (Beraud *et al.*, 2018; Zölck *et al.*, 2015). We chose to ignore tidal migrations at the outset of the thesis, thinking that, at the scale of our study are, the effects of these migrations would be insignificant. It would be interesting to add these two components to a model with a more precise definition of the coastal interface to investigate whether, indeed, the effects are negligible, or if it significantly alters the results.

In our model, we have set a fixed spawning period for each species in each zone. To better account for inter-regional and inter-annual variabilities, as well as climate changes, the spawning period could have been more realistic by basing it on external indicators. For instance, it has been demonstrated that spawning can be triggered when a certain temperature threshold is reached (Baynes *et al.*, 1993; Bedoui, 1995). Additionally, photoperiod may play a significant role in spawning initiation (Blaxter, 1969b) as well as the NAO, EA and upwelling intensity (Sims *et al.*, 2004; Vaz *et al.*, 2023).

In the previous paragraphs, I explored various factors that were omitted from our modelling efforts. However, it is important to acknowledge that we may lack the necessary data to incorporate these

factors comprehensively across diverse spatial and temporal scales. This limitation is applicable to multiple species as well. These aspects could also lead to an over-complexification of the model, as explained earlier. As a preliminary step, these considerations should be validated at a smaller, more localized scale.

3.2. Looking ahead: Advises for future larvae drift modelling studies

Overall, larval dispersal modelling is a powerful tool to evaluate impacts at the population level of different climate conditions. Based on all the points raised in this thesis and throughout this discussion, I have several recommendations to offer to future studies on larval drift on what could be done to go further.

First off, for more applied recruitment investigations or connectivity patterns studies, it is crucial to identify the potential location of habitats of interest (spawning grounds and nurseries). This can be done through suitable ecological niches studies, as in Navarro *et al.* (2023). Examining habitat availability is essential for characterizing the potential “back-up plans” of species, adhering to the “the more, the better” principle in line with the portfolio concept.

Secondly, it could be interesting to verify if those potential habitats are used with actual field surveys. This can be done using bioacoustics to locate school of fishes (only if the studied fish are pelagic; Lindseth and Lobel, 2018; Mann *et al.*, 2008), bio-tagging (Primo *et al.*, 2018), or more traditional sampling surveys targeting fish juveniles (Colloca *et al.*, 2009). If individuals can be sampled, obtaining genetic information could help to differentiate putative sub-populations (Dalongeville *et al.*, 2018). At a smaller scale, it is possible to track individuals using stable isotope, which could help distinguish precise connectivity structures (Almany *et al.*, 2007). In fact, it is of outmost importance to successfully validate models that address phenomena at fine scales (coast-estuary) with models at broader scales. Both are crucial and address distinct questions, yet they mutually depend on each other.

I would favour validations based on connectivity rather than relying solely on recruitment success, as the latter can obscure dispersal processes. A process that I find promising is in the use of indirect tools, as genetics or otolith geochemistry (Reis-Santos *et al.*, 2023). For instance, Vendrami *et al.* (2021) recreated population genomics using larvae drift simulations coupled with genetic information. Nolasco *et al.* (2018) compared observed connectivity matrices derived from elemental chemistry with predictions from a biophysical model of dispersal. Both these approaches can greatly help improve the calibration and validation of larvae drift modelling, to further infer on populations future.

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SUPPLEMENTARY MATERIAL: internship report

« Constitution de groupes de similitudes au sein d'un corpus de poissons possédant une dérive larvaire dans leur cycle de vie » Théo Schnebelin 2022

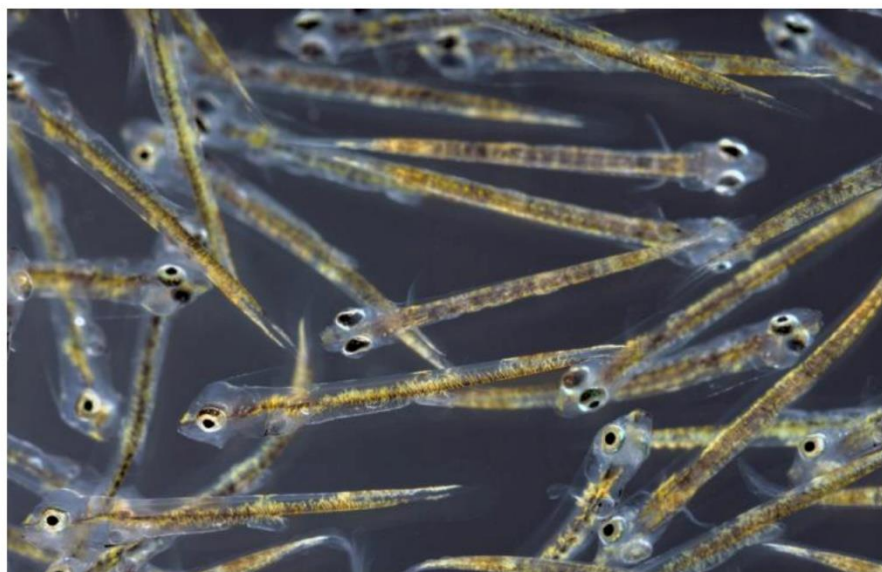
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Mention Sciences de la Vie

2021-2022 (L3)

Rapport de stage

Constitution de groupes de similitudes au sein d'un corpus de poissons possédant une dérive larvaire dans leur cycle de vie



Archives Richard Goasguen

SCHNEBELIN Théo

Dates du stage : 9/05/2022 – 24/06/2022

Durée du stage : 7 semaines

Maître de stage : Violette SILVE (doctorante)

Encadrants : Henrique Cabral (chargé de recherche) et Hilaire Drouineau (ingénieur de recherche)

Nom et adresse de la structure d'accueil : INRAE Nouvelle Aquitaine EABX – Site de Cestas-Gazinet

50 Avenue de Verdun, 33612 CESTAS

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Résumé

Le contexte climatique que nous connaissons provoque des bouleversements au sein des facteurs environnementaux qui eux même ont un effet en cascade sur les paramètres biotiques des espèces. Ces paramètres régissent le cycle de vie de nombreux organismes, dont certaines espèces de poissons possédant une dérive larvaire au cours de leur développement. Cette période est très vulnérable et sujette entièrement aux paramètres du milieu. Afin de comprendre les effets du réchauffement climatique sur ces espèces halieutiques, la modélisation est un outil fréquemment utilisé. L'objectif de cette étude est de constituer des groupes de poissons possédant des traits biologiques similaires afin de minimiser les efforts de modélisation nécessaires à l'étude des potentiels impacts du réchauffement climatique sur leur survie. L'étude porte sur vingt-huit espèces de poissons. Dans un premier temps, une étude bibliographique a été menée pour déterminer sept paramètres clefs. Par la suite une Analyse des Correspondances Multiples a été réalisée pour créer trois groupes d'espèces aux traits biologiques similaires. Le premier cluster se caractérise par des espèces côtières, pondant sur du substrat friable et possédant des durées de dérive larvaire plutôt courtes. Le deuxième quant à lui contient plutôt des espèces printanières voire estivales, qui sont également plutôt côtières. Pour finir, le troisième cluster représente des espèces hivernales, tolérantes aux températures froides et pouvant pondre sur des substrats rocheux. Grâce à cette analyse, la première étape vers la compréhension et la prédiction des effets du changement climatique sur les espèces de poissons a été réalisée.

