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Juliette Champagnat

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# THESE DE DOCTORAT DE

## L'INSTITUT AGRO RENNES ANGERS

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Spécialité : Ecologie marine

Par

**Juliette CHAMPAGNAT**

**« Modéliser l'impact des pressions anthropiques au niveau des habitats halieutiques sur la dynamique des populations de poissons marins exploités »**

Thèse présentée et soutenue à Rennes, le 04/07/2023

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### Rapporteurs avant soutenance :

Clara Ulrich Directrice de recherche, IFREMER  
Jean Christophe Poggiale Professeur, MIO

### Composition du Jury :

Présidente : Clara Ulrich Directrice de recherche, IFREMER  
Examineurs : Sarah Cubaynes Chargée de recherche, CNRS, CEFE  
Hilaire Drouineau Ingénieur de recherche, INRAE, EABX  
Karen Van de Wolfshaar Senior Scientist, Wageningen University

Dir. de thèse : Olivier Le Pape Professeur, Institut Agro Rennes, DECOD  
Co-dir. de thèse : Etienne Rivot ICPEF Enseignant-Chercheur, Institut Agro Rennes, DECOD

### Invitées

Stéphanie Tachaires OFB, Brest  
Isabelle Gailhard Rocher OFB, Brest



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## Avant-propos

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Elle a donné lieu à la rédaction de quatre articles dont trois en premier auteur. Le premier article a été accepté à l'automne 2021 dans la revue *Marine Ecology Progress Series*. Les deux suivants sont en révision dans les revues *Fish and Fisheries* et *Estuarine, Coastal and Shelf Science*. Le dernier est le fruit d'une collaboration avec Elliot Brown, amorcée lors d'un séjour de deux mois au DTU Aqua (Danemark) ; il sera soumis prochainement à la revue *ICES Journal of Marine Science*.

Lors de cette thèse plusieurs communications orales ont aussi été réalisées. Présentation des travaux de thèse lors d'un séminaire d'unité (mars 2021), du webinaire du GIP Seine Aval (avril 2021) et de réunions du groupe de travail du Conseil International pour l'Exploration de la Mer (CIEM) « Value of Coastal Habitats for Exploited Species » (juin 2021, 2022 et 2023). Un poster a été présenté à la conférence annuelle du CIEM (ASC) en septembre 2021 (édition en visioconférence). Deux présentations orales ont été réalisées lors du colloque de l'Association Française d'Halieutique (juin 2022) et du colloque annuel de l'ECSA (Estuarine and Coastal Science Association) en septembre 2022 (San Sebastian, Espagne). Deux expériences de vulgarisation scientifique ont aussi eu lieu dans le cadre de Pint of Science (mai 2022) et du concours « Ma thèse en 180 secondes » (février 2023).

Finalement, les travaux de cette thèse ont aussi contribué aux projets Seine Aval 6 CHOPIN («Contaminants organoHalogénés histOriques et d'intérêt émergent : Présence et transfert vers la sole commune – Impact de la contamination sur la Nourricerie et conséquences sur la population») et UE H2020 Seawise (Shaping Ecosystem bAsed fisheries management).



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# 1. Introduction générale

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*Illustration : Sylvie Champagnat*

## 1.1 Cycle de vie des poissons marins et zones fonctionnelles halieutiques

### 1.1.1 Cycle de vie

Les espèces de poissons marins ont un cycle de vie caractérisé par trois phases successives, les stades larvaire, juvénile et adulte (Fig. 1.1, Harden Jones 1968). Chacun de ces stades est généralement associé à des habitats spécifiques et marqué par des taux de survie très différents.

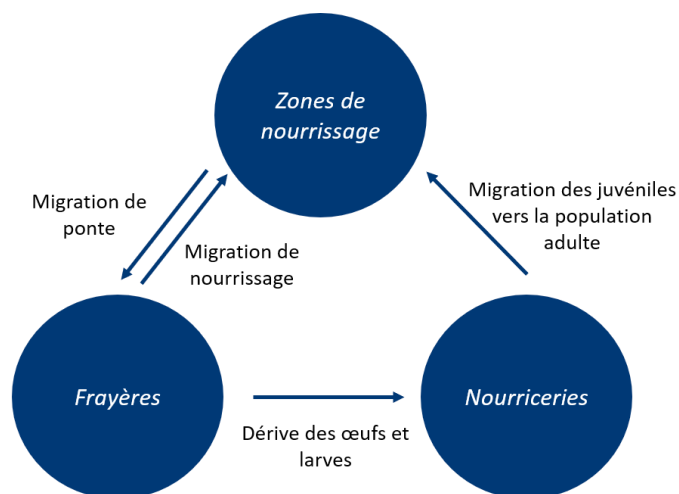


Figure 1.1 : Représentation schématique du cycle de vie d'une espèce d'intérêt halieutique (redessinée d'après Brown et al., 2018 et Harden Jones, 1968).

Le stade larvaire comprend le développement embryonnaire (œufs) et la vie larvaire (larves et post-larves) et s'étend de quelques jours à quelques mois en fonction des espèces. Durant cette période, les stades sont généralement planctoniques et soumis à de très forts taux de mortalité. Pour la plupart des espèces de poissons marins, le taux de survie de l'œuf au début du stade juvénile est de l'ordre de 1 pour 1000, voire moindre (Le Pape and Bonhommeau, 2015). En effet, à l'exception des poissons cartilagineux, et de quelques espèces comme les hippocampes, la stratégie de reproduction se caractérise par une forte fécondité (Juanes, 2007) suivi d'une forte mortalité naturelle (Gallego et al., 2012). Ce faible taux de survie, et l'absence de soin parental chez les poissons (Juanes, 2007) conditionnent leur forte dépendance aux conditions environnementales (Bakun, 1997; Houde, 2008). D'une part, la température (Gerber et al., 2014) et surtout la disponibilité en nourriture contrôlent la croissance, le développement et la survie des larves (match-mismatch hypothesis, Cushing 1995, Beaugrand et al. 2003). D'autre part, les courants marins déterminent la dispersion larvaire à large échelle (de l'ordre de 100 km pour les espèces non récifales, Nielsen et al. 1998, Sentchev & Korotenko 2004, Cowen et al. 2006, D'Aloia et al. 2015), et le succès de l'arrivée des larves dans des zones favorables à

la poursuite de leur cycle de vie (Bakun, 1997). Cette faible survie s'accompagne donc d'une forte variabilité en lien avec les aléas environnementaux au cours de la vie larvaire (Houde, 2008; Savina et al., 2016).

La période juvénile commence après la métamorphose et va jusqu'à la maturation sexuelle ; elle dure de quelques mois à plusieurs années en fonction de l'espèce. Elle se déroule sur des zones de nurricerie qui sont caractérisées par la quantité et la qualité des ressources trophiques (forte disponibilité alimentaire) qui maximisent la croissance et la survie (Islam and Tanaka, 2005; Tableau et al., 2016) mais aussi la présence de refuges et de protections qui diminuent la prédation (Manderson et al., 2000). Cependant le taux de survie de cette phase demeure faible pour une majeure partie des ressources marines : de 1 pour 100 à 1 pour 1000 (Le Pape and Bonhommeau, 2015). Pour une large partie des espèces marines de poissons exploités, les juvéniles sont très fortement concentrés sur des nurriceries côtières et estuariennes, propices à une croissance rapide, notamment du fait de leur forte productivité biologique (Brown et al., 2018; Seitz et al., 2014). Par exemple, sur les côtes françaises, les nurriceries de sole communes sont caractérisées par une faible bathymétrie (<5 m), des sédiments fins (sables fins et vases) et par l'influence forte des panaches estuariens (Le Pape et al., 2003). Les nurriceries de morue, quoique moins précisément définies, correspondent à des zones côtières et plusieurs études indiquent qu'elles pourraient être liées à la présence d'herbiers marins (notamment de *Zostera marina*, métaanalyse de Lilley & Unsworth 2014).

La phase adulte se partage entre période de reproduction et phase de nourrissage. Certaines espèces sont sémelpares, elles ne se reproduiront qu'une fois dans leur vie, c'est par exemple le cas de la plupart des espèces de saumons du Pacifique (genre *Oncorhynchus*), de l'aloise ou de la seiche. La plupart des espèces marines exploitées sont itéropares et se reproduisent plusieurs fois au cours de leur vie. Le nourrissage permet aux adultes de constituer les réserves nécessaires à la production de gamètes, et pour les adultes itéropares, de poursuivre leur croissance ralentie lors de la reproduction (Colloca et al., 1997; Enberg et al., 2008). Cette phase couvre la majeure partie de l'année durant laquelle les individus sont répartis sur les zones de nourrissage. Dépendante, dans une moindre mesure que les jeunes stades, de conditions abiotiques (conditions physico-chimiques) et biotiques (ressources trophiques, Compaire et al., 2016), cette phase de vie est généralement répartie sur des surfaces importantes, correspondant à l'aire de répartition de la population (Delage and Le Pape, 2016). La ponte correspond à une période définie, dont la durée varie selon les espèces, au cours de laquelle les individus matures se regroupent pour émettre leurs gamètes. Au même titre que les nurriceries, voire plus encore,

les frayères sont caractérisées par une très forte concentration d'individus sur un espace restreint (Palomera et al., 2007). L'emplacement des frayères résulte généralement d'un processus d'évolution long terme ayant conduit à la sélection de zones qui maximisent les chances de survie des œufs et larves : conditions physico-chimiques et d'alimentation favorables, mais aussi de dérive vers des secteurs de nurserie. Par exemple, les frayères historiques de morue de baltique sont localisées dans le bassin de Bornholm, et les bassins profonds de Gotland et Gdansk (Bagge et al., 1994) ; cependant le succès de fertilisation dépend aussi de conditions de température, de salinité et d'oxygène précises (Nissling and Westin, 1991). Ou encore, les frayères du hareng sont des zones côtières de faible profondeur, où la macrofaune végétale peut servir de substrat pour les œufs de ce poisson benthique (Kanstinger et al., 2018).

Les habitats occupés au cours des différents stades de vie étant, dans la majorité des cas, physiquement distincts, une ou plusieurs phases de migration ontogénique doivent avoir lieu. Ces phases transitoires peuvent être passives (œufs et larves) ou actives (juvéniles et adultes) et advenir entre des stades de vie ou entre deux phases saisonnières. On considère comme des voies de migration les couloirs empruntés par une espèce dans le but de rejoindre une zone hors de laquelle la poursuite de son cycle biologique n'est pas réalisable (Delage and Le Pape, 2016; Secor, 2015).

### 1.1.2 Zones fonctionnelles halieutiques

Le terme de Zone Fonctionnelle Halieutique désigne l'ensemble des eaux et substrats nécessaires à la reproduction, la ponte, l'alimentation et la croissance jusqu'à maturité (Magnuson-Stevens Fishery Act, 2007). On peut donc caractériser une zone fonctionnelle halieutique comme un habitat indispensable à la réalisation d'au moins une phase du cycle de vie d'une espèce exploitée (Delage and Le Pape, 2016; Wright, 1936). On peut identifier comme zones fonctionnelles halieutiques (cf. 1.1.1; Fig. 1.1) les frayères, les secteurs de dérive larvaire, les zones de nurserie, les zones de nourrissage des adultes et les voies de migration.

Chaque phase du cycle de vie conditionne le renouvellement de la population dans la zone fonctionnelle où elle le réalise et au-delà, sur l'aire de répartition de la population à ses différents stades. La dégradation d'une seule zone fonctionnelle est donc de nature à perturber l'accomplissement du cycle de vie et à altérer le renouvellement de la population. Cette altération peut avoir des conséquences sur l'exploitation halieutique, notamment la diminution de la ressource (Archambault et al., 2018; van de Wolfshaar et al., 2011).

### 1.1.3 Hiérarchisation de l'importance des zones fonctionnelles halieutiques pour la dynamique de population

La littérature très abondante sur les nourriceries montre que tous les habitats juvéniles ne sont pas équivalents en termes de contribution à la population adulte (Beck et al., 2001; Dahlgren et al., 2006; Minello et al., 2003). La qualité et la surface des habitats sont deux éléments complémentaires dans l'identification des habitats essentiels (Delage and Le Pape, 2016). Beck et al. (2001) mobilisent le concept de contribution relative pour identifier les nourriceries. Ils évaluent pour chaque habitat sa contribution par unité de surface au nombre d'adultes qu'il produira *in fine*. Cette définition renvoie au concept de qualité de l'habitat, qui est défini par quatre métriques : la densité, la croissance, la survie et la connectivité effective avec les habitats adultes. Dahlgren et al. (2006) élargissent la définition des nourriceries pour qu'elle intègre les habitats qui contribuent substantiellement à la population adulte même si leur contribution relative par unité de surface n'est pas des plus élevées. C'est le concept d'habitat efficace (Effective Juvenile Habitat, Dahlgren et al. 2006) qui incite à considérer tout habitat qui contribue fortement à la population. Cette définition fait ressortir la notion de surface.

Dans une optique de compréhension des facteurs contrôlant la dynamique de population et de gestion, il est important de hiérarchiser l'importance respective de chaque habitat au renouvellement d'une espèce donnée. On applique donc les concepts de surface et de qualité identifiés précédemment, non plus pour comparer des habitats propres à un même stade entre eux, mais pour identifier des couples stade-habitat particulièrement importants pour le renouvellement d'une espèce donnée. On appelle zones fonctionnelles halieutiques d'importance (ZFHI), les habitats présentant, lors d'une phase d'intérêt majeur du cycle de vie, une forte concentration d'individus sur une surface restreinte, et contribuant de manière significative au renouvellement des ressources (Dahlgren et al., 2006; Delage and Le Pape, 2016). Cette importance dépend de la concentration d'individus sur une zone fonctionnelle spatialement restreinte, indispensable pour atteindre le stade suivant (Delage and Le Pape, 2016).

Si l'on applique ce critère aux différentes zones fonctionnelles au cours du cycle de vie (cf. 1.1.1; Fig. 1.1), on peut considérer que les frayères et nourriceries sont des ZFHI. Les voies de migrations constituent également des ZFHI pour les espèces amphihalines et les espèces marines récifales des milieux tropicaux. Cependant, cette thèse s'est restreinte à l'étude des poissons marins des milieux tempérés et la suite du manuscrit n'approfondira donc pas le cas des voies de migrations.



## 1.2 De multiples facteurs de pression sur les populations marines exploitées

Les écosystèmes terrestres et aquatiques sont soumis à de multiples pressions d'origines naturelles et anthropiques. L'augmentation sans précédent de l'influence des pressions d'origines anthropiques directes ou indirectes sur l'ensemble de la planète mène à un constat : les activités humaines sont désormais la cause dominante des changements environnementaux observés (Steffen et al., 2007). Pour marquer ce tournant planétaire, la période géologique que nous vivons a été baptisée « Anthropocène » (Crutzen, 2016; Lewis and Maslin, 2015). Cette nouvelle ère géologique se caractérise notamment par le changement climatique et l'effondrement de la biodiversité (6<sup>e</sup> extinction de masse, Barnosky et al. 2011, Ceballos et al. 2015).

Les écosystèmes marins ne sont pas épargnés puisque 87 à 90 % de la surface des océans est impactée par les activités humaines (Halpern et al., 2015). Ces forts niveaux de pressions anthropiques ont mené à une dégradation des écosystèmes marins natifs partout dans le monde (Bulleri and Chapman, 2010; Halpern et al., 2008). Les populations marines sont donc exposées à de multiples facteurs de pressions tout au long de leur cycle de vie (Brown et al., 2018). Cependant, certains stades peuvent être associés spécifiquement à certaines pressions. C'est le cas du stade adulte, cible principale de l'exploitation par la pêche ; ou du stade juvénile de nombreuses espèces qui subissent dans leurs nourriceries côtières et estuariennes un fort niveau de pression anthropique (Archambault et al., 2018; Brown et al., 2018).

### 1.2.1 Prélèvement par la pêche

La pêche est généralement le premier facteur de pression retenu lorsque l'on évoque l'impact de l'Homme sur les écosystèmes marins (Hutchings, 2000; Jackson et al., 2001). Elle est considérée comme le principal facteur responsable du déclin des populations marines (Christensen et al., 2003; Myers and Worm, 2003; Pauly et al., 2005). Depuis 1970, l'abondance des poissons marins a globalement diminué de 38 % (Hutchings et al., 2010). Aujourd'hui, 35 % des stocks sont considérés comme surexploités à l'échelle planétaire (FAO, 2022). Les impacts de la pêche sont multiples : augmentation directe de la mortalité induisant une baisse de l'abondance et du potentiel reproducteur (Jackson et al., 2001) et de la diversité génétique (Smith et al., 1991), mais aussi évolution induite par la pression sélective (Conover, 2007; Olsen et al., 2004; Trippel, 1995). Ces impacts affectent la résilience des populations. Les effets de la pêche dépassent les seules espèces exploitées : captures accessoires (Alverson et al., 1994) et

rejets (Kelleher, 2005), altération de la structure des habitats par certains engins de pêche (Auster and Langton, 1999; Thrush et al., 1998; Turner et al., 1999), altération des réseaux trophiques (Österblom et al., 2007; Pauly et al., 1998). *In fine*, ces impacts sont susceptibles de mener à des changements profonds du fonctionnement des écosystèmes (Baum and Worm, 2009).

### 1.2.2 Climat et changement climatique

Le climat impacte les populations à différentes échelles temporelles : à moyen long terme (cycles climatiques et régimes océaniques, Francis et al. 1998) et à court terme (variabilité hydroclimatique interannuelle, Lehodey et al. 2006, Houde 2008). Ces fluctuations abiotiques engendrent des variations au sein des compartiments biotiques des écosystèmes ; elles modifient la disponibilité alimentaire, la compétition et la prédation pour une population donnée. Pour la gestion à court et moyen terme, la variabilité interannuelle des conditions hydroclimatiques est très structurante. En effet, la forte dépendance de la survie des premiers stades aux conditions environnementales (Hermant et al., 2010; Houde, 2008; Planque and Frédou, 1999) génère de fortes variations du recrutement, qui impactent la taille des populations et l'exploitation par la pêche.