I. Structure d'accueil

Ce stage a été réalisé au sein de l'unité EABX¹ de l'INRAE Nouvelle Aquitaine, dans l'équipe FREEMA². Cette équipe travaille autour de deux objets d'études principaux : les populations de poissons migrateurs amphihalins et les écosystèmes estuariens. Les travaux de recherche sont axés sur la caractérisation et l'évaluation de l'état et la viabilité, la compréhension et la description des évolutions des poissons migrateurs amphihalins, et des écosystèmes estuariens face aux changements globaux. L'équipe se compose de 22 chercheurs permanents, mais aussi de doctorants, de contractuels et de stagiaires. Au sein de cette unité, les études portent sur de la biologie de la conservation aussi bien que sur de la génétique. Des écotoxicologues opèrent également en relation avec les autres chercheurs plus halieutiques afin d'obtenir des visions plus globales des problématiques.

II. Introduction

Le contexte climatique que nous connaissons actuellement, provoque des changements importants dans l'équilibre des écosystèmes terrestres et aquatiques. En effet, les changements climatiques se manifestent par des changements sur le long terme au niveau des températures et des conditions météorologiques. Au niveau marin, cela peut se traduire de nombreuses façons comme des changements dans l'hydrodynamisme, dans les vents et les précipitations, ou encore dans les températures de surface de la mer. Ces paramètres abiotiques sont des facteurs clefs dans le cycle de vie de nombreux organismes, parmi lesquels certaines espèces de poissons possédant une dérive larvaire au cours de leur cycle de vie. Cette dérive a lieu entre des zones de ponte au large des côtes (frayères) et des zones dites de nourriceries. Ces nourriceries sont des zones littorales voire estuariennes dans lesquelles il y a peu de prédateurs et une abondance de nourriture, ce qui favorise le développement des juvéniles ((Cabral et al. 2022) et les références qu'il contient). C'est une période

¹ Écosystèmes Aquatiques et Changement Globaux.

² Fonctionnement et Restauration des Écosystèmes Estuariens et des populations de Migrateur Amphihalins.

très exposée, sujette à un taux élevé de mortalité, dû à la faible capacité de nage des larves, les rendant inaptes à échapper aux prédateurs ou à sortir activement de zones sans nourriture. De nombreux facteurs influent sur cette dérive larvaire, qu'ils soient abiotiques comme décrits précédemment, ou bien biotiques (localisation de la zone de ponte, densité des œufs, présence de migrations verticales dans la colonne d'eau, etc...). Certains de ces facteurs sont fonction de la température, comme par exemple la période de ponte ("déclenchée" lorsqu'une certaine température est atteinte (Imsland et al. 2003) la vitesse de développement larvaire (Fonds 1979), la mortalité due à la rencontre avec une température létale ou encore la position verticale de la larve dans la colonne d'eau (due à la densité de l'eau environnante et celle des individus). Ainsi, les changements climatiques influent sur la dérive de larves de poissons à la fois au niveau de l'environnement mais également au niveau de la biologie des espèces.

L'importance halieutique de certaines espèces de poissons rend primordial le fait d'essayer de comprendre et de prédire les effets que les changements climatiques pourraient avoir sur leurs populations. Afin d'étudier des processus à large échelle, la modélisation est préférée à d'autres approches *in situ* (van de Wolfshaar, Barbut, et Lacroix 2022). Cependant, ces modèles doivent prendre en compte de multiples processus et peuvent se révéler être très complexes (Swearer, Tremblé, et Shima 2019). En ce sens, modéliser la dérive de nombreuses espèces est une opération coûteuse aussi bien en temps de calcul qu'en ressources informatiques. Cela rend essentielle l'utilisation d'"archétypes" permettant de représenter différentes espèces en un minimum de simulations. Il est possible de déterminer ces archétypes de poissons en fonction de certains traits d'histoire de vie influant sur la survie de l'individu jusqu'à son arrivée dans une nurserie.

Le but de notre étude est donc de déterminer s'il est possible de constituer des groupes de similitudes au sein d'un corpus de poissons présentant une phase de dérive larvaire dans leur cycle de vie. Afin de répondre à cette problématique, vingt-huit espèces de poissons utilisant les côtes et estuaires comme nurseries ont été étudiés. Dans un premier temps, une grande étude bibliographique a été réalisée pour chacun afin de renseigner sept paramètres essentiels : la saison de ponte moyenne, la bathymétrie des frayères et celle des nurseries, les températures létales, la durée de la phase de larvaire, la densité des œufs au moment de la ponte et le type de sédiments présents aux frayères. Dans un second temps, une analyse des correspondances multiples a été menée dans le but de créer des clusters d'espèces aux traits d'histoire de vie similaires. Trois clusters d'espèces ont été établis, dont les caractéristiques biologiques sont discutées.

III. Matériels et méthodes

1. Obtention des données

Vingt-huit espèces de poissons ont été sélectionnées comme étant des espèces pondant sur le plateau continental Nord-Atlantique, et pour lesquelles une phase de dérive larvaire permet le recrutement dans des nurseries côtières. Une vaste étude bibliographique a permis de renseigner sept paramètres pour chaque espèce (Annexe). Lorsque les informations manquaient dans la littérature, les données ont été récoltées soit à l'aide de dires-d'experts, soit à l'aide d'informations sur des espèces proches plus documentées. Nous avons concentré la majorité des données sur le Golfe de Gascogne mais nous avons élargi à la Mer du Nord et aux côtes Ibériques lorsque les données n'étaient pas disponibles dans notre zone d'étude.