En dehors des variations climatiques naturelles citées ci-dessus, le changement climatique affecte les écosystèmes marins (Brander, 2007; Walther et al., 2002) et ses conséquences vont augmenter (IPCC, 2022). Un premier niveau de modifications liées au changement climatique concerne les caractéristiques physiques et chimiques du milieu marin (IPCC, 2022) : élévation du niveau, augmentation des températures, modification de la circulation océanique, changement de la stratification verticale, acidification et désoxygénation. Ces changements engendrent des conséquences multiples sur la vie marine, plus ou moins difficiles à quantifier et à prédire. L'élévation des températures et les modifications de stratification verticale affectent considérablement la répartition latitudinale de la production biologique. Le réchauffement des eaux influence aussi le métabolisme des individus qui détermine les taux de croissance, mais aussi les capacités reproductives des poissons (Britten et al., 2016; Huang et al., 2021). Il peut aussi modifier les distributions spatiales des espèces en lien avec leurs préférences bioclimatiques (Cheung et al., 2009; Hastings et al., 2020; Raitos et al., 2010), ce qui peut avoir des conséquences sur la prédation et la compétition (Pinsky et al., 2013). Les vagues de chaleur marines, aux conséquences désastreuses pour les écosystèmes marins, augmentent aussi en fréquence et magnitude (Frölicher et al., 2018; Holbrook et al., 2019). Un

déclin global de la biomasse marine et de la production halieutique est attendu (Tittensor et al., 2021).

### 1.2.3 Dégradation des écosystèmes côtiers

Les populations et activités humaines sont concentrées sur la frange littorale et le long des cours d'eau (Halpern et al., 2008), ce qui engendre des perturbations au niveau des écosystèmes côtiers et estuariens (Lotze, 2006) souvent plus intenses que celles observées dans d'autres zones. Ces écosystèmes abritent aussi de nombreuses activités humaines (de Groot et al., 2012) ce qui augmente encore l'intensité des pressions anthropiques auxquelles ils sont soumis (Korpinen et al., 2012). Au cours de la dernière décennie, l'impact cumulé des pressions anthropiques était le plus élevé au niveau des écosystèmes côtiers, et le taux d'accroissement de ces pressions cumulées était aussi le plus fort (Halpern et al., 2019). En France, les écosystèmes côtiers sont ceux dont le statut de conservation est le moins bon (3 % en bon état écologique, source OFB 2020).

L'occurrence de ces pressions pour les espèces utilisant des habitats côtiers et évaluées par le CIEM a été recensée par Brown et al. (2018) dans une méta-analyse (Figure 1.2). La pression la plus commune est la pollution (75 % des espèces) ; suivent l'eutrophisation (58 %), les espèces invasives (54 %), le développement côtier (i.e., perte surfacique d'habitat, 42 %) et les impacts indirects de la pêche (17 %). Dans les paragraphes suivants, on détaille l'ampleur et les conséquences des pressions majeures sur les organismes marins.

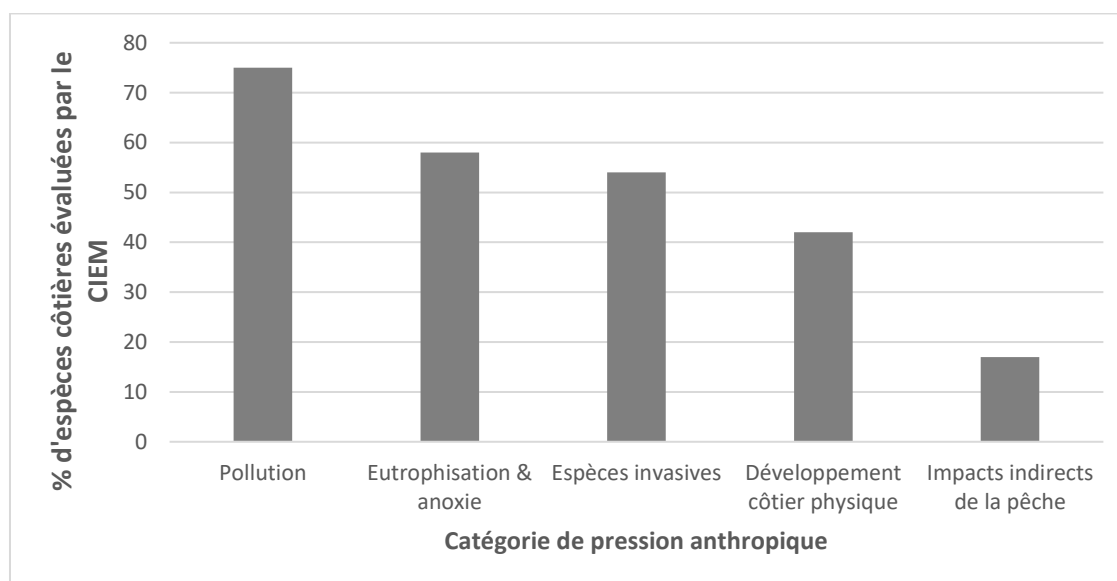


Figure 1.2 : Pourcentage (en nombre) d'espèces évaluées par le CIEM utilisant les zones côtières impactées par un type de pression anthropique (redessinée à partir de Brown et al. 2018).

### *1.2.3.1 Réduction surfacique et perte d'habitat*

Avec l'augmentation constante des populations humaines et leur agrégation proche de la côte (Airoldi and Beck, 2007; Kummu et al., 2016), l'espace pour les installations et activités est souvent gagné par artificialisation des espaces naturels, ce qui induit la perte et la fragmentation des zones côtières intertidales ou peu profondes. La construction de nouvelles structures (e.g., digues, extensions portuaires, éolien offshore ..) et leur maintien (e.g., dragage de maintenance des canaux de navigations) causent des dégradations, directes et à long terme (Grasso et al., 2018 ; Grasso & Le Hir, 2019) qui réduisent la surface des habitats côtiers. Dans l'estuaire de Seine, les modifications successives depuis 1850 ont supprimé 75 % des vasières estuariennes et transformé 33 % des habitats favorables aux juvéniles de sole en espaces terrestres (Rochette et al., 2010). Plus généralement, les grands deltas mondiaux perdaient 10 % de leur surface par décennie dans les années 2000 (Coleman et al., 2008). Ce processus n'est pas restreint aux secteurs estuariens, à l'échelle de l'ensemble des côtes anglaises et galloises, Stamp et al. (2022) ont estimé que la perte d'habitats intertidaux depuis 1843 était de 14 %, alors que la réduction des banquettes intertidales est estimée à 16 % au niveau planétaire depuis 1984 (Murray et al., 2019). Plus encore entre  $\frac{1}{4}$  et  $\frac{1}{3}$  des herbiers marins ont disparu à l'échelle planétaire (Dunic et al., 2021; Jones, 2014). Enfin les extractions de substrat (e.g., exploitation de sables et graviers, engraissement côtier via l'extraction de sable) impactent aussi directement les zones côtières (Borja et al., 2010; Peterson et al., 2014).

### *1.2.3.2 Polluants et agents toxiques*

Les activités anthropiques terrestres (industrie, extraction minière, agriculture) introduisent de nombreux xénobiotiques comme les pesticides, les métaux lourds et les composés chimiques industriels et pharmaceutiques qui se retrouvent dans les eaux de surface et contaminent les milieux estuariens et côtiers. Depuis 1970, la production de produits chimiques de synthèse a plus augmenté que les autres facteurs déterminants des changements globaux (e.g., émission de CO<sub>2</sub> ou changement d'usage des terres, Bernhardt et al. 2017). Wang et al. (2020) estiment à plus de 350 000 les composés chimiques de synthèse et leurs dérivés. Dans l'environnement ces produits chimiques sont omniprésents, notamment dans les écosystèmes aquatiques qui sont les réceptacles de l'ensemble des rejets produits par les activités humaines. Par exemple, plus de 400 composés chimiques sont trouvés dans trois rivières d'Europe centrale (Busch et al., 2016). Les xénobiotiques impactent les poissons et d'autres organismes à différents niveaux trophiques (Davis, 1999). Ils génèrent de multiples effets négatifs chez les organismes aquatiques : impact direct sur la survie (Gilliers et al., 2006; Le Pape et al., 2007), mais aussi

baisse de croissance, de capacité reproductive, de succès de migration (Feunteun, 2002; Houlihan et al., 1994; Kerambrun et al., 2012). *In fine* une baisse de densité des peuplements halieutiques est observée dans les zones polluées (e.g. -20 % de juvéniles de poissons marins dans les estuaires français contaminés, Courrat et al. 2009, Delpech et al. 2010), ce qui peut mener à un déclin de l'abondance des populations marines qui dépendent de ces habitats (Archambault et al., 2018) ainsi qu'à des pertes de biodiversité et de fonctionnalité des écosystèmes (Beketov et al., 2013; Desforges et al., 2018; Kidd et al., 2007).

La pollution plastique est aussi une menace environnementale planétaire majeure (Bhuyan, 2022; Eriksen et al., 2023) par son ubiquité et son augmentation constante (Gall and Thompson, 2015). La production mondiale de plastique était de 368 millions de tonnes en 2019 (Lebreton et al., 2017; Williams and Rangel-Buitrago, 2022), et environ 10 % de cette production se retrouve sous forme de déchet dans les écosystèmes aquatiques (Lebreton et al. 2017, Borrelle et al. 2020). La pollution plastique impacte directement la faune marine de grande taille par enchevêtrement ou ingestion : toutes les espèces de tortues sont impactées et plus de 50 % des espèces de mammifères et d'oiseaux marins (Gall and Thompson, 2015). Mais la fragmentation du plastique en particules plus petites (microplastique <5 mm ; nanoplastique <0,1  $\mu$  m) conduit aussi à des impacts sur des organismes de taille plus réduite. Ces particules se retrouvent dans un grand nombre d'organismes de tous niveaux trophiques (Berghlund et al., 2019): des copépodes (Cole et al., 2015) jusqu'aux requins (Parton et al., 2020). L'ingestion des micro- et nanoplastiques par les poissons cause blocages intestinaux, dommages physiques, altérations physiologiques et changements de comportement (Jovanović 2017, Gall & Thompson 2015, Marn et al. 2020). Les microplastiques peuvent aussi jouer le rôle de vecteur et augmenter l'exposition aux micropolluants organiques (Granek et al., 2020; Issac and Kandasubramanian, 2021).

#### *1.2.3.3 Eutrophisation et appauvrissement en oxygène*

Les activités terrestres peuvent induire des apports excessifs de nutriments, d'origines industrielle, urbaine (effluents de stations d'épuration) et agricole (lessivage des engrais organiques et minéraux). L'accumulation de ces nutriments excédentaires au niveau des milieux côtiers et des estuaires conduit à l'eutrophisation des habitats. Si une eutrophisation moyenne peut augmenter la production dans certains systèmes (Österblom et al., 2007), l'augmentation de la charge nutritive a généralement des effets néfastes sur les écosystèmes côtiers (Diaz and Rosenberg, 2008; Rabalais, 2015).

Une des conséquences les plus visibles de l'eutrophisation est l'augmentation incontrôlée de la production de macroalgues vertes, normalement régulée par une faible concentration en nutriments (Fletcher, 1996; Merceron et al., 2007). La prolifération massive d'algues vertes est en augmentation dans le monde en termes d'occurrence, d'abondance et de durée (Fletcher, 1996; Smetacek and Zingone, 2013; Ye et al., 2011; Zhou et al., 2015). Les habitats juvéniles et les frayères des ressources halieutiques peuvent être perturbés (Carl et al., 2008; Isaksson et al., 1994) et *in fine* les densités de poissons et la diversité spécifique sont impactées négativement (Le Luherne et al., 2016).

Mais, plus encore que les marées vertes, la principale conséquence de l'eutrophisation est une production phytoplanctonique excessive, qui conduit à des événements hypoxiques voire anoxiques (Diaz and Rosenberg, 2008; Rabalais, 2015). Ces phénomènes sont en augmentation à l'échelle planétaire (Diaz and Rosenberg, 2008) et accentués par le réchauffement climatique qui limite la disponibilité en oxygène (Pörtner and Knust, 2007). Les événements anoxiques ont de multiples conséquences directes et indirectes sur les organismes aquatiques ; ils modifient leur métabolisme, écologie et traits d'histoire de vie (Chabot and Dutil, 1999; Domenici et al., 2007; Herbert and Steffensen, 2005; Pichavant et al., 2001), jusqu'au fonctionnement global de l'écosystème (Breitburg, 2002; Diaz and Rosenberg, 2008; Wu, 2002). À l'échelle individuelle, on observe une réduction des taux de croissance et de survie des jeunes stades de poissons en période hypoxique (Maes et al., 2007; Petersen and Pihl, 1995; Teschner et al., 2010), et des mortalités massives en cas d'anoxie (Shimps et al., 2005) avec des réductions drastiques des habitats colonisés (Craig and Crowder, 2005; Powers et al., 2005). Les ressources halieutiques dépendantes des zones affectées sont considérablement réduites comme en Californie (Hughes et al., 2015) ou en Baltique (Kraufvelin et al., 2018).

#### 1.2.3.4 *Invasions biologiques*

Les écosystèmes côtiers et estuariens sont particulièrement enclins à l'introduction d'espèces non natives du fait des activités qu'ils accueillent. La navigation de bateaux de commerce maritime est une source majeure et croissante d'introduction d'espèces via le fouling, et le rejet des eaux de ballast (Nunes et al., 2014; Seebens et al., 2017, 2013). L'aquaculture (Grosholz et al., 2015; Nunes et al., 2014) et particulièrement les activités conchylicoles peuvent aussi être un vecteur d'introduction via le transfert de coquillages allochtones et de leurs épibiontes. Les espèces introduites prolifèrent facilement dans ces habitats productifs (Paavola et al., 2005). Elles impactent la productivité des habitats en captant les nutriments et la production primaire

(Arbach Leloup et al., 2008; Cloern, 1982) et modifient profondément leurs structures physiques, au détriment des ressources halieutiques (Kostecki et al., 2011; Le Pape et al., 2004).

#### 1.2.4 Interactions entre les différentes pressions

L'ensemble des pressions que les populations subissent dans les habitats côtiers n'agissent pas de façon isolée, mais interagissent pour former une combinaison complexe d'impacts cumulatifs (Halpern et al., 2008; Lotze, 2006; Vasconcelos et al., 2014). Au vu de la multiplicité des pressions et de la complexité du cycle de vie des populations marines, les effets peuvent se cumuler en termes de types de pression, mais aussi en termes d'exposition à différentes phases du cycle de vie des espèces (Brown et al., 2018). Les effets cumulés non linéaires (i.e. effets de plusieurs pressions supérieurs à la somme de leurs effets isolés) sont fréquents, voire majoritaires (Crain et al. 2008 ; Piggott et al. 2015 ; Côté et al. 2016), ce qui appuie l'intérêt d'étudier ces interactions.

#### 1.2.5 Les ZFHI - des habitats qui concentrent les pressions anthropiques

Les écosystèmes côtiers et estuariens sont indispensables pour de nombreuses espèces de poissons marins (Beck et al., 2001; Elliott and Hemingway, 2002). En Atlantique Nord-Est, 44 % des espèces commerciales pour lesquelles le CIEM délivre un avis, dépendent de ces milieux pour au moins un stade de vie ; ces espèces représentent 77 % des débarquements commerciaux en poids (Seitz et al., 2014). Pour une large partie (Brown et al., 2018), cette dépendance s'exerce au stade juvénile ( $\frac{1}{3}$  des espèces,  $\frac{2}{3}$  des débarquements) ou lors de la reproduction (17 % des espèces,  $\frac{1}{3}$  des débarquements). Des niveaux de dépendance comparables sont rencontrés ailleurs dans le monde (e.g., USA : Fodrie & Mendoza (2006), Lellis-Dibble et al. (2008) ; Golfe du Mexique : Peterson (2003) ; Indopacifique : Bradley et al. (2022) ; échelle mondiale : Brown et al. 2019).

Du fait des nombreuses pressions exercées sur les habitats côtiers, une forte proportion d'espèces de poissons utilisant ces habitats comme ZFHI sont impactées. Par exemple, en Atlantique Nord-Est, 92 % des espèces poissons qui utilisent les zones côtières et sont évalués par le CIEM, sont impactés par des pressions anthropiques, 71 % subissent des pressions de plusieurs types et 38 % sont impactés à de multiples stades. Si l'on considère les ZFHI d'importance mentionnées plus haut, 67 et 78 % de ces espèces sont impactées sur les habitats de frayère et de nurricerie, respectivement (Brown et al., 2018). À l'échelle planétaire, on estime que la fonctionnalité de nurricerie des milieux côtiers et estuariens a été réduite d'un

facteur au moins égal à deux du fait du cumul de ces pressions (Barbier et al., 2011; Worm et al., 2006).

D'autres ZFHI sont non côtières mais concentrent des pressions anthropiques. Un exemple connu est le ciblage par la pêche de frayères où certaines espèces forment des zones d'agrégations transitoires de pondeurs (Erisman et al., 2017; Grüss, 2014).

### **1.3 Variabilité de la réponse des populations en fonction des traits d'histoire de vie**

La réponse d'une population à des pressions dépend de ses caractéristiques intrinsèques et notamment des traits d'histoire de vie (THV) des individus (on considère ici les traits d'histoire de vie moyens des individus d'une population) : longévité, croissance, fécondité, migration, survie (Andersen et al., 2017). L'évolution des traits d'un organisme est une réponse adaptative aux variations environnementales et à la mortalité différentielle subie ou à l'allocation de ressources à certains stades de vie (Roff, 1992; Stearns, 1992). La théorie des histoires de vie étudie les forces qui façonnent les traits d'histoire de vie, la corrélation des traits entre eux et leur relation avec les contraintes écologiques. Elle vise aussi à prédire les réponses démographiques face à des perturbations aux échelles temporelles et spatiales variées (Winemiller, 2005).

A l'échelle des populations, l'articulation des THV au cours du cycle de vie contrôle notamment le taux de croissance des populations. Les THV peuvent fluctuer en réponse à des processus biotiques (prédation, compétition, parasitisme) ou abiotiques (variabilité environnementale au sein des habitats successifs). La variation des THV sous l'effet de processus densité-dépendants peut induire une baisse du taux de croissance de la population à forte densité et au contraire stimuler l'accroissement de la population à faible densité. Les processus densité-dépendants compensatoires exercent une rétroaction négative sur les populations et tendent donc à les stabiliser (Rose et al., 2001). Christensen et Goodyear (1988) définissent la réserve compensatoire comme l'excès de capacité reproductive lorsque la population est fortement réduite et que la mortalité compensatoire ne s'exerce pas. Cette réserve reflète la capacité d'une population à compenser les variations de mortalité, mais elle n'est pas nécessairement liée à la stabilité (variabilité interannuelle) de la population au cours du temps (Rose et al., 2001).

Plusieurs cadres conceptuels ont été développés pour expliquer les liens entre THV, capacité compensatoire et réponses des populations à des pressions comme les variations



environnementales (Winemiller, 2005), la mortalité par pêche (Horbowy and Hommik, 2022; Kindsvater et al., 2016b) ou des épisodes de mortalité pulsés (Langangen et al., 2023; White et al., 2022).

Les pressions mentionnées précédemment agissent à différents stades du cycle de vie des espèces marines, parce qu'elles sont spatialisées, tout comme les stades de vie associés à des ZFH distinctes. La sensibilité d'une espèce à une pression donnée est spécifique du stade impacté (durée et survie de la transition, importance au cours de son cycle de vie) et dépend du niveau de concentration des individus dans la ZFH impactée par la pression. L'exploration du lien entre cycle, stratégies d'histoire de vie et conséquences des dégradations anthropiques sur les ZFHI pour les populations est nécessaire pour aborder ces aspects de façon générique.

## **1.4 Stratégie de modélisation pour quantifier l'impact des pressions exercées sur l'habitat pour les populations de poissons marins exploités**

L'impact d'un large panel de pressions anthropiques au niveau des habitats sur les poissons marins est de longue date analysé au niveau local, à l'échelle des individus, pour un stade vie donné (Beck et al., 2001; Heck et al., 2003; Minello et al., 2003; Vasconcelos et al., 2014). En revanche, la quantification de ces impacts à l'échelle des populations, à la distribution large et variable au cours de leur cycle de vie, reste très lacunaire (Brown et al., 2018) et limitée à de rares cas d'étude (Lipcius et al., 2019; Litvin et al., 2018; Nagelkerken et al., 2015).

Pour comprendre la dynamique des populations et leurs réponses à de multiples pressions (par exemple celles exercées sur les ZFHI), la modélisation est un outil incontournable. En effet elle permet de donner corps à un problème complexe et de proposer une représentation simplifiée des différents processus. Le modèle sert aussi à transformer les connaissances et les données en informations utilisables pour diagnostiquer l'état des populations et prédire leur évolution sous divers scénarios de fluctuations environnementales ou de gestion (Bernier et al., 2000; Legay, 1997; Roqueplo, 1997).

### 1.4.1 Quel grain biologique - modèle IBM ou modèle de population ?

La modélisation en écologie requiert des hypothèses simplificatrices. Une des questions que l'on peut se poser pour la modélisation d'une population est la suivante : la représentation des individus est-elle nécessaire, ou peuvent-ils être agrégés en une variable d'état unique ? Et donc est ce que la représentation des caractéristiques spécifiques de chaque individu (physiologiques,

comportementales, génétiques et phénotypiques) est utile pour la question que l'on cherche à investiguer (DeAngelis, 2018) ?

Les modèles individus centrés (individual based model, IBM) représentent une population comme composée d'individus (ou de super individus). Leur capacité à intégrer la variabilité inter-individuelle est leur atout majeur. Ils peuvent incorporer de nombreux mécanismes à l'échelle individuelle (DeAngelis & Grimm 2014, DeAngelis 2018), représenter les variations des traits des individus en fonction de l'environnement qu'ils expérimentent, ou représenter de façon mécaniste l'impact de l'habitat tel que mesuré lors d'expérience en laboratoire ou sur le terrain (Lipcius et al., 2019). Le stade de dérive larvaire est souvent modélisé avec des IBM pour évaluer l'influence des processus hydrodynamiques sur le devenir des larves dans un milieu hétérogène du fait de leur forte dispersion (Rochette et al., 2012; Savina et al., 2016). Les modèles DEB (Dynamic Energy Budget) sont un cadre de modélisation unifié pour représenter un individu en termes d'acquisition de ressources et d'allocation de celle-ci à diverses fonctions (maintenance, croissance et reproduction) ainsi que les conséquences pour ses THV (Kooijman, 2010). Ils sont souvent utilisés dans le cadre d'approches IBM pour extrapoler à une population des résultats d'expériences en laboratoire, par exemple l'exposition à des xénobiotiques ou à des conditions anoxiques (Lavaud et al., 2019; Mounier et al., 2020). Ces IBM à la résolution fine peuvent aussi être utilisés comme sous-modèles pour représenter des stades spécifiques au sein d'un modèle intégré de population (e.g. stade de dérive larvaire, Rochette et al. 2013).

Les étapes de calibration et de validation des IBM nécessitent de nombreuses données, à l'échelle individuelle et populationnelle, difficilement accessibles pour les populations marines. L'existence et la fiabilité de ces données déterminent le domaine d'application du modèle, la confiance dans son réalisme et sa capacité à représenter la réponse des populations à des scénarios (Rose et al., 2015). Les analyses et interprétations des résultats issus de modèles IBMs sont donc dans l'ensemble plus difficiles que ceux issus de modèles de populations (DeAngelis and Grimm, 2014). Ces contraintes ont aiguillé notre choix de modèle vers un modèle de population, plutôt qu'un IBM.

La question du grain biologique peut se poser à une résolution supérieure, c'est-à-dire pour la structure en âge et en stades de la population. Modéliser une population non structurée revient à faire l'hypothèse que les caractéristiques de celle-ci sont identiques au cours des différents stades de vie. Quoique plus simple et moins demandeuse en données, cette représentation ne permet pas le traitement des cycles de vie complexes associés à l'utilisation de différents

habitats. Elle est d'ailleurs plus rarement utilisée dans la gestion ou pour la prise de décision, même si elle peut s'avérer utile pour des populations particulières dépendantes d'un habitat spécifique (e.g., population d'huître dans la baie de Chesapeake, Lipcius et al. 2015).

Ainsi, une solution intermédiaire entre la modélisation individuelle et un modèle de population non structuré apparaît comme appropriée pour analyser la réponse d'une population au cycle de vie structuré en stades distincts aux pressions vécues sur des habitats qui changent au cours du cycle ontogénique.

#### 1.4.2 Modèle de population structuré en âge et/ou en stades

##### *1.4.2.1 Modèle en temps continu ou discret*

Plusieurs catégories de modèles émergent selon la représentation qu'ils font du temps. Une première catégorie regroupe des modèles en temps continu utilisant une ou plusieurs ODE (Ordinary Differential Equation). Ces modèles permettent d'analyser analytiquement la dynamique de population. Ils sont souvent utilisés pour explorer les conditions d'existence d'états stables multiples. Les modèles à pas de temps discrets sont plus répandus, notamment parce que les données sont souvent disponibles sur un pas de temps discret, mais aussi par simplicité mathématique.

##### *1.4.2.2 Modèle d'évaluation de stock : impact de la pression de pêche sur la population adulte*

Les modèles de dynamique de population de type « analyse de cohortes » (Shepherd, 1999) sont largement utilisés dans le cadre de l'évaluation des stocks de poissons marins. Ils visent à évaluer l'état d'une population exploitée à un temps donné (e.g., une année) et éventuellement à réaliser des projections à court terme, afin de fournir des avis de gestion. Dans ce cadre, la pêche est considérée comme le principal (si ce n'est le seul) impact anthropique appliqué à la population, et en général seule la fraction exploitable de la population est représentée.

##### *1.4.2.3 Boucler le cycle avec une relation stock-recrutement : indispensable, mais complexe*

Les approches de modélisation par cohortes ne permettent pas de représenter la dynamique du renouvellement des populations. Il semble naturel de chercher à lier le recrutement (l'abondance des juvéniles issus de la reproduction) à la biomasse féconde adulte qui l'a produit, c'est l'objectif des relations stock-recrutement (SR). Ces relations sont un enjeu majeur de la dynamique des populations et de son application aux sciences halieutiques car elles permettent de représenter la propagation des effets de différentes pressions sur la dynamique

du renouvellement de la population et ainsi de simuler la dynamique d'une population sur plusieurs générations. Elles permettent aussi d'estimer des points de références biologiques (Hilborn and Walters, 1992; Punt et al., 2001), qui sont indispensables à la gestion. Cependant, au vu des caractéristiques des premiers stades de vie (*cf.* 1.1.), le recrutement est très fluctuant, en lien avec la variabilité (peu prévisible) des facteurs de l'environnement qui contrôlent la faible survie des jeunes stades (Bakun, 1997; Houde, 2008). La paramétrisation des relations SR est donc difficile car les séries temporelles de données d'abondance de recrues sont souvent courtes et de surcroît très incertaines (Le Pape et al., 2020). Elles sont peu informatives pour estimer des valeurs de paramètres SR (Burrow et al., 2013; Myers and Barrowman, 1996; Zhou, 2007).

De plus en plus d'évaluations de stock reposent sur des modèles intégrés qui permettent l'intégration d'un grand nombre de séries temporelles de données (Carvalho et al., 2021; Hoyle et al., 2022; Maunder and Punt, 2013; Punt et al., 2020). Ces modèles intègrent généralement une relation stock-recrutement dont les paramètres sont estimés lors de la calibration du modèle. Certains développements récents permettent d'intégrer des données environnementales comme variables explicatives de certains processus, notamment le recrutement (du Pontavice et al., 2022; Stock and Miller, 2021).

#### 1.4.2.4 Modèles de cycle de vie

Les modèles de dynamique de population structurés en âge et en stades sont des outils adaptés pour représenter le cycle de vie. Plusieurs modèles structurés en âge et/ou stades ont investigué les effets de la qualité et de la quantité d'habitats sur la dynamique de population. Par exemple en exprimant les paramètres spécifiques de certains stades comme des fonctions des caractéristiques des habitats, comme la température (Honea et al., 2009; Scheuerell et al., 2006; Stelzenmüller et al., 2010), le débit d'une rivière (Ruiz et al., 2009; Scheuerell et al., 2006), la structure (Honea et al., 2009; Mizerek et al., 2011; Scheuerell et al., 2006) ou la taille (Camp et al., 2020) de l'habitat, l'oxygène (Rose et al., 2018), les xénobiotiques (Ono et al., 2019), ou la combinaison de facteurs environnementaux (Rahikainen et al., 2017).

#### 1.4.2.5 Approche « data driven » (statistique) vs « process driven » (hypothèses)

Les modèles peuvent être classés sur un gradient allant de modèles empiriques à des modèles plus mécanistes. Les approches empiriques s'appuient principalement sur l'information contenue dans les données, et utilisent souvent des approches statistiques pour s'ajuster aux données ; on peut donc les qualifier de « data driven ». Les modèles mécanistes reposent sur la

formalisation mathématique d'hypothèses sur les processus démographiques et écologiques. A ce titre ils sont plutôt qualifiés de « *process driven* ».

Les données de suivi utilisées pour déterminer les tendances des populations de poissons (e.g., CPUE) incluent rarement un suivi simultané de la quantité et qualité de l'habitat à des échelles spatiales permettant l'inclusion de ces variables d'habitat comme variables explicatives. Et même lorsque ces données existent, les approches d'analyses inférentielles restent uniquement corrélatives et ne permettent pas de dresser des conclusions, car d'autres facteurs interviennent.

Les approches expérimentales permettent de comprendre comment les attributs de l'habitat influencent la physiologie, le comportement, et aussi les taux vitaux (survie, croissance, reproduction). Cependant les données sont souvent générées par des expériences à petite échelle, ou en laboratoire, au niveau d'un groupe limité d'individus non représentatif de la population entière, et qui dépend du design expérimental.

En intégrant les relations entre les caractéristiques de l'habitat et leurs effets sur les taux vitaux, la modélisation mécaniste peut servir de pont entre les études réductionnistes à petite échelle et les fluctuations observées par les programmes de suivi à plus large échelle. Les études mécanistes réductionnistes peuvent servir à formuler des relations, et les programmes de suivi à évaluer (e.g. calibrer ou valider) le modèle à l'échelle de la population.

#### 1.4.3 Un bilan sur la modélisation de l'impact de l'habitat

Une revue des modèles permettant de quantifier l'impact des habitats sur la dynamique des populations marines exploitées (Lipcius et al., 2019) permet de dresser un constat général : ces modèles sont peu nombreux, l'intégration de l'habitat est rare dans l'analyse de la dynamique de population, et quasi inexistante dans l'appui à la gestion.

D'autre part, une très large majorité des trop rares modèles qui existent est « *data driven* ». Ces approches utilisent la statistique pour s'ajuster aux données et nécessitent une grande quantité de données pour être calibrées et/ou validées. Cela implique que ces modèles sont très spécifiques du cas d'étude et difficilement transférables à d'autres populations. Ceci est une limite forte à leur dissémination et donc à la prise en compte des habitats et des pressions qu'ils subissent dans les décisions de gestion.

## 1.5 Questions de recherche

Les parties précédentes ont souligné la forte dépendance des poissons marins aux écosystèmes côtiers et estuariens qui sont des ZFHI pour de nombreuses espèces exploitées, mais aussi le fort niveau de dégradation de ces habitats du fait des activités anthropiques. La quantification de l'impact de ces pressions humaines à l'échelle des populations reste cependant rare (Lotze, 2006 ; Sundblad & Bergström, 2014 ; Vasconcelos et al., 2014), notamment parce qu'il est difficile de passer de l'échelle locale et individuelle des pressions subies à des conséquences sur l'ensemble de la population, à une échelle spatiale bien plus large (Lipcius et al., 2019).

Or ces connaissances sont essentielles pour guider les actions de gestion dans un contexte où des compromis entre de multiples activités humaines sont nécessaires (Rönnbäck et al., 2007 ; Rose et al., 2018 ; Sundblad & Bergström, 2014). Les approches de modélisation existantes sont généralement très spécifiques d'un cas d'étude et très coûteuses en données. Cela implique qu'elles sont difficilement transférables à d'autres populations, ce qui limite fortement leur dissémination et la prise en compte des habitats dans les décisions de gestion.

Pour généraliser la quantification de ces pressions sur les habitats, il serait utile de développer une approche mécaniste plus générique et « process-driven » c'est-à-dire (i) avec une structure en âge et en stades suffisamment flexible pour représenter des populations aux histoires de vie très variables ; (ii) dont une paramétrisation des scénarios d'habitat puisse s'appliquer au niveau de différents stades de vie ; (iii) dont la paramétrisation repose sur des données relativement accessibles pour un grand nombre d'espèces.

Le présent travail de thèse a cherché à développer des approches de modélisation visant à quantifier de l'impact des pressions anthropiques subies par les ZFHI sur la dynamique des populations de poissons marins exploités. Plus précisément, ce travail a pour objectif d'apporter des éléments de réponse aux questions suivantes :

- (1) Comment quantifier de façon réaliste l'impact de la dégradation des habitats juvéniles sur la dynamique d'une métapopulation ?

Cette première question a été abordée au travers d'un exemple spécifique (la métapopulation de sole de la Manche Est) et de scénarios coconstruits de façon multidisciplinaire. Cette démarche très « data driven » a servi de point d'ancrage pour développer une approche de modélisation plus générique et « process driven » dans la suite de la thèse.

(2) Les différentes espèces d'intérêt halieutique sont caractérisées par des THV variés. La réponse des populations aux pressions subies au niveau des nourriceries dépend-elle de ces traits ? Quels sont les THV qui contrôlent cette réponse ?

Pour répondre à ces questions, nous avons développé une approche de modélisation structurée par stades et par âge suffisamment flexible pour pouvoir représenter différentes stratégies de vie et proposé une paramétrisation générique de scénarios de dégradation de l'habitat (en surface et en qualité) sur les nourriceries.

(3) Quel serait l'impact de la restauration de nourriceries côtières communes à plusieurs populations d'espèces exploitées par les pêcheries françaises et européennes, à l'échelle d'une unité de gestion ?

Pour investiguer cette question, le modèle a été appliqué à quatre espèces d'intérêt halieutique de la Manche Est présentant des traits d'histoire de vie et des degrés de concentration sur les secteurs de nourricerie contrastés (sole, plie, merlan, bar). Des scénarios de restauration de surface et de qualité spécifiques des nourriceries côtières de Manche Est ont été conçus et simulés.

(4) Quel est l'impact relatif de pressions anthropiques sur les nourriceries et les frayères pour une population ? Quelle est la réponse des populations lorsque ces pressions à différents stades de vie se combinent ? Les réponses dépendent-elles des traits d'histoire de vie des populations ?

Pour explorer ces questions, le modèle générique développé a été étendu pour évaluer l'impact de l'hypoxie sur les nourriceries et les frayères des trois espèces exploitées de Mer Baltique aux traits d'histoire de vie contrastés (plie, morue, hareng). Des scénarios marginaux ont été simulés pour évaluer les réponses spécifiques à la perturbation de l'habitat au sein des nourriceries et des frayères, puis cumulés pour appréhender l'impact des dégradations de l'habitat au sein des ZFHI tout au long du cycle de vie des espèces.

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## **2. Modélisation de l'impact de la restauration locale d'une nourricerie estuarienne sur la dynamique d'une métapopulation**

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*Illustration : Sylvie Champagnat*



## Introduction du chapitre 2

Les écosystèmes côtiers et estuariens abritent des habitats de nurricerie pour de nombreuses espèces de poissons exploités (Beck et al., 2001; Lefcheck et al., 2019; Litvin et al., 2018; Seitz et al., 2014), mais font face à des forts niveaux de pressions anthropiques (Halpern et al., 2008). Bien que l'impact de ces pressions locales sur les juvéniles soit largement documenté (Brown et al., 2018), leurs conséquences à l'échelle des populations sont encore rarement quantifiées (Lipcius et al., 2019; Vasconcelos et al., 2014).

Le chapitre 2 de cette thèse évalue comment les multiples pressions anthropiques au niveau d'une nurricerie estuarienne affectent la dynamique de métapopulation de la sole commune de Manche Est. Ce stock, composé de trois sous-populations (Randon et al., 2021), dépend des habitats côtiers et estuariens de Manche Est, et notamment de l'estuaire de Seine, pour sa croissance juvénile (Riou et al., 2001; Rochette et al., 2010). L'estuaire de Seine a subi d'importantes modifications morphologiques causées par des constructions portuaires et des travaux de chenalisation. Depuis 1850 ce sont 33 % des habitats favorables aux juvéniles de sole qui ont été artificialisés (Avoine et al. 1981, Ducrotoy & Dauvin 2008, Rochette et al. 2010). Par ailleurs, plusieurs décennies de forts niveaux de contamination chimique (Barjhoux et al., 2018; Lellis-Dibble et al., 2008), ont provoqué d'importantes altérations de la qualité des habitats juvéniles (Amara et al., 2007; Courrat et al., 2009; Gilliers et al., 2006).