2. Transformation des variables

Sept variables ont été sélectionnées afin de permettre la comparaison entre espèces de poissons : la bathymétrie des frayères et celle des nurseries, les températures létales, la longueur moyenne de la phase de larvaire, la densité des œufs au moment de la ponte et le type de sédiments présents aux

frayères. Afin de minimiser les imprécisions, et de rassembler toutes les variables sous la même forme, le choix a été fait de transformer les données en variables qualitatives à différentes modalités. Ces modalités ont été réalisées sous le logiciel R (R Core Team (2022)) à l'aide du package "adegenet" (Jombart, T. (2008)). L'analyse de clustering consiste à la construction de groupes. Le cluster va chercher à minimiser les différences entre les données appartenant aux mêmes groupes et dans le même temps à maximiser les différences entre différents groupes. Pour ce faire, l'analyse se base sur l'algorithme des K-means. Cet algorithme sépare les données en clusters, homogènes et compacts. C'est-à-dire qu'il choisit un nombre de centres définis par l'opérateur. Ensuite, il affecte tous les individus au centre de classe le plus proche, pour former des classes d'individus. Un calcul des centres de gravité est effectué, puis l'opération est répétée jusqu'à que l'algorithme converge. La distance euclidienne est la base de l'algorithme des k-means.

Les bornes des modalités obtenues pour chaque variable sont définies dans les paragraphes ci-dessous.

La période de ponte a été séparée en deux modalités. Une saison moyenne a été déterminée en fonction de la période de ponte : "*spring*" d'Avril à Juin ; "*summer*" de Juillet à Septembre ; "*autumn*" d'Octobre à Décembre ; "*winter*" de Janvier à Mars. La deuxième variable permet de renseigner l'étalement de la période de ponte et a été classée en trois modalités : "*short*" pour une durée de la période de ponte inférieure ou égale à 3 mois ; "*medium*" entre 4 et 5 mois et pour finir "*long*" si elle est supérieure ou égale à 6 mois.

La bathymétrie de la zone de ponte et celle des nourriceries sont également rangées dans trois catégories : pour les nourriceries, "*shallow*" correspond à des nourriceries où la profondeur est inférieure à 20m, "*medium*" lorsqu'elle se trouve entre 20 et 45m et pour finir "*deep*" lorsqu'elle est supérieure à 45m. Pour les nourriceries, "*shallow*" a été utilisé lorsque la frayère se situait à des profondeurs inférieures à 50m, "*medium*" de 50 à 150m et "*deep*" lorsque la profondeur des frayères excédait les 150m.

Concernant les températures létales, les gammes de températures viables pour chaque espèce ont été relevées et ont ensuite été classées en "*cold*" pour inférieure à 10°C, "*medium*" entre 10 et 20 °C et "*hot*" pour celles supérieures à 20°C. La durée du stade larvaire (appelée par la suite dans les graphiques PLD pour "Pélagique Larval Duration"), est rangée en : "*short*" pour les durées inférieures à 40 jours, "*medium*" entre 40 et 70 jours et "*long*" pour celles supérieures à 70 jours. La densité des œufs au moment de la ponte est définie selon leur position dans la colonne d'eau. Soit les œufs flottent ("*buoyant*"), soit ils sont démersaux (référés comme "*heavy*"). Pour finir, le dernier paramètre concerne le type de sédiment présent dans les frayères et les nourriceries. Il est classé en deux catégories : soit il est friable (vase, sable ou gravier) et est alors qualifié de "*soft*" soit il est qualifié de "*rock*" lorsqu'il est susceptible de contenir des fonds rocheux.

3. Regroupement des espèces selon leurs traits

3.1. L'Analyse de Correspondances Multiples (ACM)

L'ACM permet de résumer l'information contenue dans un grand nombre de variables qualitatives. Il nous est ainsi possible d'interpréter et de mettre en évidence des associations entre variables. L'ACM a été réalisée à l'aide du package "FactoMineR" (Sebastien Le et al. (2008)). Deux dimensions ont été gardées dans l'analyse, qui représentent 31.3% de variance expliquée.

3.2 Classification Hiérarchique sur Composantes Principales

Une fois l'ACM effectuée, les espèces ont été regroupées à l'aide d'une classification hiérarchique sur composantes principales.

Cette fonction permet l'exploration des données après une analyse multivariée identifiant ainsi les espèces similaires dans notre jeu de données. Cette méthode permet d'effectuer à la fois la classification ascendante hiérarchique ainsi que le partitionnement en k-means.