Dans cette étude, nous développons une approche qui permet d'évaluer l'effet conjoint de la réduction locale de quantité et de qualité d'une nurricerie estuarienne sur la productivité et le potentiel d'exploitation du stock de sole de Manche Est. Pour cela, nous utilisons un modèle de cycle de vie structuré spatialement, qui permet de simuler la dynamique de métapopulation et de quantifier l'impact des pressions anthropiques locales subies par les juvéniles, concentrés au sein de nurriceries d'emprises spatiales restreintes, sur le renouvellement global du stock. En amont de ce projet de thèse (Savina-Rolland et al., 2021), le modèle, basé sur le travail d'Archambault et al. (2016), a été complété par des estimations concernant la structure spatiale de la métapopulation (Lecomte et al., 2020; Randon et al., 2021) et ajusté aux données les plus récentes dans un cadre hiérarchique bayésien pour estimer les paramètres. Ce modèle est utilisé pour simuler des scénarios de restauration de la nurricerie de l'estuaire de Seine, coconstruits dans une approche multidisciplinaire (hydrosédimentologie, chimie, écotoxicologie et écologie), portant sur l'impact de deux pressions anthropiques :

- (1) L'artificialisation et le dragage de l'estuaire et leurs impacts sur les processus de transport sédimentaire et la surface de nurricerie résultante ;
- (2) L'exposition de l'estuaire de Seine à de forts niveaux de pollution chimique et les conséquences sur la survie et fécondité future des juvéniles de sole.

Les effets de l'augmentation des surfaces et de la qualité de la nurricerie de Seine ont été évalués séparément puis conjointement. La représentation de la structure de métapopulation au sein du modèle a permis d'évaluer les conséquences de chaque scénario à l'échelle de la sous-population dépendante de l'estuaire de Seine et à l'échelle de la Manche Est.

## Multidisciplinary assessment of nearshore nursery habitat restoration for an exploited population of marine fish

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J. Champagnat<sup>1,\*</sup>, J. B. Lecomte<sup>1,2</sup>, E. Rivot<sup>1</sup>, L. Douchet<sup>1</sup>, N. Martin<sup>1</sup>, F. Grasso<sup>3</sup>, F. Mounier<sup>4</sup>, P. Labadie<sup>5</sup>, V. Loizeau<sup>6</sup>, N. Bacq<sup>7</sup>, O. Le Pape<sup>1</sup>

<sup>1</sup>DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, IFREMER, INRAE, 35042 Rennes, France

<sup>2</sup> DECOD (Ecosystem Dynamics and Sustainability), IFREMER, INRAE, Institut Agro, 44311 Nantes, France

<sup>3</sup> DYNECO/DHYSED, Hydro Sediment Dynamics Lab, IFREMER, 29280 Plouzané, France

<sup>4</sup> DataReportR, 33610 Canéjan, France

<sup>5</sup> Univ. Bordeaux, CNRS, UMR 5805 EPOC, 33405 Talence, France

<sup>6</sup> PFOM/LARN, LEMAR UMR 6539, IFREMER, 29280 Plouzané, France

<sup>7</sup> GIP Seine-Aval, 76176 Rouen, France

### Abstract

Nearshore habitats are essential for many marine fish species but are subject to anthropogenic stressors. Assessing the consequences of essential fish habitat degradation on population dynamics and productivity is challenging. We address this by focusing on a metapopulation of the common sole *Solea solea*, a high-value, exploited flatfish in the Eastern English Channel (EEC). Multidisciplinary data and expert knowledge were compiled to build feasible restoration scenarios for the availability of suitable habitat (measured in habitat surface extent) and chemical quality of juvenile habitats in the highly anthropized Seine estuary, the largest estuary and potentially a sole nursery area of primary interest in the EEC. Scenarios were simulated with a spatially structured life-cycle model to investigate the consequences of local restoration on restricted nursery habitats in the estuary. Restoring surface extent and habitat quality in the Seine estuary dramatically enhances spawning stock biomass (+18%) and fishery catches (+13%) in the EEC. Restoring habitat quality has a greater effect than restoring habitat surface. Because of the low connectivity between subpopulations of sole in the EEC, most of the local

restoration benefits remain regional and affect the subpopulation that directly depends on the Seine nursery, with only moderate spread to the entire EEC. Our study emphasizes the utility of spatial simulation models for integrating multidisciplinary knowledge and assessing the consequences of local anthropogenic pressures at wider metapopulation scales. We provide a means of building robust methods to assess the benefits of nearshore habitat restoration for enhancing fish populations and fisheries and integrate habitat value into the sustainable management of exploited species.

KEY WORDS: Common sole · *Solea solea* · Life-cycle model · Population dynamics · Anthropogenic pressures · Coastal degradation · Essential fish habitat

## 2.1 Introduction

Nearshore ecosystems host essential habitats for numerous fish species (Lellis-Dibble et al., 2008; Seitz et al., 2014). In particular, estuarine and coastal ecosystems provide food and refuge and are considered nurseries for the juveniles of many exploited fish stocks (Beck et al., 2001; Lefcheck et al., 2019; Litvin et al., 2018). For instance, one-third of the commercially important species for which advice is provided by the International Council for the Exploration of the Sea (ICES) in the Northeast Atlantic uses coastal and estuarine systems as nursery grounds, and they account for two-thirds of the commercial landings (in weight; Seitz et al. 2014, Brown et al. 2018). While they represent essential nursery habitats, coastal and estuarine areas also face high levels of anthropogenic pressures (Halpern et al., 2008). Near populated areas, the need for new space for human activities often results in the loss of nearshore habitat, and degradation of the quality of remaining areas due to eutrophication, chemical pollution and introduction of non-native species, for example. The vast majority of commercially important fish species using coastal and estuarine nurseries experience cumulative anthropogenic impacts notably through the degradation of both the quantity and quality of these habitats (Brown et al., 2018). However, despite the well-documented impacts of local anthropogenic disturbances on the juveniles of nearshore nursery dependent species (Brown et al., 2018), the consequences of these impacts at the population scale are still poorly understood and urgently need to be quantified (Lipcius et al., 2019; Vasconcelos et al., 2014) and integrated into management (Kraufvelin et al., 2018).

The common sole *Solea solea* is a widely distributed flatfish species in the eastern Atlantic and adjacent seas, with high commercial interest. The Eastern English Channel (EEC; Fig. 2.1) stock of common sole serves as a relevant case study to assess how multiple local anthropogenic

pressures on nearshore juvenile habitats can affect population dynamics and related fisheries at a wider scale. For this flatfish population, reproduction takes place in early spring. After hatching, pelagic larvae drift towards shallow coastal and estuarine nursery grounds (Rochette et al., 2012), where individuals settle as benthic juveniles for approximately 2.5 yr (Riou et al. 2001, Rochette et al. 2010, Fig. 2.1). At sexual maturity, soles move to wider and deeper feeding and spawning areas (Archambault et al., 2016; Rochette et al., 2013). The Seine estuary (Fig. 2.1) is one of the nursery areas for the common sole in the EEC (Riou et al., 2001). It is a highly anthropized area with degradation of both surface area and habitat quality that impacts sole juveniles (Le Pape et al., 2007). This estuary has experienced important morphological changes from channel dredging and the building of dikes and harbors, with a resulting substantial reduction in suitable shallow muddy nursery areas (Rochette et al., 2010). In addition, this area has been facing high levels of chemical contamination for decades (Barjhoux et al., 2018; Lellis-Dibble et al., 2008), causing reductions in habitat quality for juveniles (Amara et al., 2007; Courrat et al., 2009; Gilliers et al., 2006).

In this study, we developed an approach that enables the assessment of the cumulative effects of reductions in both local juvenile habitat extent and quality on sole stock productivity in the EEC. This study relies on a spatially structured life-cycle model used to simulate the dynamics of this metapopulation and quantify the impacts of natural and anthropic stressors on population renewal. Specifically, the model was used to assess how local anthropogenic impacts faced by juveniles in the Seine estuary affect stock productivity in the EEC using simulations of restoration scenarios for the Seine nursery grounds. The scenario design allowed the integration of multidisciplinary knowledge, through collaboration among scientists from several fields (hydrosedimentology, chemistry, ecotoxicology and ecology), to determine the potential impacts of 2 main anthropogenic pressures on the nursery function of this estuary:

- (1) Land reclamation and channel dredging and their impacts on mud and sand transport processes for nursery habitat surface extent (henceforth, surface); and
- (2) Exposure to high levels of pollutants in the Seine estuary and their consequences for the survival and future fecundity of juvenile sole.

Marginal effects of structural and chemical improvements to the nursery were evaluated as well as cumulative impacts. The metapopulation structure of the population model allowed an assessment of the consequences of each restoration scenario at the scale of the subpopulation that directly depends on the Seine estuary and at the scale of the whole EEC.

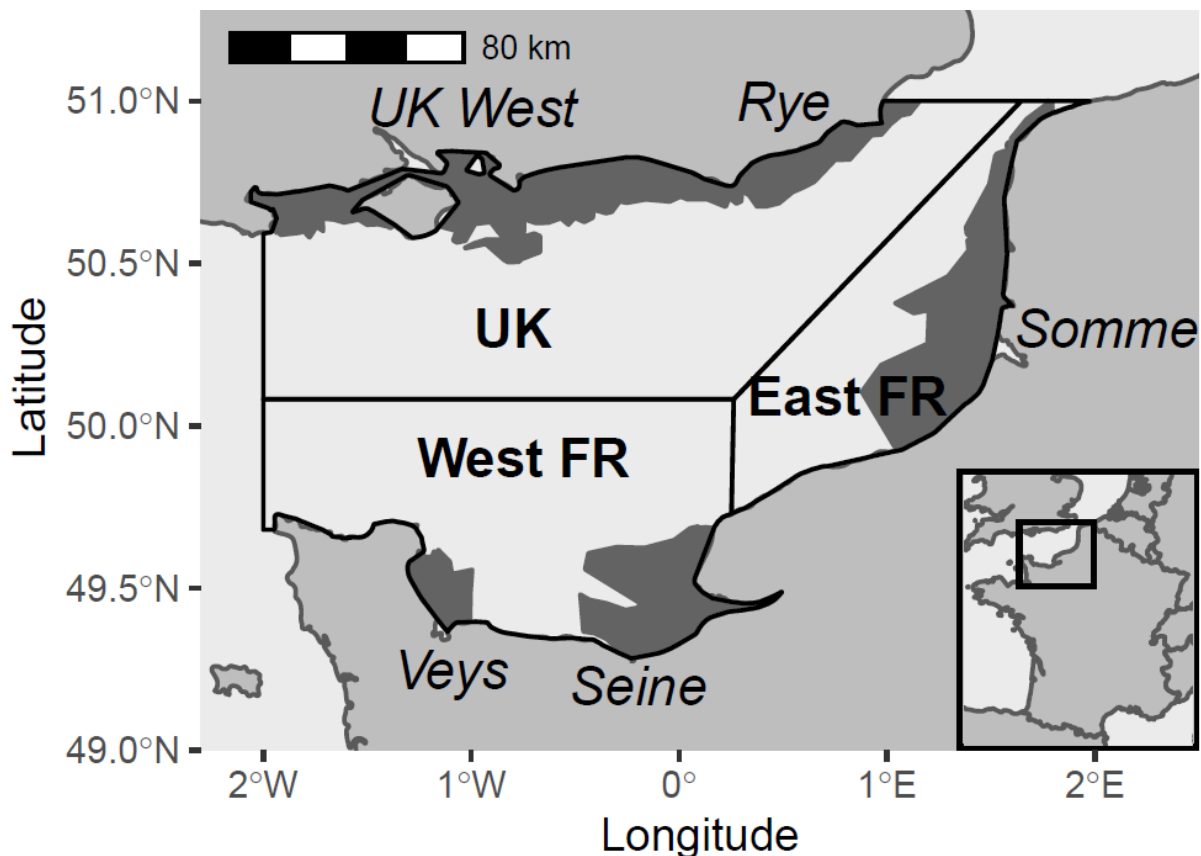


Figure 2.1. Study area with the 3 components of the Eastern English Channel sole population (UK, West FR, East FR) and the 5 coastal and estuarine nursery sectors (in dark grey with the adjacent related name in italics). Inset: general location of the study area in Western Europe

## 2.2 Materials and methods

### 2.2.1 Life-cycle model of the EEC sole stock

The metapopulation dynamics in the EEC were simulated based on the spatially structured and age structured life-cycle model developed by Archambault et al. (2016) and were updated with data up to 2019 and new recent information about fish connectivity between subpopulations. The life-cycle model (Fig. 2.2) involved the following key structural assumptions. (1) The spatial structure of the EEC sole populations relies on the previously identified 3 subpopulations (UK, East France (FR hereafter), and West FR) and 5 nursery areas for juveniles, each belonging to a subpopulation (UK West and Rye: UK; Somme: East FR; and Seine and Veys: West FR) (Fig. 2.1). (2) Eggs and larvae are transported from each of the 3 spawning areas and die or settle in 1 of the 5 nursery sectors (Rochette et al., 2012). The drift and survival matrix was parameterised from the outputs of a biophysical model that provided larval survival and dispersal from spawning areas to the 5 nursery sectors (Savina et al. 2016, 4 km horizontal

resolution). (3) Within each nursery sector  $i$ , settled larvae experienced compensatory density-dependent mortality between settlement and the end of the growth period of the age-0 juveniles. Density dependence was modelled through nursery specific Beverton-Holt relationships parameterised with  $\alpha_i$  the maximum survival rate, and  $K_i$ , the carrying capacity per unit of surface (Archambault et al., 2014; Iles and Beverton, 2000). (4) Older juveniles experience natural mortality (i.e. encompassing all mortality sources except fishing) until they reach age 2, then leave nurseries and disperse among the 3 subpopulations of adult fish. (5) The 3 subpopulations consist of 14 age classes between the ages of 2 and 15 yr that experience natural and fishing mortality. (6) Fish aged between 2 and 15 yr move among the 3 subpopulations. Connectivity was parameterised based on new information about low adult connectivity that was determined by state-space modelling of multidecadal mark–recapture data (Lecomte et al., 2020), analysing growth and demographic rates (Randon et al., 2018), markers at the individual scale (genetics and morphometry of otoliths; Randon et al. 2020), and conducting a holistic analysis combining these various methods (Randon et al., 2021). Extreme *a priori* hypotheses on metapopulation structure impacts on adult-mediated connectivity (i.e. no interregional connectivity after larval drift/full mixture) previously proposed by Archambault et al. (2016) were therefore replaced by a connectivity matrix estimated from mark–recapture data (Lecomte et al., 2020) that disperses individuals of age 2 to 15 yr annually between the 3 subpopulations with a low, but non-null, mixing rate (Table S2 in Supplement 1 at [www.intres.com/articles/suppl/m680p097\\_supp.pdf](http://www.intres.com/articles/suppl/m680p097_supp.pdf)).

A Bayesian hierarchical framework using Monte Carlo Markov chain methods (Archambault et al., 2016) was used to estimate all model parameters by assimilating an extensive data set. Details about the model, including equations for population dynamics, updated data, Bayesian method used to fit the model, and parameter values are given in Supplement 1. Once fitted to the data, the model was used to simulate the effects of nursery habitat restoration at the local scale in the Seine estuary on the dynamics of the metapopulation at the 2 broader scales, from the West FR subregion, where the Seine estuary is located, to the EEC sole stock.

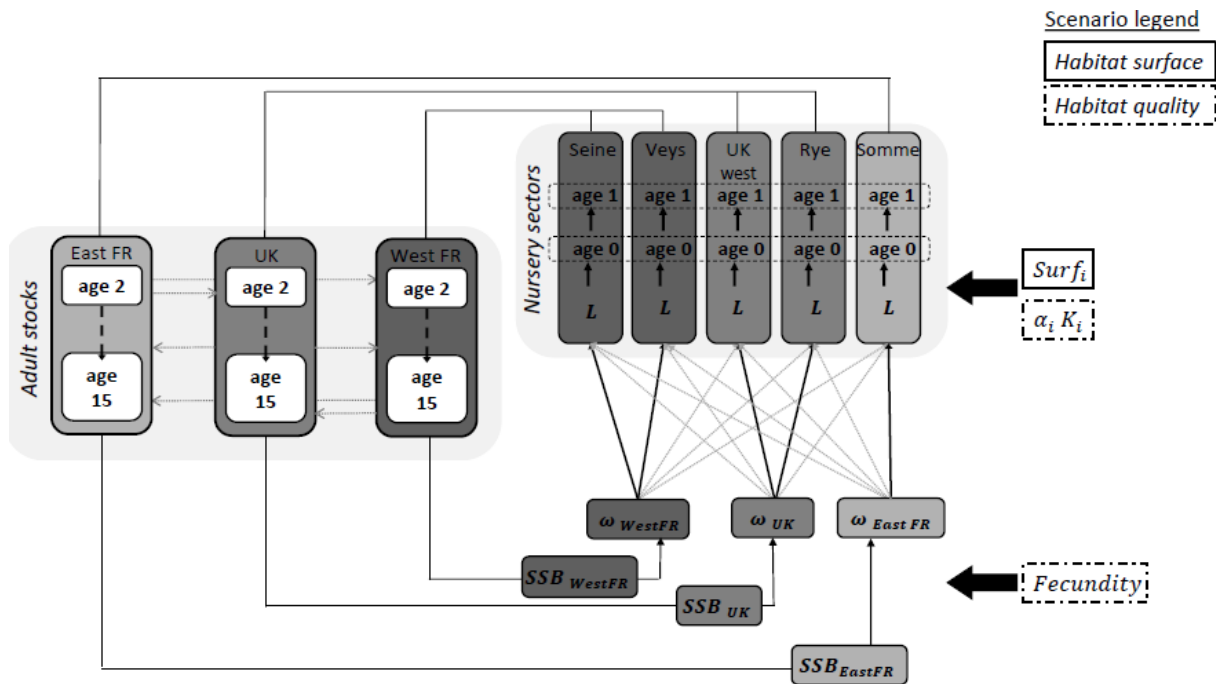


Figure 2.2. Structure and main parameters of the spatial life-cycle simulation model.  $SSB$ : spawning stock biomass,  $\omega$ : no. of eggs  $L_i$ : no. of larvae. Age 0 to 15: abundance of each age group. Dark arrows: distribution of individuals among spatial components. Light grey arrows: subpopulation connectivity (which exists but is quantitatively very low). On the right side, parameters affected by restoration scenarios are in boxes:  $Surf$  (surface),  $\alpha$  (maximal survival rate), and  $K$  (carrying capacity per unit of surface) specific to each nursery  $i$ , and fecundity. In the Seine estuary, these parameters are modified according to the simulated restoration scenarios (Table 2.1)

## 2.2.2 Scenarios of Seine estuary habitat restoration

The available scientific data and expert knowledge on anthropogenic pressures in the Seine estuary and on their consequences for sole juvenile habitat were combined to establish achievable scenarios relative to the current state. The goal was to assess the potential of the restoration scenarios in one of the nursery areas, the highly degraded Seine estuary, to enhance the metapopulation of sole at the EEC scale.