IV. Résultats :

1. Analyses des Correspondances Multiples (ACM)

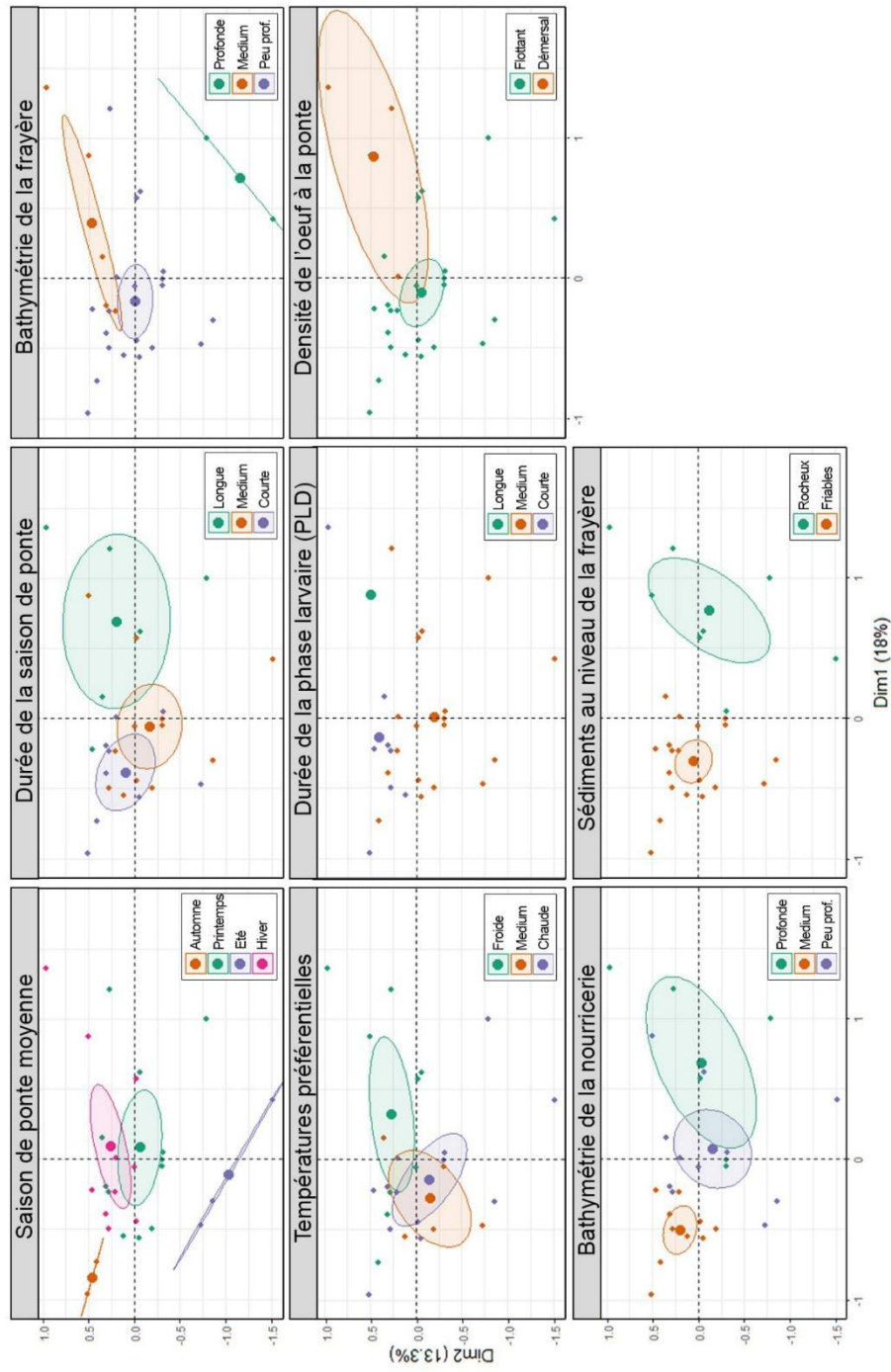


Figure 1 : Résultats de l'Analyse des Correspondances Multiples pour les 28 espèces de poissons.

Nous pouvons mettre en évidence une corrélation entre la saison de ponte moyenne et le préférentiel de températures. Ainsi, une espèce pondant en hiver possède une plus grande tolérance aux températures froides. Cependant nous n’observons pas de lien particulier entre la saison moyenne de ponte et la durée de la dérive larvaire.

D’autres variables semblent également corrélées, comme la bathymétrie de la frayère et la densité de l’œuf au moment de la ponte. Si la profondeur de la frayère est entre 50 et 150 mètres, les œufs pondus seraient démersaux. A l’inverse une bathymétrie faible de la frayère correspondrait à une ponte d’œufs flottants.

Dans une moindre mesure, la sédimentation présente aux frayères semble également répondre à la bathymétrie de cette dernière. Une espèce pondant dans de plus grandes profondeurs semble être moins sensible à la présence de roches dans le substrat.

2. Classification hiérarchique sur composantes principales

Dans un deuxième temps, afin de créer des clusters d’espèces aux traits d’histoire de vie similaires, une classification hiérarchique sur composantes principales a été réalisée sur deux dimensions de l’ACM. On observe que trois groupes d’espèces se dessinent (Fig.2). Les caractéristiques biologiques de ces clusters d’espèces de poissons ont été définies dans le tableau 1.

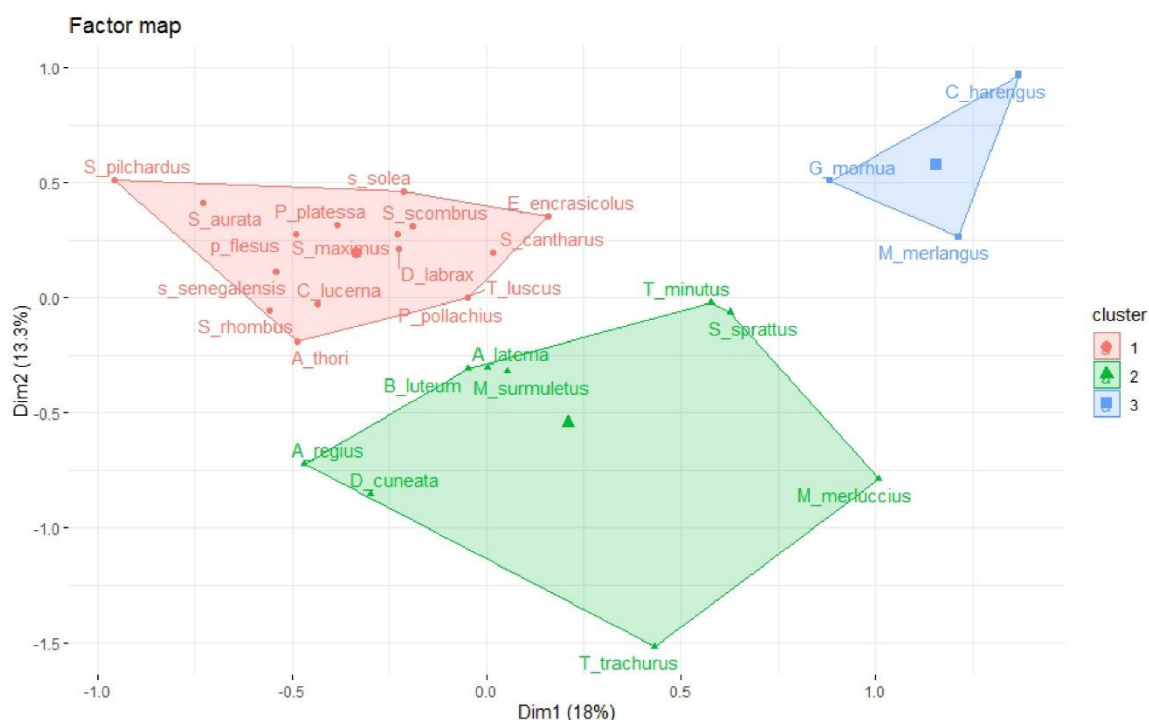


Figure 2. Groupements d’espèces obtenus à l’aide de la classification hiérarchique sur composantes principales. Les caractéristiques biologiques correspondant aux différents groupes sont visibles dans le tableau 1. Les clusters contiennent respectivement 16, 9 et 3 espèces.

Le premier cluster (Tab.1) se caractérise par des espèces côtières, pondant sur du substrat friable et possédant des durées de dérive larvaire plutôt courtes. Le deuxième quant à lui contient plutôt des espèces printanières voire estivales, qui sont également plutôt côtières. Pour finir, le troisième cluster représente des espèces hivernales, tolérantes aux températures froides et pouvant pondre sur des substrats rocheux.

Tableau 1 : Pourcentage d'individus dans chaque cluster correspondant aux traits biologiques étudiés.

	Cluster 1				Cluster 2				Cluster 3			
	Hiver	Printemps	Été	Automne	Hiver	Printemps	Été	Automne	Hiver	Printemps	Été	Automne
Saison de ponte moyenne	50,00	37,50	-	12,50	11,11	55,56	33,33	-	66,67	33,33	-	-
Étalement de la période de ponte	Court	Medium	Long		Court	Medium	Long		Court	Medium	Long	
	43,75	43,75	12,50		22,22	55,56	22,22		-	33,33	66,67	
Bathymétrie de la frayère	Peu profond	Medium	Profond		Peu profond	Medium	Profond		Peu profond	Medium	Profond	
	81,25	18,75	-		77,78	-	22,22		33,33	66,67	-	
Températures viables	Froides	Medium	Chaudes		Froides	Medium	Chaudes		Froides	Medium	Chaudes	
	31,25	50,00	18,75		22,22	55,56	22,22		100,00	-	-	
Durée larvaire	Courte	Medium	Longue		Courte	Medium	Longue		Courte	Medium	Longue	
	43,75	56,25	-		-	100,00	-		33,33	33,33	33,33	
Densité de l'œuf	Lourd	Flottant			Lourd	Flottant			Lourd	Flottant		
	6,25	93,75			-	100,00			66,67	33,33		
Bathymétrie de la nourricerie	Peu profond	Medium	Profond		Peu profond	Medium	Profond		Peu profond	Medium	Profond	
	37,50	62,50	-		55,56	-	44,44		33,33	-	66,67	
Sédiments au niveau de la frayère	Friable	Rocheux			Friable	Rocheux			Friable	Rocheux		
	100,00	-			55,56	44,44			-	100,00		

V. Discussion

1. Relations entre les traits biologiques

L'ACM a indiqué une relation entre la saison de ponte moyenne et le préférentiel de température des espèces. En effet, une espèce hivernale est tolérante aux températures froides, tout comme une pondant en période estivale est tolérante aux températures chaudes. Ce résultat était attendu et permet en un sens de valider la vraisemblance de nos résultats pour ces deux variables.

Au contraire, nos résultats ne mettent pas en évidence de lien entre la saison moyenne de ponte et la durée de la dérive larvaire (PLD). Il aurait été possible de nous attendre à ce que les espèces avec une PLD longue correspondent aux espèces qui sont pondues en hiver. En effet, lorsque la température est basse, les processus biologiques sont plus lents et donc le développement larvaire prend plus de temps. Or, bien que les espèces hivernales évoluent dans des températures plus froides, cela ne veut pas nécessairement dire que leur durée larvaire est longue. Par exemple, le bar européen et la sole commune possèdent le même référentiel thermique (entre 9 et 17°C, (Pickett et Pawson 1994) pour le bar, (Koutsikopoulos et Lacroix 1992) pour la sole) mais le bar est connu pour avoir un développement larvaire relativement long au contraire de la sole pour laquelle il est plus court, et ce pour les mêmes températures (en moyenne 55 jours pour le bar (Beraud et al. 2018) et 35 jours pour la sole (Barbut et al. 2019)). La durée de la phase larvaire étant un processus spécifique à chaque espèce, il est donc assez normal que nous n'ayons pas eu de relation avec la saison de ponte moyenne.

Nos résultats semblent également montrer une similitude entre la ponte d'œufs démersaux et l'atteinte d'une zone de nourricerie possédant une bathymétrie forte. C'est un résultat que l'on peut

essayer d'expliquer. En effet, la position verticale d'un œuf est lié à sa densité ainsi qu'à la densité de l'eau environnante, qui elle-même dépend de la salinité et de la température (Coombs 1981). L'osmorégulation permet le maintien de la densité de l'œuf et sa position dans la colonne d'eau (Coombs 1981). La densité de l'eau de mer implique une stratification des masses d'eau, qui a son importance dans le transport des œufs vers les nourriceries (Millero et al. 1978). Les œufs transportés par les courants de surface possèdent un transport efficace sur de plus longues distances, les eaux de surface étant plus chaudes et moins denses. Au contraire, lorsque l'eau est plus froide et dense, ce sont les courants profonds qui jouent, pouvant rendre le transport des œufs plus difficile sur de longues distances (Pacariz et al. 2014). Il a été prouvé que la densité des œufs est un facteur déterminant pour la dispersion ou la rétention des larves d'espèces de poissons (Nissling, Nyberg, et Petereit 2017). Nous pouvons poser l'hypothèse, qu'un œuf flottant sera alors plus facilement transporté vers les côtes et estuaires, qui sont des nourriceries de bathymétries peu profondes. Un œuf démersal quant à lui atteindra des nourriceries moins littorales, avec des bathymétries plus grandes.

Pour finir, il est possible d'observer une corrélation entre la bathymétrie de la frayère et le type de sédiment présent. Les espèces avec une bathymétrie de frayère faible ou moyenne, seraient susceptibles de présenter un fond sédimentaire "friable". Tandis que les espèces avec une bathymétrie de frayère forte seraient moins dérangées par la présence de roches dans le substrat. Bien que ce lien semble logique de prime abord, la cartographie des substrats présents dans le Golfe de Gascogne indique la présence de roches au bord des côtes, tandis que les zones plus au large sont parsemées de vase et autres substrats friables (SHOM 2011). Cependant nous ne sommes intéressés qu'à la cartographie des substrats au sein du Golfe de Gascogne, mais nos espèces d'intérêt sont distribuées dans de nombreuses autres zones. De plus, dans notre analyse les espèces dont le substrat au moment de la ponte était qualifié de "rocheux" ne sont pas des espèces pondant uniquement sur des rochers, mais des espèces qui ne sont pas dérangées par la présence de ces derniers. Ainsi la friabilité du substrat au large n'est pas un facteur discriminant pour ces espèces.

2. Regroupement des espèces selon leurs traits biologiques et limites de l'approche utilisée

Les résultats obtenus après le cluster effectué sur l'ACM, ont permis de regrouper certaines espèces entre elles, selon leur ressemblance. Ce regroupement semble faire sens, puisque nous retrouvons dans chaque cluster des espèces sensiblement proches (le sprat et le chinchard pour le premier cluster, l'anchois et la sardine pour le deuxième cluster ou encore le hareng commun et le merlan pour le troisième cluster).

Notre modèle d'étude présente toutefois des limites. Certaines de nos espèces d'intérêt sont peu étudiées pour les variables que nous avons choisies. Nous avons eu recours à des experts pour compléter les informations manquantes, ce qui peut comporter son lot d'incertitudes. Il est nécessaire de revenir vers des études de terrain ou d'expérimentation, afin de paramétrer au mieux des modèles de dérive complexes.