### 2.2.2.1 Habitat loss, land requirement, and channel dredging

During recent decades, extensive morphological changes have occurred in the Seine estuary in relation to human activities, such as land reclamation, dredging, and channelization (Avoine et al., 1981; Ducrottoy and Dauvin, 2008). The induced evolution of sediment dynamics has been estimated by a 3D hydrosediment dynamic model for 3 critical years: 1960, 1975, and 2010 (Schulz et al. 2018, Grasso & Le Hir 2019; model spatial resolution: cells from  $30 \times 100$  m<sup>2</sup> in the estuary to  $2 \times 2$  km<sup>2</sup> towards the open waters). The resulting modification in bathymetry



and sediment structure (Fig. 2.3) impacted the surface of the Seine nursery habitats. The loss of juvenile habitat surface was estimated using the method developed by Rochette et al. (2010). The habitat suitability model describing sole juvenile distribution according to physical descriptors on historical maps was applied to predict the young of the year density at each point of a grid characterised by its bathymetry and type of sediments (Fig. 2.3). The predicted density of sole at each grid point was then integrated (summed) over the area of the whole estuary. Thus, we estimated how the variations in surface and structure (bathymetry  $\times$  sediment type) impacted juvenile abundance at the scale of the nursery. Finally, standardising the historical total abundance of sole juveniles based on 2010 estimates provided a proxy of the evolution of nursery habitat capacity through successive morphological changes in the estuary during recent decades (Rochette et al., 2010). This abundance ratio is a proxy of habitat capacity change because it represents how the number of juveniles supported by the nursery evolve in relation to habitat surface and structure: 1.15 and 1.08 (+15 and +8%, respectively) when comparing the surface in 2010 to that in 1960 and 1975 (Fig. 2.3). In our simulations, we multiplied Seine capacity (denominator of Eq. S4 in Supplement 1) by 1.15 and 1.08 when applying the surface scenario related to 1960 and 1975, respectively (Fig. 2.3).

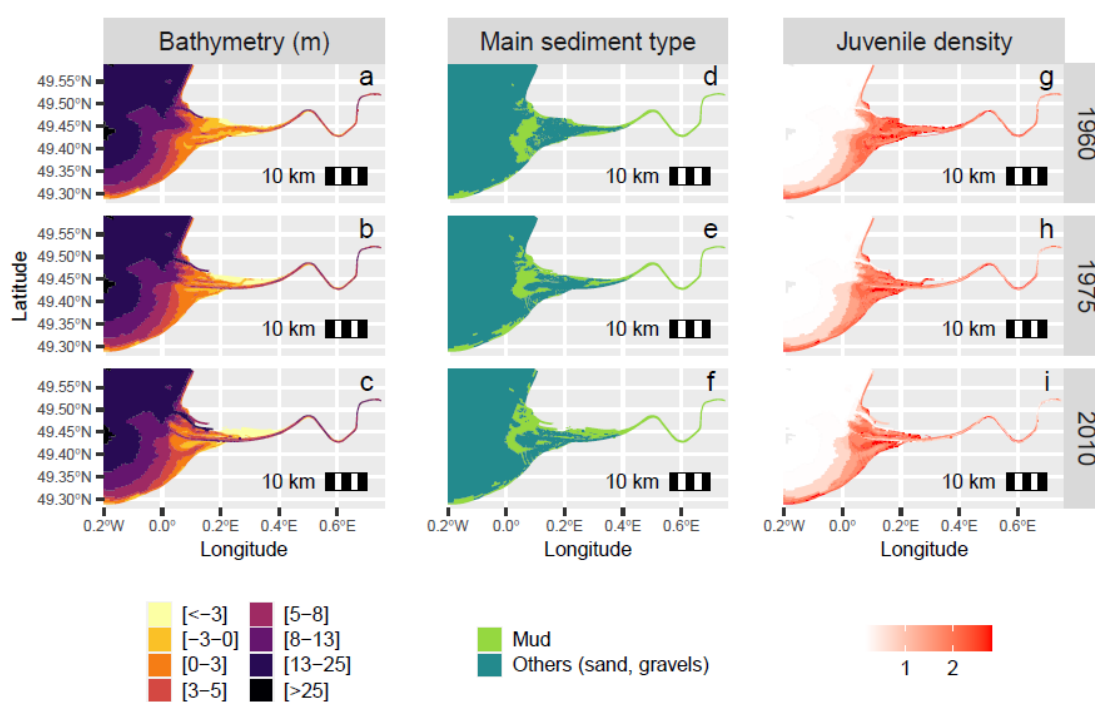


Figure 2.3. Hydrosedimentary evolution of the Seine estuary between (a,d,g) 1960, (b,e,h) 1975 and (c,f,i) 2010 and induced evolution of sole juvenile densities. (a–c) Bathymetry relative to mean sea level. (d–f) Superficial sediment nature over the first cm, averaged from June to September; adapted from Grasso & Le Hir (2019). (g–i) Juvenile (young of the year) predicted relative density for each cell of the grid map based on the habitat suitability model. **Bold** values in the top left corner are indices of suitable nursery habitat, relative to 2010

### 2.2.2.2 *Habitat contamination*

The Seine estuary has been heavily affected by strong chemical contamination for decades (Gilliers et al., 2006; Meybeck et al., 2007; Tappin and Millward, 2015), especially in terms of organic micropollutants. For instance, contamination levels are several times higher than in any other coastal and estuarine area on the Atlantic and EEC coasts of France: >10-fold for polychlorinated biphenyls (PCBs), 3-fold for dichlorodiphenyltrichloroethane (DDT), 2-fold for lindane, and 2-fold for polycyclic aromatic hydrocarbons (PAHs) (Gilliers et al., 2006). Two approaches were conducted to quantify the impact of high exposure to pollutants on the demographic rates of sole juveniles. We first reviewed the available literature to assess the effect of pollutant exposure on the demographic rates of marine juvenile fish in nearshore nursery grounds (for an exhaustive description of the systematic review, see Supplement 2). The analysis aimed to compile data to estimate a range of values for the effects of pollutants on 2 demographic traits of juvenile fish: survival and future fecundity. From the 1638 studies obtained by a Web of Science search and a complementary search (Supplement 2), 50 references provided quantitative information on survival rates and mortality (based on 195 individual case studies: 1 experiment  $\times$  1 species; Table S2.2.1 in Supp. Mat. 2.2), while only 1 reference addressed the future fecundity of juvenile marine fish. These references used a diverse range of approaches (i.e. field studies or laboratory-controlled experiments), species (30), pollutants (i.e. metals, organic pollutants or mixtures, cocktail in sediment, and microplastics), levels of exposure (from realistic levels of contamination to several orders of magnitude higher to estimate lethal concentration for 50% of the organisms) and durations of exposure (2 d to 1 yr). Thus, both the low sample size and its high heterogeneity did not allow for a reliable aggregation or the statistical treatment of these data to estimate a range of changes in survival or future fecundity related to realistic *in situ* exposure to pollutants.

Therefore, because the systematic literature review did not allow us to derive robust estimates of pollutant effects, we relied on expert knowledge to form assumptions about the effect of pollutants on juveniles and design sensible scenarios resulting from habitat quality restoration.

(1) Immediate impact on survival rate. No experiment or *in situ* analysis allowed us to estimate the impact of pollutants on juvenile sole survival in the Seine estuary. However, despite inputs of larvae similar to those in the other nursery sectors in the EEC (Rochette et al., 2012), the Seine estuary presents lower densities of juvenile sole (Riou et al., 2001; Rochette et al., 2010). Nursery-specific estimates of post-settlement larval survival (i.e. Beverton-Holt parameters controlling the mortality from larval settlement to the end of the first summer of life) indicate

that settled larvae experience moderate density independent mortality ( $\alpha$ , the maximum survival rate) but face low carrying capacity ( $K$ , the carrying capacity per unit of surface) in this estuary with regard to that in other nursery sectors (Rochette et al. 2013, Archambault et al. 2016; see parameter estimation Table S2.1.2). High levels of contamination have been noted as an explanatory factor of this low nursery habitat suitability for sole (Archambault et al., 2018; Gilliers et al., 2006; Le Pape et al., 2007).

To mimic the impact of habitat quality restoration and its consequences on juvenile survival, the  $\alpha$  and  $K$  parameters in the Seine estuary were increased to the values estimated for a less contaminated estuarine nursery (Archambault et al., 2018) (Fig. 2.2). The Bay of Veys, a neighboring estuarine system close to the Seine, with similar larval inputs but much lower levels of contamination (e.g. 10-fold less for PCBs; Tappin & Millward 2015), was chosen as the reference for the restored quality level for the Seine estuary (Rochette et al., 2010). To analyse the sensitivity to this hypothesis, scenarios were run with a range of values; we used the quartiles (qt) of the Bay of Veys  $\alpha$  and  $K$  posterior distributions after checking the absence of correlation between them (Pearson's correlation parameter =  $-0.078$ ). This approach resulted in testing 3 hypotheses by taking the lower (1st qt), median (2nd qt) and upper (3rd qt) quartiles for ( $\alpha$ ,  $K$ ).

(2) Carry-over impact on future fecundity. Eichinger et al. (2010) designed an experiment to quantify the impacts of feeding exposure to a mixture of 4 PCB congeners on sole biology from their juvenile to adult stages. During this 3 yr chronic contamination experiment, 6 mo old juveniles were exposed to environmentally relevant pollutant concentrations (i.e. the mussel contamination levels measured in the Seine estuary in 2010 for PCBs) in their food. Hatching success of the eggs produced by the broodstock resulting from this experiment showed a reduction in egg viability: only 18% of the eggs spawned by the sole feeding on contaminated food hatched in comparison to 56% of the eggs for the control (F. Mounier unpubl.; calculated from the raw data of the aforementioned laboratory experiment). This level of loss in hatching success was in accordance with experimental investigations on dab (Fonds et al., 1995) and zebrafish (Daouk et al., 2011). In our study, the impact of habitat contamination on fecundity was parameterised using the results from that experimental approach. We considered scenarios where the fecundity in the current state corresponding to a contaminated environment was only 32% (i.e. 18/56) of the one that would be achieved in a restored, uncontaminated environment. As a proper associated range of probabilities could not be determined, we tested the effect of

50 or 100% restoration (altered fecundity increased to 50 or 100% of the reference level, respectively).

### 2.2.3 Simulation details and scenario comparisons

For each scenario, the population was simulated under a constant fishing mortality value set to the average value of the last 5 yr derived from the Bayesian fitting procedure:  $F_{\text{West FR}} = 0.183$ ,  $F_{\text{UK}} = 0.260$ ,  $F_{\text{East FR}} = 0.317$ . The allocation and survival matrix for larval drift was calculated as the mean of the historical time series (Archambault et al., 2018). Weights at age from 2019 (ICES, 2020) were used to calculate the age-specific fecundity. Parameter uncertainties were not considered, so their values were fixed to the mode of their respective posterior distribution (Archambault et al., 2018). However, the simulations were stochastic, as they included environmental random noise at several stages, and the dominant stochasticity was logically in the recruitment process. Monte Carlo simulations were run for 300 years, and then the first 100 years were discarded. The remaining 200 years were considered random draws within the ergodic equilibrium state of the system. Simulations were repeated with different parameter values depending on the scenarios. We defined the reference scenario as the baseline model configuration with all parameters derived from the model calibration (Table S2.1.2). Table 2.1 summarises the designated scenarios and their combinations, which were run to analyse the marginal and combined effects of restoration in the Seine estuary (surface and quality). Our scenarios of habitat quality restoration referred specifically to contamination reduction and the impacts on juvenile survival and future fecundity. In practice, both aspects would be affected, but to analyse the marginal effects of the 2 processes, they were run separately and in combination. As mentioned above, habitat quality scenarios were designed based on expert knowledge and did not rely on direct experiments or modelling outputs. Therefore, it was decided to run the scenarios with a range of values (Table 2.1) to assess the potential uncertainty of this expert knowledge (cf. Section 2.2.2.). The average of the sole stock biomass of spawners at equilibrium ( $SSB_{\text{eq}}$ ) and of the amount of fishing capture at equilibrium ( $C_{\text{eq}}$ ) calculated over the last 200 yr of the simulations were used as indicators of restoration outcome/success. The relative percentage of the gain/loss between the explored scenario ( $S_{\text{ce}}$ ) and the reference scenario ( $S_{\text{ce}_{\text{ref}}}$ ) was calculated as follows:

$$\% \text{ gain/loss} = 100 \times \left[ 1 - \frac{\text{Indicator}_{S_{\text{ce}}}}{\text{Indicator}_{S_{\text{ce}_{\text{ref}}}}} \right] \quad (1)$$

with indicator = SSB or C.

*Table 2.1. Scenarios and associated types of habitat restoration in the Seine estuary. Year considered for the nursery surface: the historical surface of suitable nursery habitat used in the simulation, where 2010 = reference; 1960 and 1975 = restored states with surface increases of 15 and 8%, respectively. Future fecundity: reference = fish from the Seine nursery exhibit altered reproductive capacities (i.e. 32% of other regional fecundity values); fully restored = the scenario corrected this value to the level of other regional fecundity values; half restored = the value was increased to half of the restored value. Juvenile survival: modification of stock-recruitment parameters ( $\alpha$  and  $K$ ) used for the Seine nursery, where reference = actual estimates of the Seine estuary; restored = parameters from the Bay of Veys were used. Lower, median or upper hypothesis = quartile (first, median or third, respectively) of the  $\alpha$  and  $K$  parameter distribution used in the simulation to test sensitivity*

Scenario	Parametrization used for simulation		
	Year considered for the nursery surface	Future fecundity	Juvenile survival
<b>Reference</b>	2010	Reference	Reference
<b>Surface restoration</b>	1960	Reference	Reference
	1975		
<b>Habitat quality restoration on future fecundity</b>	2010	Half-restored	Reference
		Fully restored	
<b>Habitat quality restoration on juvenile survival</b>	2010	Reference	Restored – lower, median or upper hypothesis
<b>Habitat quality restoration (juvenile survival and future fecundity)</b>	2010	Fully restored	Restored – median hypothesis
<b>Quality and surface restoration</b>	1960	Fully restored	Restored – lower, median or upper hypothesis

## 2.3 Results

Given the metapopulation structure of the EEC sole, the simulation results were available at 2 spatial scales: regional (West FR, East FR, UK) or global (EEC). The restoration scenario outcomes mainly impacted the West FR subpopulation (i.e. the subpopulation in which the Seine estuary is located; thus, in which partial nursery restoration would be implemented), so most results are presented at this scale. Some results will also be shown for each region and globally to provide a general understanding of how the structure of the metapopulation interacts with the restoration results.

### 2.3.1 Reference scenario

The equilibrium state obtained under the reference scenario (Table 2.1) stabilised to mean local SSB of 5584, 6936, and 6716 t for West FR, UK, and East FR subpopulations, respectively (19

236 tons at the EEC scale). The mean catch at equilibrium for each subpopulation was 963, 1729, and 1995 t for West FR, UK, and East FR, respectively (4687 tons in the EEC).

### 2.3.2 Marginal impacts of restoration scenarios

#### 2.3.2.1 *Surface restoration*

Restoring the Seine nursery surfaces to the levels in 1975 and 1960 increased SSB at the regional scale in West FR by 5.9 and 9.5% (Fig. 2.4), respectively. The greater the surface area was (1960 > 1975; Fig. 2.3), the larger the SSB was. Catches followed similar increases for restoration to the levels in 1975 and 1960 (+5.9 and 9.6%, respectively).

Local restoration in the Seine estuary enhanced the subpopulation in the West FR region (where this estuary is located, Fig. 2.1), but the positive impacts only weakly diffused to other regions. The increases in biomass and catches at the EEC stock scale were almost similar in weight to those observed in the West FR region. When scaled to the whole EEC for the 1975 and 1960 scenarios, the SSB increased by 2 and 3.5%, and the catches increased by 1.7 and 2.8%, respectively (Fig. 2.4).

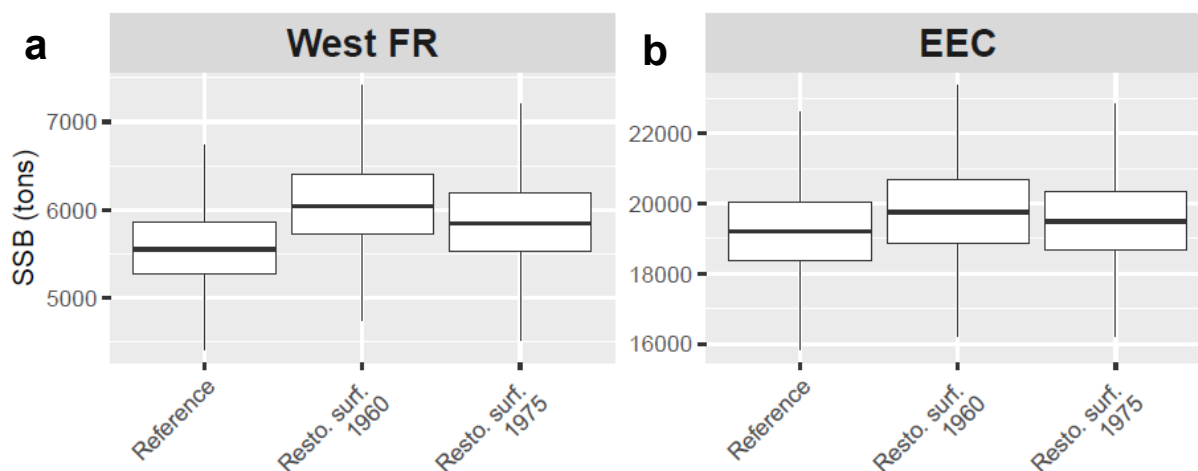


Figure 2.4. Distribution of estimated stock spawning biomass (SSB) for the surface restoration (*Resto. surf.*) scenarios to 1960 and 1975 nursery surfaces (a) in the West FR Region and (b) at the Eastern English Channel (EEC) stock scale; note different y-axis scales. Horizontal line: median; upper and lower boxes: third and first quartiles, respectively; whiskers:  $1.5 \times$  interquartile range

#### 2.3.2.2 *Effects of habitat quality restoration on juvenile survival*

Restoration of the habitat quality for juvenile survival alone had a substantial impact on the SSB of the West FR subpopulation, with lower, median or upper hypotheses having an increasing effect. They produce a 13.6, 33.6, and 58.5% increase in SSB, respectively (Fig. 2.5a

hereafter the results of these hypotheses will be noted as median [lower, upper]%) and a quantitatively comparable effect on catches (+34.1 [13.8, 59.5]%).

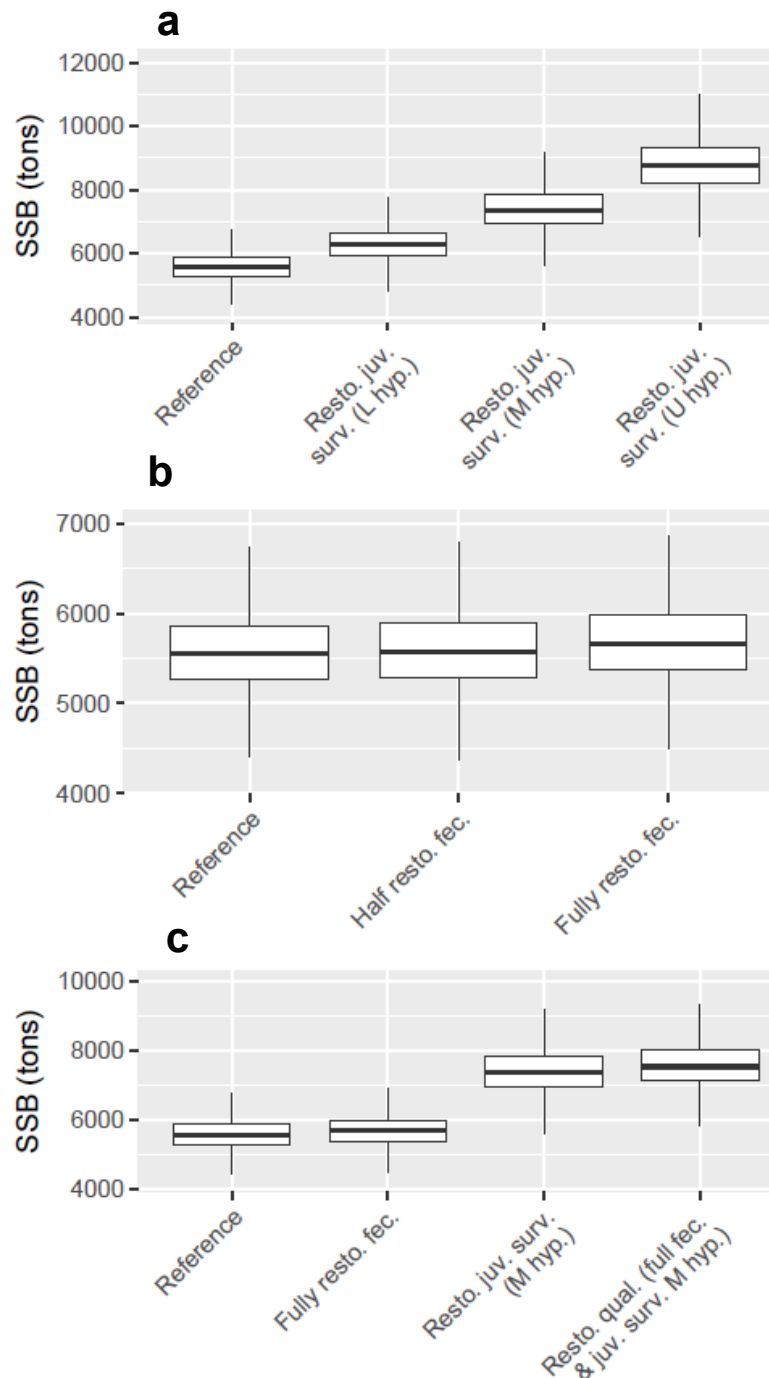


Figure 2.5. Distribution of estimated stock spawning biomass (SSB) in the local West FR region for the habitat quality restoration scenarios in relation to (a) juvenile survival (resto. juv. surv.), (b) future fecundity (resto. fec.), and (c) both elements combined (resto. qual.). Represented restoration hypotheses: lower (L hyp.), median (M hyp.) and upper (U hyp.) survival values and half or fully restored future fecundity. Boxplot parameters as described in Fig. 2.4

### 2.3.2.3 *Effects of habitat quality restoration on future fecundity*

Habitat quality restoration for fecundity had only a weak effect on the SSB and catches at equilibrium. The SSB gains in the West FR region among the reference and half-restored and fully restored habitat quality regarding fecundity only were only +0.9 and 2.7%, respectively (Fig. 2.5b), with similar low effects on catches.

### 2.3.3 Impacts of combined restoration scenarios

#### 2.3.3.1 *Habitat quality restoration (juvenile survival and future fecundity)*

The effect of the combined quality scenario slightly differed from the effect of the restoration scenario on survival only, outlining the weak effect of improving fecundity (Fig. 2.5c). SSB and catch improvements in the West FR region reached 36.6 [16.4, 62]% and 37.2 [16.6, 63]%, respectively, when considering a complete restoration of fecundity.

#### 2.3.3.2 *Quality and surface restoration*

When all the restoration scenarios were combined, the overall gains reached 50.5 [27.7, 80.2]% and 51.3 [28.1, 81.6]% for SSB and catches, respectively, in the West FR region (Fig. 2.6c). Regarding low connectivity, the SSB increase was very limited in the UK region (3 [1.5, 3.3]%) and moderate in the East FR (6.2 [4.7, 9.3]%), with similar minimal improvements in catches (Fig. 2.6a,b). At the EEC scale, the increase was quantitatively (i.e. in weight) similar to that observed in the West FR region but diluted at the scale of the EEC at 17.5 [9.6, 27.7]% and 13.2 [7.5, 21.4]% for SSB (Fig. 2.6d) and catches, respectively.



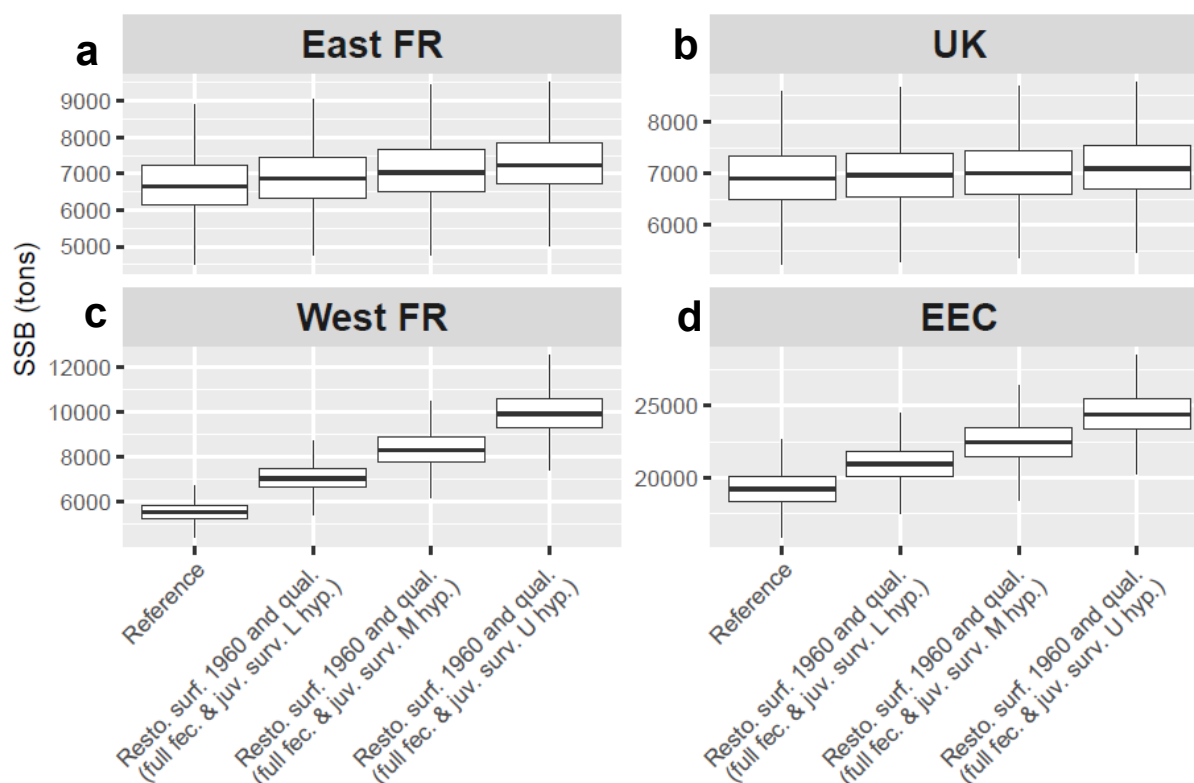


Figure 2.6. Distribution of estimated stock spawning biomass for the combined (surface and quality: resto. surf. and qual.) habitat restoration scenarios in the (a) East FR, (b) UK, and (c) West FR region and (d) at the Eastern English Channel (EEC) stock scale. Note different y-axis scales. The 3 hypotheses (lower, median and upper, indicated as L, M and U hyp.) of juvenile survival (juv. surv.) are combined with the full fecundity (full fec.) restoration hypothesis and the 1960 surface restoration scenario. Boxplot parameters as described in Fig. 2.4

## 2.4 Discussion

### 2.4.1 Strengths of a multidisciplinary approach to quantify consequences of habitat degradation

Despite the degradation of habitats in nearshore nurseries being well studied (Brown et al., 2018), quantitative estimates of the impact on fish populations remain rare (Rose et al., 2003; Vasconcelos et al., 2014). The present approach demonstrated the benefits of compiling and analysing multidisciplinary scientific data and expert knowledge (fish life cycles, population dynamics and connectivity, hydro sediment dynamics, chemistry, and ecotoxicology, i.e. bioaccumulation and toxic impacts) to address the impact of habitat degradation on exploited species. The results provide significant insights into the consequences of multiple pressures on juvenile sole in the Seine estuary. The restoration of both the surface extent and chemical quality of habitat in the Seine estuary dramatically enhanced spawning stock biomass and fisheries catches in the EEC.

#### *2.4.1.1 Impacts of metapopulation structure*

Considering the low connectivity within the metapopulation at the EEC scale (Lecomte et al., 2020; Randon et al., 2021), the effects of the restoration scenarios in the Seine estuary enhanced the SSB and catches in the West FR region (where the Seine nursery is located; Fig. 2.1) and did not diffuse much into other regions in the EEC (Fig. 2.6). The increase in spawning biomass and catches in the EEC only resulted from the increase in West FR. This result supports the integration of the common sole meta population structure into the EEC stock for the assessment of the consequences of both fishing pressure (Randon et al., 2021) and nursery habitat degradation/restoration.

#### *2.4.1.2 Large effect of nursery size but limited restoration potential*

A previous investigation of habitat structure restoration in the Seine estuary by Archambault et al. (2018) assumed restoring the Seine estuary to its early 19th century state using a factor of +72% for the restoration of the nursery habitat and suggested that substantial catch and SSB increases could be obtained. By integrating outputs from a 3D numerical model of sediment transport (Grasso and Le Hir, 2019), our analysis provided an intermediate milestone, with a restoration factor of +15% between 1960 and the current state (+8% for 1975). This restoration factor value also highlights that the critical loss of nursery surfaces in the Seine estuary occurred mainly before 1960. Fish habitat restoration has been studied for a diversity of habitat types, and its efficacy has generally been shown to enhance populations and associated fishery yields (Camp et al., 2020; Duarte et al., 2020; Taylor and Creighton, 2018). For juveniles of many exploited fish species, combinations of bathymetry and sediment types are key factors of habitat suitability (Rochette et al., 2010; Seitz et al., 2014), and both components are driven by hydrodynamic mechanisms linked to multiple human activities (Grasso and Le Hir, 2019). However, surface restoration faces constraints related to historical land reclamation, construction of dikes and dredging (Ducrotoy and Dauvin, 2008) and is complex to implement. This is why only a limited part of historical loss could be restored.

#### *2.4.1.3 Low sensitivity to reproductive success*

The marginal effect of fecundity improvement at the population scale was very limited (Fig. 2.5b), in accordance with the very weak correlation between the SSB and recruitment (Archambault et al., 2018). For many harvested marine species, spawner biomass is poorly correlated with the number of surviving offspring (i.e. recruitment) (Cury et al., 2014; Minto et al., 2008). This is particularly true for nursery dependent fishes, for which juvenile production

is limited by the carrying capacities of their nurseries (Archambault et al., 2014; Iles and Beverton, 2000; Myers, 2001). In the case of the EEC common sole population, the number of age-0 juveniles as measured in autumn is poorly correlated with stock size (Rochette et al., 2012). Specifically, saturation of sole juveniles (i.e. carrying capacity) in the Seine nursery is reached for a number of settled larvae at least one order of magnitude lower than the mean larval supply along the time series. Consequently, in our simulations the influence of an alteration of 32% in egg viability on recruitment was logically very low, but this might not be true for higher levels of fishing mortality (Archambault et al., 2018) and for other stocks/species.

#### *2.4.1.4 Uncertain but potentially high interest in restoring juvenile survival*

The simulations highlighted the sensitivity of the population dynamics to the improvement in juvenile survival rates (i.e. a 3-fold higher increase for the median scenario compared to the scenario of restoring the nursery surface to that in 1960). Therefore, pollution mitigation has a high potential for ecological benefits in the Seine estuary. This restoration type has more generally been outlined for enhancing juvenile fish production in estuaries (Courrat et al., 2009; Teichert et al., 2016). However, the outcomes of restoring habitat quality on juvenile survival remain highly sensitive to the uncertainty in the level of improvement in survival rates (here represented by the lower, median, and upper hypotheses) and should therefore be interpreted with caution. Using Veys estuary estimations of mortality rates for the Seine estuary juveniles was a strong but sensible assumption that relied on the similarities between the estuaries that are very close in distance, provide habitat for the same subpopulation (Lecomte et al., 2020; Randon et al., 2021), and have similar larval inputs (Rochette et al., 2012).

#### 2.4.2 Weaknesses of the approach

Numerous studies have pointed out the toxic effects of exposure to pollutants on juvenile sole (Davoodi and Claireaux, 2007; Foekema et al., 2008; Wessel et al., 2010), including studies that focus on the Seine estuary (Amara et al., 2007; Gilliers et al., 2006). Other general lab studies have shown that the future reproductive success of fish exposed to pollutants at the juvenile stage can be altered through decreases in fecundity, egg viability, and survival (Daouk et al., 2011; Fonds et al., 1995; Horri et al., 2018). However, the quantitative effects of exposure to pollutants on marine juvenile fish survival and future fecundity in the wild remain unknown. Consequently, our scenario of restoring juvenile survival relied on expert knowledge (Rochette et al., 2010) and should be interpreted with caution. Because of the complexity of fish life

histories and the multiple sources of natural variation in their abundances, predicting the effects of pollutants on wild fish populations is challenging (Hamilton et al., 2016), and estimates of consequences on demographic rates and population dynamics are lacking (Ono et al., 2019; Rose et al., 2003). There are still unmet requirements for mechanistic and holistic approaches to understanding and quantifying habitat-specific mortality rates to predict the effects of coastal habitat degradation on the dynamics of exploited marine populations (Boyd et al., 2018; Vasconcelos et al., 2014). There is an urgent need to develop integrative studies to address this issue.

### 2.4.3 Support decision making for management

Our results highlighted the potential effectiveness of the restoration of both the surface and quality of suitable juvenile habitat in the Seine estuary to increase the size and productivity of the sole population in the EEC. Restoring both nursery habitat size and quality would increase the West FR subpopulation by 51 [28, 80]%. This would represent a gain of 18 [10, 28]% in SSB at the EEC stock scale, for an increase in average annual catches of 616 [330, 955] t for commercial fisheries. Our study also suggests that in the Seine estuary, to enhance the population, reducing pollutants (i.e. restoring habitat quality) might be more efficient than restoring surface habitat. Management actions directed at the restoration of juvenile coastal habitats have already achieved significant benefits for the population size of exploited marine fish species and related fisheries. Restoring these coastal habitats may be even more beneficial than regulating fishing effort on adult fish (Hughes et al., 2015; Levin and Stunz, 2005; van de Wolfshaar et al., 2015). For the EEC sole population, local nursery restoration could also coordinate with fisheries management to enhance SSB and catches (Archambault et al., 2018). The present approach demonstrated how scientists from various fields were able to acquire, compile and apply multidisciplinary knowledge and scientific information together to answer questions about the impacts of local habitat restoration on exploited fish populations at a wider scale. In the Seine estuary, ongoing management measures aim to restore the surface (Ducrotoy and Dauvin, 2008) and quality of estuarine habitats, with some results already observable, such as significant decreases in pollutant levels (Meybeck et al., 2007; Tappin and Millward, 2015). For instance, between the 1990s and 2010s, observations from a water quality monitoring system in the Seine estuary (data source: IFREMER; [http://envlit.ifremer.fr/resultats/acces\\_aux\\_donnees](http://envlit.ifremer.fr/resultats/acces_aux_donnees)) recorded reductions of 68% in PCB-153, 81% in DDT, and 40% in lead (updated contamination data measured in *Mytilus edulis*, as described by (Courrat et al., 2009)). The present analysis showed the critical importance of such

local restoration actions, which could complement fisheries management plans to efficiently enhance marine life and fisheries-related ecosystem services (Cordier et al., 2011). Ecological initiatives to restore estuaries may suffer from a global lack of information and/or knowledge regarding how to establish step-by-step objectives and to evaluate an entire restoration project (Capderrey et al., 2016). This study is a step forward for understanding how restoration may affect fish population dynamics.

## Conclusion du chapitre 2

Le chapitre 2 visait à évaluer, à l'aide d'un modèle de cycle de vie spatialisé, comment les multiples pressions anthropiques au niveau de la nurricerie de l'estuaire de Seine affectent la dynamique de métapopulation de la sole commune de Manche Est. Pour cela, des données et connaissances expertes de multiples champs disciplinaires (cycle de vie, dynamique de population, dynamique hydrosédimentaire, chimie et écotoxicologie) ont été compilées et analysées pour construire des scénarios de restauration de l'estuaire de Seine. L'impact de ces scénarios sur la dynamique de métapopulation de sole a été simulé à l'aide d'un modèle de cycle de vie représentant la dynamique de la métapopulation.

La restauration de la qualité chimique et de la surface de l'estuaire de Seine génère d'importantes augmentations de la biomasse féconde et des captures en Manche Est. Ces augmentations résultent quasi exclusivement des conséquences positives de la restauration pour la sous-population située au sud-ouest de la Manche Est alimentée directement par la nurricerie de l'estuaire de Seine. En effet, la faible connectivité entre les trois sous-populations (Lecomte et al., 2020; Randon et al., 2021) induit une très faible (mais non nulle) diffusion dans les sous-populations.