Certaines de nos modalités ("Eté" et "Automne" dans la variable de la saison moyenne de ponte ; "profonde" pour la bathymétrie de la frayère ou encore "Longue" pour la durée de la phase larvaire), nous n'avons qu'entre une et trois espèces représentantes. Or l'ACM est particulièrement sensible aux

modalités rares et y accorde trop de poids ce qui est susceptible d'amener des erreurs dans la formation de nos clusters.

Pour finir, le choix du nombre de dimensions à garder pour réaliser l'ACM est aussi déterminant. Une ACM ne porte pas nécessairement beaucoup de variances expliquées sur ces axes, car les données sont simplifiées en les traitant qualitativement. Il est donc compliqué d'obtenir en peu de dimensions, une grande part de variance expliquée. De plus, la méthode des coudes ou test d'accumulation de variances (Cattell 1966) était difficilement applicable à notre analyse (voir annexe). Il existe donc deux écoles : garder un minimum de dimensions (souvent deux), ou en prendre suffisamment pour avoir une grande variance expliquée. Le problème est que plus l'on choisit de dimensions, plus la variance qu'ils portent est artificielle car ils sont contraints de se placer orthogonalement aux autres axes déjà calculés. Selon ce nombre d'axes gardés, les clusters finaux peuvent être radicalement différents.

Pour pallier ce problème, d'autres approches permettant de traiter à la fois des données quantitatives et qualitatives pourraient être envisagées comme par exemple l'Analyse Factorielle des Données Mixtes (« Analyse factorielle de données mixtes », s. d.). C'est d'ailleurs ce sur quoi j'ai travaillé à la fin de mon stage, dont les résultats préliminaires peuvent être consultés en annexe.

VI. Conclusion

En définitive, vingt-huit espèces de poissons utilisant les côtes et les estuaires comme nourriceries ont été étudiés afin de déterminer et constituer des groupes de similitudes au sein d'un corpus de poissons présentant des phases de dérive larvaire dans leur cycle de développement. Une étude bibliographique de grande échelle a été concentrée sur sept traits biologiques qui ont par la suite fait l'objet d'une analyse de correspondances multiples. Les sorties de l'ACM ont été analysées pour vérifier que les corrélations affichées faisaient sens avant d'aller plus loin et constituer trois groupes d'espèces distincts, caractérisés selon les modalités de nos variables qualitatives. Le premier groupe s'est vu regrouper des espèces côtières, pondant sur du substrat friable et possédant des durées de dérive larvaire plutôt courtes. Le deuxième cluster quant à lui contenait plutôt des espèces printanières voire estivales, qui étaient également plutôt côtières. Pour finir, le troisième cluster représentait des espèces hivernales, tolérantes aux températures froides et pouvant pondre sur des substrats rocheux. Cette étude a ainsi rendu possible le regroupement d'espèces aux traits similaires en utilisant une méthode reproductible. L'objectif final de déterminer des archétypes qui sont nécessaires à la modélisation de la dérive de ces espèces est donc atteint. Ce travail pourra donc servir de base pour une étude de modélisation de la dérive de certaines espèces halieutiques. Cette technique permet d'atteindre une modélisation plus économique en termes de temps et d'énergie en réduisant le nombre de simulations nécessaires. Ainsi l'impact des facteurs environnementaux sur ces espèces pourra être étudié, en n'en modélisant qu'une ou deux par cluster pour extrapoler les résultats aux autres espèces du même groupe. Cette étude a permis de réaliser un pas de plus vers la compréhension et la prédiction des effets du réchauffement climatique sur les espèces halieutiques les plus importantes.

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Annexes :

1. Données obtenues pour chaque espèce :

Tableau 2 : Données obtenues pour les espèces. Les astérisques indiquent lorsque l'information a été obtenue par dires-d'experts.

Espèces	Début de la période	Fin de la période	de ponte	Periode de ponte moyenne	Etatement	Densité des œufs pondus	Sédimentation	Bathymétrie de la frayère	Gamme de température létale	PLD	Bathymétrie de la nourricerie	Références		
<i>Solea solea</i>	december	may	winter	7	Buoyant	soft	30	100	8	18	35	10	35	(Koutsikopoulos et Lacroix 1992) ; (Garlan et Marchès, s. d.) ; (Wegner, Damm, et Purps 2003)
<i>Solea senegalensis</i>	march	june	spring	4	Buoyant	soft	30	100	12	30	35	10	35	(« Meteorciel - Température de la mer (Sea Surface Temperature) » s. d.) ; (Imsland et al. 2003)
<i>Platichthys flesus</i>	january	april	winter	4	Buoyant	soft	20	50	8	15	*45	10	35	(Skerritt 2010) ; (Bos et Thiel 2006) ; (Yin et Blaxter 1987) ; (Ustups et al. 2013)
<i>Pleuronecta platessa</i>	february	march	winter	2	Buoyant	soft	20	40	2	12	50	10	30	(Brule 1987) ; (Wegner, Damm, et Purps 2003) ; (Houde et Zastrow 1993) ; (Rijnsdorp, Van Stralen, et Van Der Veer 1985)
<i>Dicentrarchus labrax</i>	december	april	winter	5	Buoyant	soft	50	90	8	18	65	1	50	(Laboratoire d'ichtyologie générale et appliquée 1997) ; (Dambrine et al. 2021) ; (Bos et Thiel 2006) ; (Pickett et Pawson 1994) ; (Jennings et Pawson 1992)
<i>Engraulis encrasicolus</i>	march	august	spring	6	Buoyant	soft	50	150	12	30	40	5	20	(Uriarte, Prouzet, et Villamor, s. d.) ; (Bos et Thiel 2006) ; (Houde et Zastrow 1993) ; (Allain et al. 2003)
<i>Sardina pilchardus</i>	november	january	autumn	3	Buoyant	soft	20	25	10	21,3	40	1	50	(Bos et Thiel 2006) ; (Blaxter 1969) ; (Houde et Zastrow 1993) ; (McFadzen, Coombs, et Halliday 1997)
<i>Argyrosomus regius</i>	may	july	summer	3	Buoyant	soft	20	40	10	30	*50	*5	*20	(« Bioline International Official Site (site up-dated regularly) » s. d.) ; (Bos et Thiel 2006) ; (Duncan et al. 2012) ; (Vallés et Estévez 2013)
<i>Gadus morhua</i>	january	april	winter	4	Buoyant	rock	50	200	7,	11	100	1	10	(Cohen 1990) ; (Bos et Thiel 2006) ; (Houde et Zastrow 1993) ; (Lilley et Unsworth 2014)
<i>Trisopterus luscus</i>	december	april	winter	5	Buoyant	soft	*20	*100	*5	*15	*50	5	20	(Cohen 1990) ; (Vieira et Bordalo 2000)
<i>Trisopterus minutus</i>	december	march	winter	4	Buoyant	rock	20	100	8	11	*50	*20	*50	(Cohen 1991) ; (Magnussen et Magnussen 2009)
<i>Merlangius merlangus</i>	january	september	spring	9	Demersal	rock	20	150	*5	*17	50	*10	*50	(Cohen 1990) ; (Cohen 1991)