Au sein des scénarios testés, les réponses varient fortement. La restauration de la surface d'habitat à son état de 1960 induit une augmentation modérée (10 %) de la biomasse féconde pour la sous-population du sud-ouest. Ces chiffres contrastent avec le très fort potentiel de restauration (+36 %) mis en évidence par Archambault et al. (2018) pour un retour à l'état de 1850, mais s'expliquent car la plus forte dégradation de la nurricerie de Seine est advenue avant 1960.

La restauration marginale de la fécondité des adultes matures issus de l'estuaire de Seine a eu des effets très limités (+3 % de biomasse féconde pour la sous-population). Ces résultats sont cohérents avec la très faible corrélation entre SSB et recrutement pour ce stock (Archambault et al., 2018; Rochette et al., 2012), comme pour la plupart des poissons marins (Cury et al., 2014; Minto et al., 2008). Le faible lien entre biomasse féconde et recrutement est encore accentué pour les poissons plats nurriceries-dépendants, comme la sole, dont le recrutement est essentiellement déterminé par la capacité d'accueil de leurs nurriceries (Iles & Beverton 2000, Myers 2001, Archambault et al. 2014), sauf lorsque le niveau de biomasse féconde devient très faible.

La restauration de la survie juvénile, en lien avec une amélioration de la qualité chimique, permet une forte augmentation de la biomasse féconde, mais dont le niveau exact reste très incertain : + 34 [14-59] %. En effet, en dépit des nombreuses études démontrant les effets toxiques des polluants sur les juvéniles de sole en Manche Est (Amara et al., 2007; Gilliers et al., 2006), les effets quantitatifs à l'échelle de la population demeurent difficiles à estimer (Brown et al., 2018; Vasconcelos et al., 2014) et ce scénario internalise la grande incertitude sur le niveau de restauration potentiel.

Cette étude s'inscrit dans la lignée d'un ensemble de travaux menés afin de quantifier de l'impact de la dégradation de la nourricerie de Seine sur la dynamique de population de sole de Manche Est (Rochette et al. 2010, Rochette et al. 2013, Archambault et al. 2018). Elle en est la version la plus aboutie et s'appuie sur une représentation précise de la dynamique de la métapopulation (notamment en lien avec un effort important dédié à la paramétrisation du modèle par une approche statistique poussée) et des scénarios de restauration rassemblant l'expertise et les connaissances les plus récentes de plusieurs champs disciplinaires. La grande quantité de données et d'expertise requise pour calibrer le modèle et concevoir les scénarios est associée à une très grande spécificité au cas d'étude. La quantité de données nécessaires et l'effort fourni pour la paramétrisation rend la transférabilité de cette approche très limitée.

Si l'on souhaite multiplier les cas d'étude pour informer les décisions de gestion il semble nécessaire de se tourner vers une approche plus parcimonieuse et plus générique, facilement adaptable à différentes populations.

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### 3. Modélisation de l'impact de la dégradation/restauration des nourriceries sur la dynamique de populations marines de poissons aux histoires de vies contrastées

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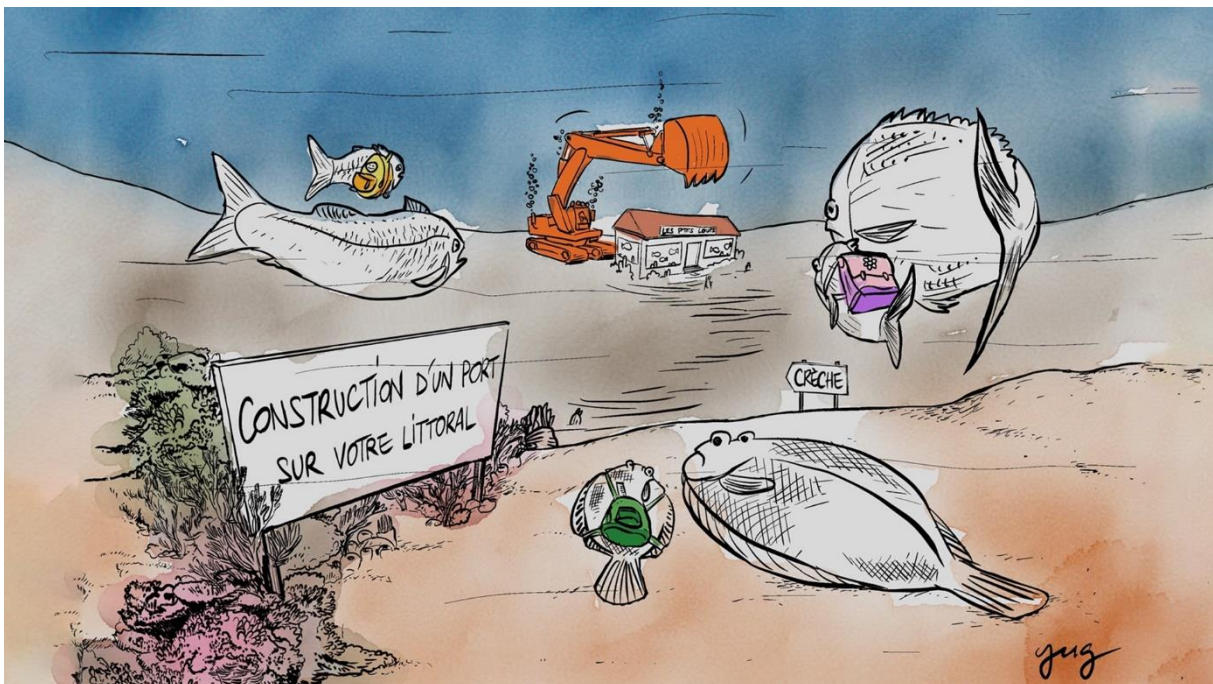


Illustration : Guy Le Besnerais



## Introduction du chapitre 3

L'introduction générale du manuscrit a pointé le faible nombre d'approches permettant de quantifier l'impact des dégradations d'habitat sur la dynamique des populations marines (Lipcius et al., 2019). Le rôle des zones côtières et estuariennes comme ZFHI est pourtant déterminant pour les espèces marines exploitées (Seitz et al., 2014) et leur niveau de dégradation par de multiples pressions anthropiques très élevé (Brown et al. 2018). Le chapitre précédent illustre le travers de la plupart des approches de modélisation existantes : une grande spécificité aux cas d'étude marquée par des modèles souvent ajustés finement aux données disponibles, qui exige une grande quantité de données et d'expertise locale ; et qui génère en retour une faible transférabilité des modèles. Ces considérations dressent le portrait-robot d'une approche qui permettrait d'étudier l'impact des pressions anthropiques au niveau des ZFHI sur la dynamique de diverses populations aux histoires de vie contrastées : une approche plus « processus driven » et plus facilement transférable à des espèces variées.

Pour répondre à ces besoins, nous proposons dans le chapitre 3 une approche de modélisation plus générique qui se concentre sur les nourriceries. Pour rendre compte des processus advenant au sein des habitats juvéniles, nous développons une expression de la relation SR qui dépend directement de la surface et de la qualité de la nourricerie. Cette relation est incorporée dans un modèle structuré en âge et en stades pour simuler la dynamique d'une population exploitée sous différents scénarios de dégradation/restauration de l'habitat des juvéniles. Le modèle est conçu de façon à pouvoir être paramétré relativement aisément pour un large panel d'espèces à partir d'informations issues de la littérature ou des rapports d'évaluation.

Dans un premier temps (chapitre 3.1), le modèle est appliqué dans un cadre théorique à trois espèces marquées par de larges contrastes dans leurs histoires de vie : une espèce à cycle de vie court (anchois), et deux autres longévives mais présentant des dynamiques SR (fécondité/survie des jeunes stades/steepness) opposées (plie et raie fleurie). La paramétrisation des impacts anthropiques sur les nourriceries permet d'exprimer explicitement les paramètres de la relation SR en fonction de multiplicateurs de qualité et de surface d'habitat. Des simulations sont conduites pour explorer la réponse des populations aux scénarios de dégradation/restauration de surface ou de qualité de l'habitat des juvéniles, puis analyser comment les réponses varient selon les espèces pour le gradient d'histoires de vie couvert.

Dans une seconde partie (chapitre 3.2), l'approche est appliquée à un cas d'étude original pour quantifier l'impact de la restauration de zones de nourricerie communes à quatre espèces

commerciales de Manche Est : le bar, la sole, la plie et le merlan. Le modèle est calibré pour ces quatre espèces nourricerie-dépendantes à partir de données issues d'évaluation de stock et de la littérature. Des scénarios réalistes de restauration de surface et de qualité sont construits à partir d'une quantification des pertes (i) de surface d'habitats côtiers en Manche Est depuis 1870 ; (ii) de densité de juvéniles selon la contamination des estuaires (Courrat et al., 2009). Ces scénarios sont simulés séparément puis conjointement pour évaluer le potentiel de restauration de la biomasse féconde et du potentiel d'exploitation durable pour les différentes populations, en lien avec leurs THV et leur degré de concentration sur les habitats juvéniles.

### 3.1 Response of marine fish population productivity to juvenile habitat modifications depends upon life histories

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Champagnat J.<sup>1\*</sup>, Rivot E.<sup>1</sup>, Le Pape O.<sup>1</sup>.

<sup>1</sup>DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, IFREMER, INRAE, 35042 Rennes, France

\*Corresponding author: [juliette.champagnat@institut-agro.fr](mailto:juliette.champagnat@institut-agro.fr)

#### Abstract

Coastal and estuarine habitats are essential for both growth and survival at juvenile stages for a large proportion of marine fish, but are exposed to a variety of threats. Still, the quantitative impacts of anthropic-mediated nursery degradations on exploited population dynamics and productivity are rarely addressed. We developed a comprehensive steepness-based parameterization of the stock-recruitment relationship that directly depends upon juvenile habitat quality and surface area, and used a generic age- and stage-structured model to simulate exploited population dynamics under scenarios of nursery degradation/restoration. Population responses to juvenile habitat modification were estimated for three species with contrasting life histories. Modifying the surface area of nursery habitat has a predictable direct scaling effect on the population size and affects the biomass and the fishing yield, similarly for various life histories. Modification of habitat quality affects both the population size and the shape of the productivity curve, leading to more complex responses of biomass and fishing yields that depend upon combinations of life history traits. Populations with low steepness; hence lower resiliency to fishing, are the most sensitive to the degradation of habitat quality. Our study emphasises the critical impact of juvenile habitat modification on population dynamics and productivity and the urgent need to integrate habitat consideration into the management of exploited marine species. Our framework is a generic tool, transferable to a large panel of case studies, to quantify the consequences of coastal habitat degradation/restoration for the dynamics of marine exploited fish populations.

Keywords: Anthropogenic pressures; Coastal degradation; Coastal restoration; Essential fish habitat; Nurseries; Population model.

### 3.1.1 Introduction

Nearshore ecosystems are highly productive areas (Costanza et al., 1997) that serve as essential fish habitat for numerous marine species (Miller et al., 1984). They support and maximise survival and growth of juvenile stages by providing food and refuges (Beck et al., 2001; Lellis-Dibble et al., 2008). Coastal and estuarine areas are used as nurseries by one third of commercially important species assessed by the International Council for the Exploration of the Sea (ICES) in the Northeast Atlantic, which account for two third of the commercial landings in weight (Brown et al., 2018; Seitz et al., 2014). Such high levels of dependence to coastal nurseries are common worldwide on various latitudinal range for exploited species (Bradley et al., 2022; E. J. Brown et al., 2019; Fodrie and Mendoza, 2006; Lellis-Dibble et al., 2008; Peterson, 2003). The available surface area and the quality of coastal and estuarine habitats are of critical importance for recruitment levels, productivity and sustainable catch potential of these coastal nursery-dependent species (Gibson, 1994; Le Pape & Bonhommeau, 2015; Rijnsdorp et al., 1992). However, coastal and estuarine ecosystems host many human activities (de Groot et al., 2012; Šiaulys et al., 2012) and therefore suffer numerous pressures and threats (Korpinen et al., 2012), like contamination, eutrophication, invasive species and surface area losses (Brown et al., 2018). This high level of pressure has led to widespread degradation and destruction of native ecosystems worldwide (Bulleri & Chapman, 2010; Halpern et al., 2008).

Although the impact of local anthropogenic pressures on nursery-dependent juveniles has been widely documented (Brown et al., 2018), quantitative estimations of the consequences of these pressures at the population scale remain scarce (Lotze, 2006; Sundblad & Bergström, 2014; Vasconcelos et al., 2014). Still, upscaling individual and local responses to evaluate impacts at the scale of populations is essential for guiding effective management actions (Lipcius et al., 2019; Rönnbäck et al., 2007; Rose et al., 2018; Sundblad & Bergström, 2014). Population models with key demographic parameters depending upon habitat variables have been developed to simulate the impact of habitat scenarios on population dynamics and/or fisheries yields (Archambault et al., 2018; Camp et al., 2020; Mizerek et al., 2011; Rose et al., 2018; Scheuerell et al., 2006). Those studies emphasise the utility and interest of considering habitat in populations models, but suffer from important limitations. These population models are strongly case-specific, highly data-demanding, and hardly transferable to other case studies. This points out an important gap in knowledge and methodology and highlights the need to build generic approaches easier to transfer and to parameterise to quantify the impact of habitat

degradation for a wide range of coastal nursery-dependent marine fish populations (Brown et al., 2018).

Stock-recruitment relationships (SRR) are key component of stage-based population models. SRRs are needed for forward simulation of population dynamics, estimations of biological and management reference points and hence are essential for management strategies evaluation (Punt et al., 2001). The shape of the SRR especially determines the resilience to exploitation and environmental disturbance (Keith & Hutchings, 2012; Lee et al., 2012; Mangel et al., 2010). It is even more critical in our approach because the recruitment stage encompasses the mortality processes happening in nursery grounds and hence directly depends upon both the quality and the quantity of nursery habitat. Still, parameterising SRR remains highly challenging. Indeed, time series of stock-recruits at population scale generally provide little information on the values of the parameters of the stock-recruitment model (Myers et al., 1999; Rose et al., 2001; Zhou, 2007). Meta-analysis approaches have been used to overcome this variability by averaging the noise across multiple populations (Britten et al., 2016; Myers et al., 1999) and taxa (Archambault et al., 2014; Thorson, 2020). A key interest of such hierarchical analyses is that they provide generic stock-recruitment patterns related to life history traits. Especially such approach was applied to estimate steepness for all taxa of marine fish (Thorson, 2020). Steepness characterises the drop-off in recruitment when the spawning potential is reduced. It is formally defined as the proportion of equilibrium unfished recruitment produced when the spawning biomass is reduced to 20% of its unfished level (Mace & Doonan, 1988). Interestingly, steepness has no dimension, which allows comparison between species. Steepness theoretically ranges between 0.2 and 1. A value near 0.2 corresponds to nearly linear SRR hence associated with very weak density dependence in the eggs to recruit mortality. By contrast, a value near 1 indicates a very strong density dependence with a recruitment roughly constant up to 20% of pristine biomass (Mangel et al., 2013; Myers et al., 1999; Punt and Dorn, 2014). It has been demonstrated that fish population response to fisheries is partly determined by its life history traits (LHT) (Kindsvater et al., 2016b), and especially by steepness (Horbowy and Hommik, 2022): high steepness values are associated with maintained productivity when heavily depleted and hence high resilience to fishing overexploitation (Brodziak et al., 2015; Mangel et al., 2013).

In this paper, we developed a generic age- and stage-structured population model to simulate population dynamics under scenarios of nursery degradation or restoration. As a key component of our approach, we used a comprehensive steepness-based parameterization of the stock-

recruitment relationship that directly depends upon habitat quality and surface area of nursery habitats. The model was applied to three different species selected after preliminary analysis for their contrasting LHT. We performed simulations to explore the response of population productivity and fisheries yield to different scenarios of degradation/restoration of nursery habitat quality and surface area, and explore how those responses vary across a range of contrasting life histories.

### 3.1.2 Material and methods

#### 3.1.2.1 *Model overview*

Population dynamics is simulated by a deterministic life cycle model (fully described in Supp. Mat. 3.1.1) structured by age ( $a$  subscript) and stage with a year time step ( $y$  subscript).

Fish are assumed to recruit at age  $a_{rec}$ . For all ages classes  $a_{rec} < a \leq a_{max}$ , population abundance ( $N$ ) is described by equation 1:

$$N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y}+F_{a,y})} \quad (\text{eq. 1})$$

with  $M$  and  $F$  the natural and fishing mortality rates, respectively.

Recruitment is the critical component of this model as it accounts for the habitat-mediated mortalities during juvenile stage. The mortality from eggs to recruited juvenile is assumed to follow a compensatory density dependent mortality process as a result of intra-cohort competition for trophic resources and/or space (Beverton & Holt, 1957). The dynamic of a cohort facing density-dependent mortality between the eggs and the recruitment stage can be written as a partial differential equation in continuous time (Quinn & Deriso, 1999; equation 2):

$$\frac{1}{N_t} \times \frac{dN_t}{dt} = -M_{DI} - M_{DD} \frac{N_t}{S} \quad (\text{eq. 2})$$

with  $N_t$  the cohort abundance at any instant  $t$ ,  $M_{DI}$  and  $M_{DD}$  the instantaneous density-independent and density-dependent mortality rate,  $S$  the surface area of the nursery ground.  $M_{DI}$ ,  $M_{DD}$  and  $S$  are considered constant over time. A strong hypothesis in this model is that the parameters  $M_{DI}$  and  $M_{DD}$  are considered constant and homogenous in space over the entire surface area of the nursery, meaning that the habitat quality is homogeneous over the entire surface of the nursery.