<i>Dicologlossa cuneata</i>	June	september	summer	4	Buoyant	soft	20	50	10	21	*50	5	20	(Laboratoire d'ichtyologie générale et appliquée 1997) ;(García-Isarich et al. 2006) ;(Herrera et al. 2011)
<i>Arnoglossus laterna</i>	April	August	Spring	5	Buoyant	soft	*20	*50	5	23	*50	15	45	(Baltus et Van der Veer 1995)
<i>Scomber scombrus</i>	May	June	Spring	2	Buoyant	soft	80	120	6	22	40	5	10	(Collette et Nauen 1983) ; (Studholme et al. 1999) ; (Houde et Zastrow 1993)
<i>Mullus surmuletus</i>	May	June	Spring	2	Buoyant	rock	20	50	*7	*30	*50	*5	*20	(N'Da et Déniel 1993)
<i>Spondylosoma cantharus</i>	February	April	Winter	3	Demersal	soft	20	100	*5	*30	*50	*5	*20	(Gonçalves et Erzini 2000) ;(Mouine, Ktari, et Chakroun-Marzouk 2011) ;(Gordo et Cabral, s. d.)
<i>Sparus aurata</i>	October	December	Autumn	3	Buoyant	soft	30	50	4	17,5	50	*5	*30	(Daan 1987) ;(« Fisheries and Aquaculture - Cultured Aquatic Species - Sparus aurata » s. d.) ;(Houde et Zastrow 1993) ;(De Mitcheson et Liu 2008) ;(Gordo et Cabral, s. d.)
<i>Scophthalmus maximus</i>	May	June	Spring	2	Buoyant	soft	25	80	5	15	39	1	6	(Eryilmaz 2015) ;(Houde et Zastrow 1993) ;(Haynes et al. 2011) ;(Voipio 1981)
<i>Scophthalmus rhombus</i>	April	June	Spring	3	Buoyant	soft	*20	*100	11	17,5	*60	*5	*30	(Jones 1972) ;(Atlas de la mer et du littoral 2016)
<i>Buglossidium luteum</i>	March	June	Spring	4	Buoyant	soft	*20	*50	10	*30	*50	15	45	(Baltus et Van der Veer 1995)
<i>Sprattus sprattus</i>	February	July	Spring	6	Buoyant	rock	*20	*100	5	*18	*50	*5	*20	(de Silva 1973)
<i>Merluccius merluccius</i>	January	July	Spring	7	Buoyant	rock	100	200	6	*30	*50	*20	*50	(Cohen 1991) ;(Hilario Murua, Motos, et Marrale, s. d.) ;(H. Murua et Motos 2006) ;(Cohen 1991)
<i>Clupea harengus</i>	October	March	Winter	6	Demersal	rock	15	200	5	11,5	40	*20	*50	(Brophy et Danilowicz 2003) ;(Geffen 2009) ;(Houde et Zastrow 1993)
<i>Trachurus trachurus</i>	April	July	Summer	4	Buoyant	rock	50	400	5	*30	*60	1	30	(Eltink et Vingerhoed 1989) ;(Coombs, Morgans, et Halliday 2001) ;(Prista et al. 2003)
<i>Chelidonichthys lucerna</i>	November	March	Winter	5	Buoyant	soft	*20	*100	5	*30	*50	*5	*30	(Boudaya et al. 2008) ;(Alonso-Fernández et al. 2013) ; (Rodrigues et al. 2019)
<i>Pollachius pollachius</i>	January	April	Winter	4	Buoyant	soft	20	100	5	*10	*50	*5	*20	(Cohen 1990) ;(Cohen 1991) ; (Ahlstrom 1962)
<i>Arnoglossus thori</i>	April	July	Spring	4	Buoyant	soft	10	30	16	*30	*50	10	30	(« La reproduction des poissons plats (téléostéens - pleuronectiformes) en baie de Douranez » s. d.) ; (Deniel 1990)

2. Variance portée par les dimensions de l'ACM :

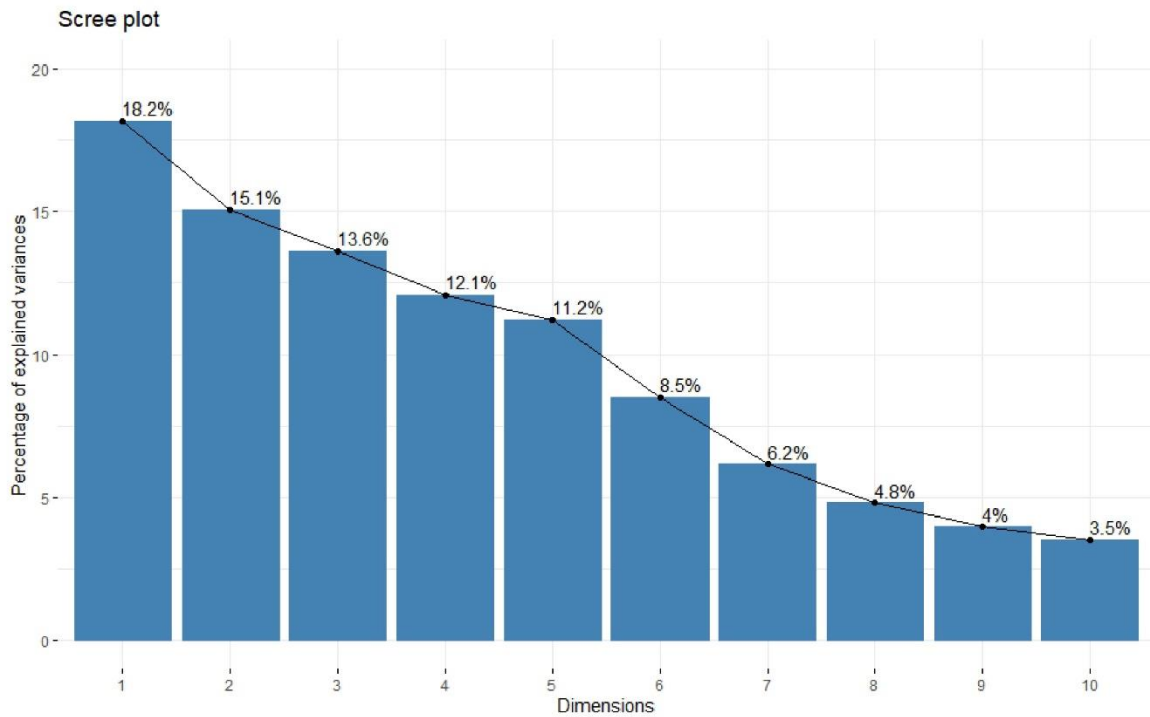


Figure 3 : Scree plot permettant de visualiser les variances expliquées portées par les dimensions.

3. Une autre approche : L'AFDM :

Une analyses FAMD a été réalisée. Elle permet de traiter à la fois des données quantitatives et qualitatives. Voici donc les résultats préliminaires de cette analyse.

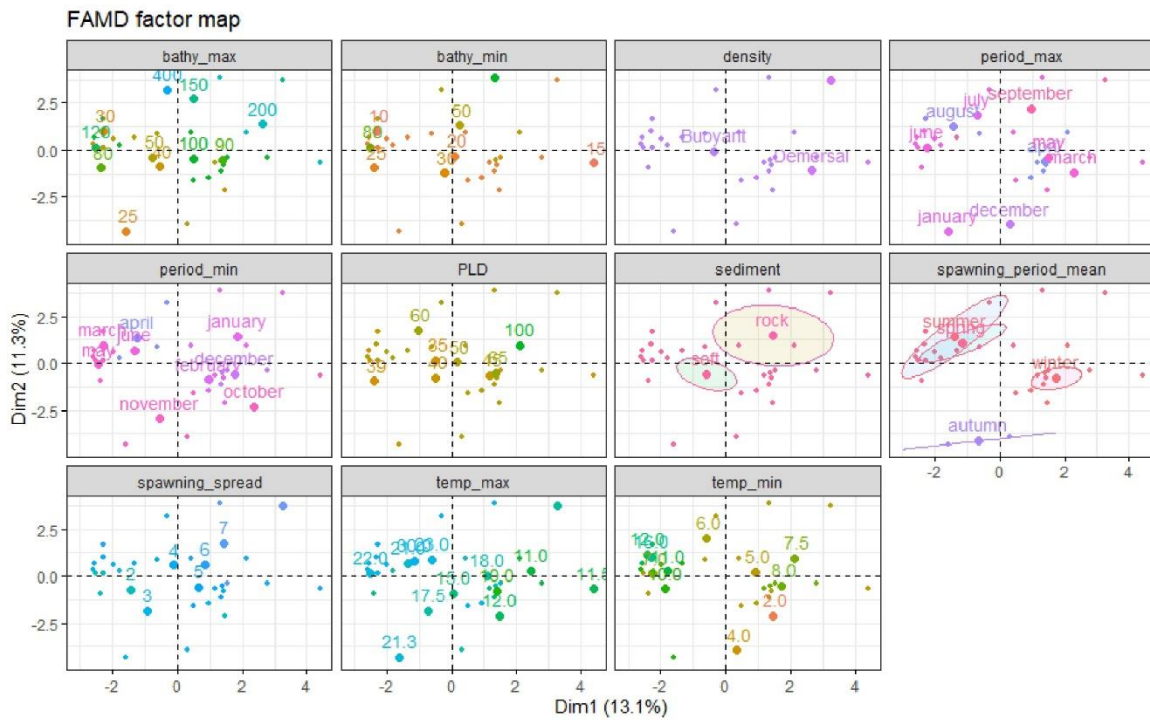


Figure 4 : Résultats de l'Analyse Factorielles des Données Mixtes pour les 28 espèces de poissons.

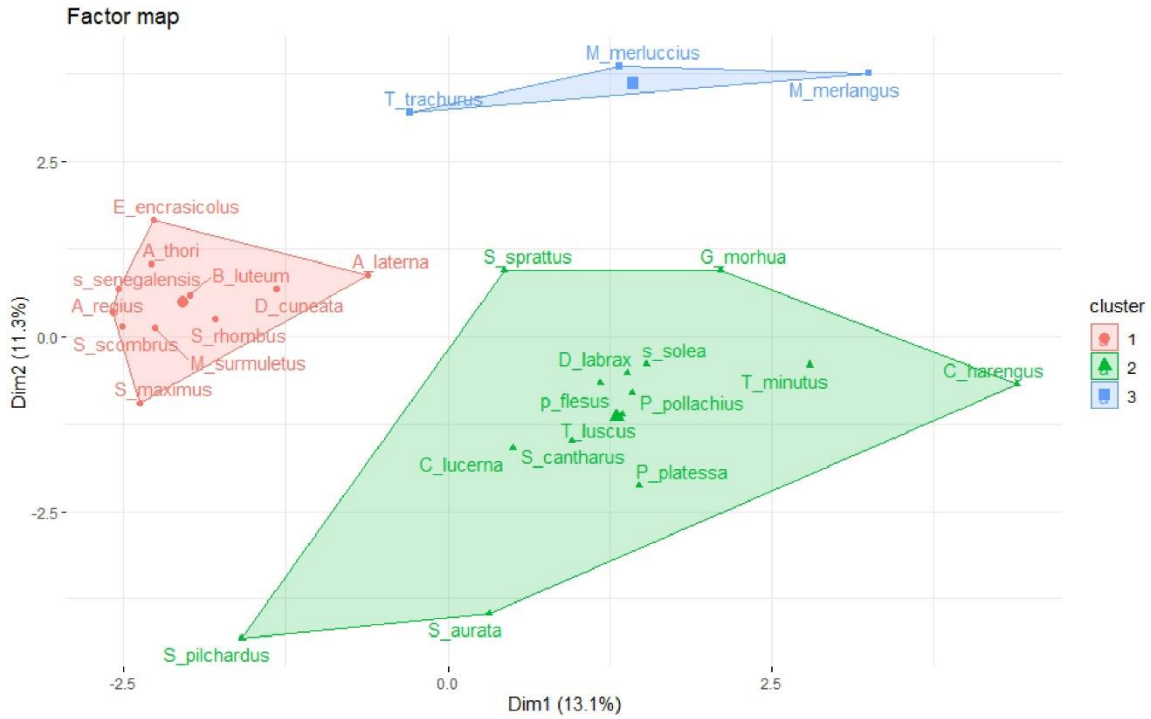


Figure 5 : Groupements d'espèces obtenus à l'aide de la classification hiérarchique sur composantes principales. Les caractéristiques biologiques correspondant aux différents groupes sont visibles dans le tableau 1. Les clusters contiennent respectivement 11, 14 et 3 espèces.