Each year, the number of eggs potentially spawned is computed based on adult abundance, female proportion, probability of being mature, weight at age and fecundity. Starting from an initial number of eggs denoted  $\omega_{y-a_{rec}}$  that first survive to the larval drift with density-independent survival  $e^{-M_{larvae}}$  before settling in the nursery areas, the recruitment  $N_{a_{rec},y}$  is defined as the number of juveniles that survive the time range between spawning and recruitment.  $N_{a_{rec},y}$  is obtained by the integration of equation 2 during a duration  $a_{rec}$ , starting with an initial abundance  $\omega_{y-a_{rec}} \times e^{-M_{larvae}}$ :

$$N_{a_{rec},y} = \frac{e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \omega_{y-a_{rec}}}{1 + \frac{1}{S} \times \frac{M_{DD}}{M_{DI}} \times (e^{M_{DI} \times a_{rec}} - 1) \times e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \omega_{y-a_{rec}}} \quad (\text{eq. 3})$$

Equation 3 is a logistic Beverton-Holt relationship (Quinn & Deriso, 1999) parameterised in terms of instantaneous mortality rates  $M_{DD}$  and  $M_{DI}$ , and the total surface area of the nursery  $S$ . It can be reparametrised in terms of steepness  $h$  and its asymptote,  $K$  interpreted as the carrying capacity of the nursery (the maximum number of juveniles that a nursery area can produce; (Del Monte-Luna et al., 2004). Under the hypothesis that habitat quality is homogeneous in space,  $K$  writes as the product of a carrying capacity per unit of surface  $K^*$ , that denotes the quality of habitat (and that is function of the rates  $M_{DI}$  and  $M_{DD}$ ) and  $S$  the surface area of the nursery. Hence equation 3 can also be written as (see SuppMat 2 for more details on the derivations):

$$N_{a_{rec},y} = \frac{4h \times \omega_{y-a_{rec}}}{\bar{W}(1-h) + \frac{1}{S} \times \frac{4h}{K^*} \times \omega_{y-a_{rec}}} \quad (\text{eq. 4})$$

with  $\bar{W}$  the average number of eggs produced by a recruit during its lifetime (see SuppMat 3.1.2). There is a one-to one relationship between the parameterizations in equation 3 and in equation 4. The carrying capacity per unit of surface can be derived from equation 3 as (equation 5):

$$K^* = \frac{M_{DI}}{M_{DD}} \times \frac{1}{(e^{M_{DI} \times a_{rec}} - 1)} \quad (\text{eq. 5})$$

The steepness  $h$  is defined as (equation 6):

$$h = \frac{e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}{4 + e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}} \quad (\text{eq. 6})$$

### 3.1.2.2 Habitat scenarios

Parameterization of the SRR in terms of instantaneous mortality rates  $M_{DI}$  and  $M_{DD}$  and surface area  $S$  in equation 3 provides a comprehensive parameterization of scenarios of habitat quality and surface areas. Parameterization of scenarios of restoration/degradation of the surface area of nursery is straightforward with a multiplier ( $\lambda_{surface}$ , henceforth, surface multiplier) directly applied to the surface area of nursery habitat  $S$  in equations 3 or 4. Scenarios of restoration/degradation of the quality of juvenile habitat were parameterised by applying a multiplier to the instantaneous mortality rates  $M_{DI}$  and  $M_{DD}$ . For example, a contaminated and/or eutrophic estuary can lead to physiological disabilities resulting in an increase of juvenile density-independent mortality, but can also affect trophic resources and consequently the density-dependent mortality term (Brown et al., 2018; Champagnat et al., 2021). Because no information was available to define how a quality scenario would impact differently  $M_{DI}$  and  $M_{DD}$ , we assumed a common multiplier ( $\lambda_{quality}$ ) for  $M_{DI}$  and  $M_{DD}$  as a default hypothesis. We use  $\frac{1}{\lambda_{surface}}$  as a multiplier of surface area so that  $\lambda_{quality} > 1$  and  $\lambda_{surface} > 1$  both simulate habitat degradation; whereas values  $<1$  represent restoration.

The carrying capacity and steepness as a function of surface and quality multiplier can then be calculated from equations 5 and 6:

$$K(\lambda_{surface}, \lambda_{quality}) = K^*(\lambda_{quality}) \times \frac{S}{\lambda_{surface}} \quad (\text{eq. 7})$$

with the carrying capacity per unit of surface that only depends upon habitat quality

$$K^*(\lambda_{quality}) = \frac{M_{DI}}{M_{DD}} \times \frac{1}{(e^{M_{DI} \times \lambda_{quality} \times a_{rec}} - 1)} \quad (\text{eq. 8})$$

and the steepness that also only depends upon habitat quality

$$h(\lambda_{quality}) = \frac{e^{-M_{DI} \times \lambda_{quality} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}{4 + e^{-M_{DI} \times \lambda_{quality} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}} \quad (\text{eq. 9})$$

The derivative of steepness and carrying capacity with respect to quality and surface multipliers are given in SuppMat 4.

### 3.1.2.3 Parameterising the model for species with contrasting life history and stock-recruitment traits

Parametrization of the full life cycle model requires both LHT (natural mortality, maximum age, age at maturity, growth and fecundity) and stock-recruitment parameters. Most of them



can be extracted from the package Fishlife (Thorson, 2020; Thorson et al., 2017) which applies a multivariate model with a taxonomic structure to fish records from Fishbase (Froese & Pauly, 2022) and stock-recruitment series from the RAM database (Myers et al., 1995). The multivariate framework ensures that correlations among variables are considered while the hierarchical structure strengthens estimation for taxa with insufficient data. All together it provides a consistent framework to 1) select species with contrasting life histories, 2) parametrise our age-structured model for selected species.

Considering a large and contrasted selection of 86 exploited marine fish species for which the European Scientific, Technical and Economic Committee for Fisheries has stock status (Scientific, Technical and Economic Committee for Fisheries (STECF), 2019), we conducted a PCA on LHT (age at maturity, asymptotic size, natural mortality and steepness) to select species with highly contrasting life history (see SuppMat 3 for details on species selection). European anchovy (*Engraulis encrasicolus*, Engraulidae), European plaice (*Pleuronectes platessa*, Pleuronectidae) and cuckoo ray (*Leucoraja naevus*, Rajidae) were chosen. They were highly scattered on the first two dimensions of the PCA and good representatives of a short-lived species (anchovy), and two long-lived species with contrasting steepness and fecundity values (plaice and cuckoo ray) (Table 3.1.1).

In addition to parameters from FishLife, other parameters needed to complete the model were drawn from the literature (e.g., length-weight relationship and fecundity, SuppMat 3.1.3). The age at recruitment,  $a_{rec}$ , was set a 1 for all species, which implies a hypothesis of density dependent processes impacting only the survival from larval to age 1. The carrying capacity of the nursery ( $K$ ) is a scaling factor of population size and the baseline value was arbitrarily set to  $10^6$  for all species. Because the carrying capacity writes as the product of carrying capacity per unit of surface and the nursery habitat surface area, we specified  $K^* = 1$  and  $S = 10^6$ , for all species. Baseline values of  $M_{DI}$  and  $M_{DD}$  (values for  $\lambda_{quality} = 1$ ) were derived by reversing equations 7-8-9:  $M_{DI}$  is derived from steepness, larval mortality and mean number of eggs produced by a recruit during its lifetime (eq. 9) while  $M_{DD}$  is totally determined by the values of  $M_{DI}$  and  $K^*$  (Table 3.1.1).

*Table 3.1.1: Life history traits for the three-example species in the baseline configuration.  $a_{mat}$  and  $a_{max}$  refer to maturity and maximum age,  $M$  is natural mortality,  $h$  is steepness,  $r$  is the intrinsic rate of population increase (all extracted from FishLife, Thorson, 2020).  $e^{-M_{larvae}}$  is the survival resulting after eggs and larval mortality (Le Pape and Bonhommeau, 2015).  $\bar{W}$  is the mean number of eggs produced by a recruit during its lifetime in the absence of fishing, computed based on species LHT. Baseline values of density-independent mortality rate  $M_{DI}$  is calculated from eq. (6). Density-dependent mortality rate  $M_{DD}$  is deduced from  $K^*$  and  $M_{DI}$  (eq. 5).*

Species	$a_{mat}$	$a_{max}$	$M$	$h$	$e^{-M_{larvae}}$	$\bar{W}$	$r$	$M_{DI}$	$M_{DD}$
<b>European anchovy</b>	1	5	0.91	0.7	$10^{-3}$	$5.4 \times 10^4$	0.66	1.7	0.37
<b>Cuckoo ray</b>	9	18	0.20	0.42	1	39.7	0.07	2.6	0.2
<b>European plaice</b>	4	28	0.14	0.82	$10^{-3}$	$4.7 \times 10^5$	0.25	3.2	0.13

#### 3.1.2.4 Simulations

The model was used to simulate population dynamics under various habitat scenarios (i.e., combinations of  $\lambda_{surface}$  and  $\lambda_{quality}$ ). Habitat scenarios were run by setting multipliers of surface and quality to values between 0.25 and 1.25. First marginal effects were investigated by varying one of the two multipliers, the second one being fixed to one. Then cumulated effects were evaluated by exploring all possible combinations of  $\lambda_{surface}$  and  $\lambda_{quality}$  within the explored range.

For each scenario, the effect habitat scenarios combined to fishing pressure was assessed by exploring a wide range of fishing mortality rates ( $F$  from 0 to 1.5). The population was simulated with constant conditions ( $F$  and all parameters) during 1000 years to reach an equilibrium state. Results were used to empirically construct the equilibrium curve relating Catch ( $C$ ) and Spawning Stock Biomass ( $SSB$ ) at equilibrium, from which we deduced catches, spawning biomass and fishing mortality at the Maximum Sustainable Yield ( $C_{MSY}$ ,  $SSB_{MSY}$  and  $F_{MSY}$ , respectively) widely used key indicators of the stock status and management reference points (Hilborn & Walters, 1992).

Consequences of habitat changes on stock-recruitment parameters and population dynamics under exploitation were investigated through the gain/loss relative to the baseline scenario calculated as the impact factor (equation 10):

$$impact(scenario) = \log\left(\frac{indicator_{scenario}}{indicator_{baseline}}\right) \text{ (eq. 10)}$$

with indicator being  $h$ ,  $K$ ,  $F_{MSY}$ ,  $SSB_{MSY}$  or  $C_{MSY}$ , alternatively.

Model simulations were performed with R, all scripts used are available on <https://github.com/jchampag/GenericLifeCycle>.

### 3.1.3 Results

First, a detailed interpretation of the results on European plaice is presented, with details on the consequences of changes in both habitat size and quality. Then the differences between species will be highlighted to analyse the sensitivity to life history.

#### 3.1.3.1 *European plaice*

##### Marginal habitat scenarios

The explored range of multipliers results in large variations of  $h$  and  $K$  values (Fig. 3.1.1). Modifying the surface area of nurseries ( $\lambda_{surface}$ ) logically affects the carrying capacity  $K$ , defined as a product of carrying capacity per unit of surface and nursery surface area. The steepness is independent of the surface of nursery habitat (eq. 6) and consequently, remains at its baseline value for this scenario. By contrast, scenarios affecting the quality of nursery habitat ( $\lambda_{quality}$ ) induce modifications of both steepness and carrying capacity (eq. 8 and 9). The steepness changes almost linearly with quality multiplier. Carrying capacity declines with quality multiplier, with a higher rate of change induces than for the surface multiplier. It can be noticed that  $K$  response to both multipliers is non-symmetrical for degradation/restoration because of its nonlinear (inverse or exponential) relation with multipliers (eq. 7 and 8).

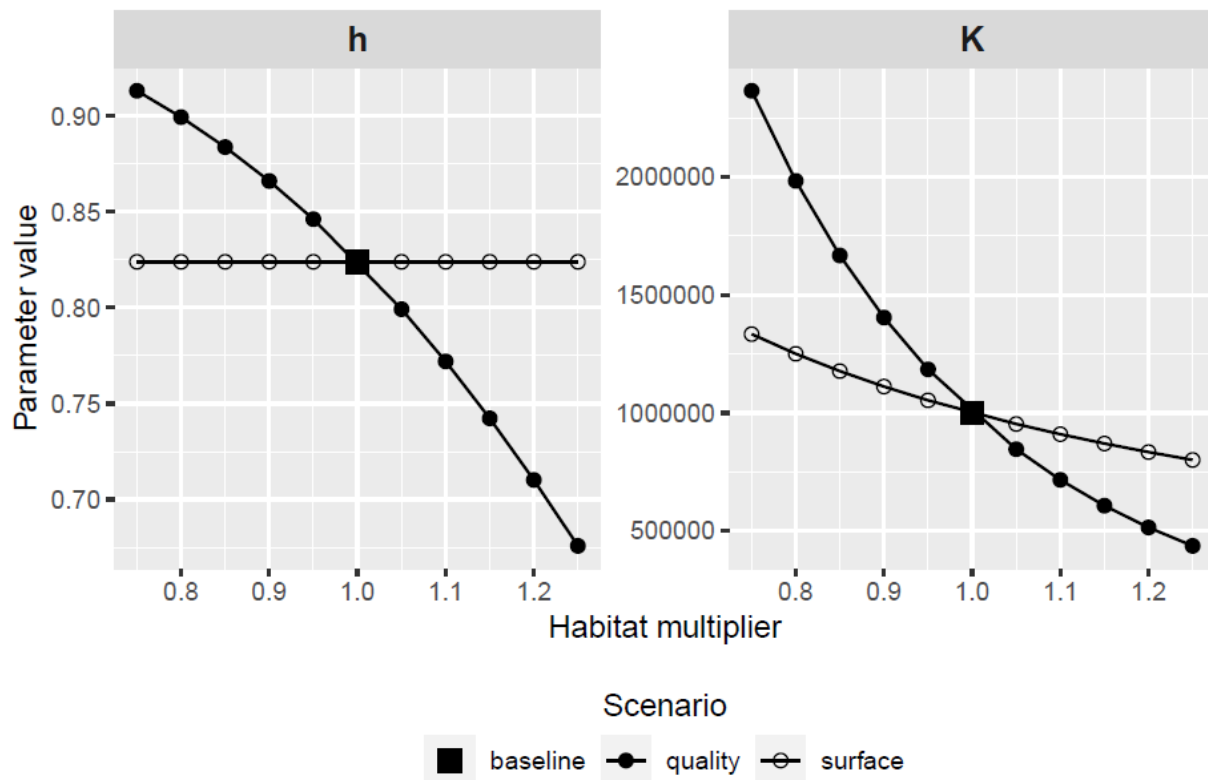


Figure 3.1.1: Effect of modifying quality (plain black points) and surface area (white points) of juvenile habitat compared to the baseline (black bold square) on the steepness ( $h$ ) and carrying capacity ( $K$ ) of the European plaice. Habitat multiplier  $>1$  (resp.  $<1$ ) correspond to a habitat degradation (resp. improvement).

Modifications of stock-recruitment parameters affect population dynamics and productivity. Equilibrium productivity curves are modified by both habitat scenarios with noticeable differences between scenarios of surface and quality (Fig. 3.1.2).

Modifying the surface area of juvenile habitat only impacts  $K$  (that sets the size of the population) hence only impacts the scale of the productivity curve, with increased (resp., decreased) level of biomass and catches at  $MSY$  ( $SSB_{MSY}$  not shown,  $C_{MSY}$  Fig. 3.1.2) for restoration (resp. degradation) scenarios. But  $h$ , hence  $F_{MSY}$ , remains unchanged.

By contrast, modifying habitat quality affects both  $K$  and  $h$  parameters, and hence not only increase (resp., decrease) yields for restoration (resp., degradation) scenarios but also increase (resp., decrease) fishing mortality maximising the catch ( $F_{MSY}$ , grey dots in Fig. 3.1.2). It is also worth noting that the response of catches at  $MSY$  to quality scenarios is quantitatively higher than to surface scenarios because the carrying capacity is an exponential function of the habitat multiplier (eq. 8) when it is a linear function of the surface multiplier (eq. 7) (but see also Supp. Mat. 3.1.4).

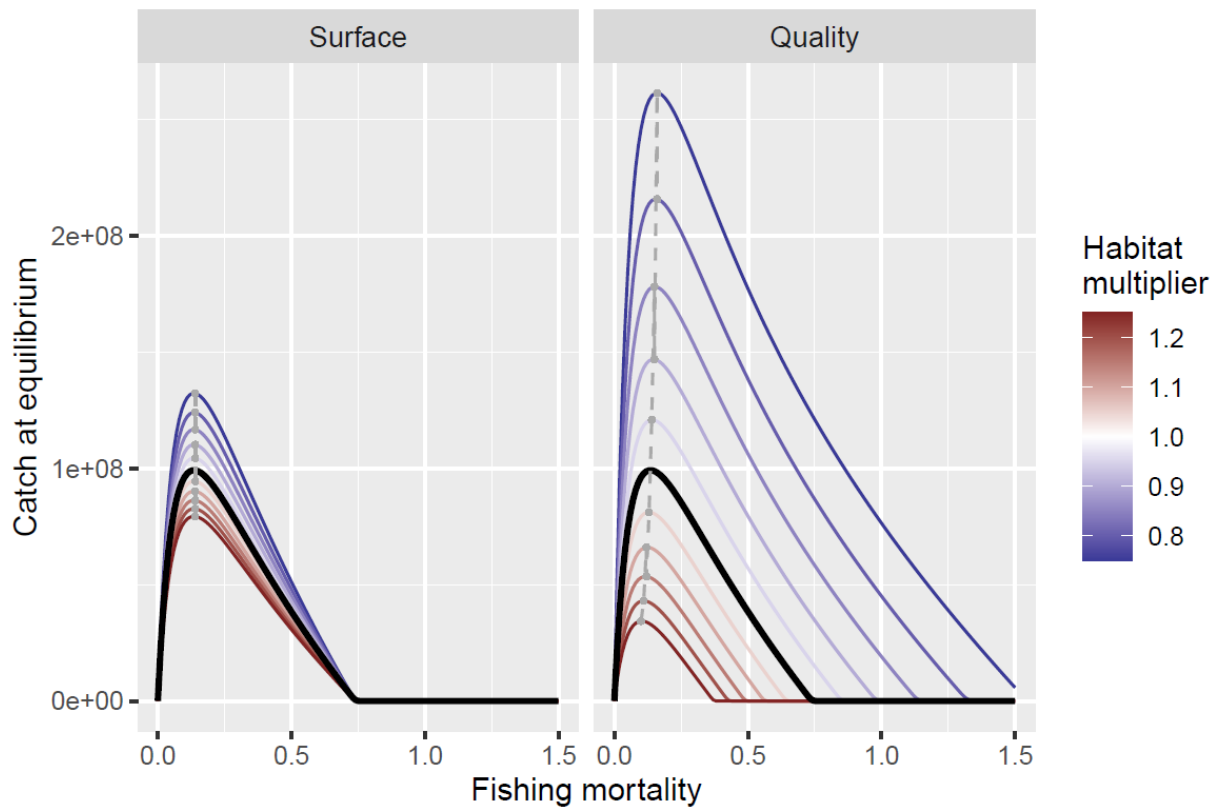


Figure 3.1.2: Effect of modifying the surface area (left panel) and the quality (right panel) of juvenile habitat on equilibrium productivity curves of the European plaice. Black line is the baseline scenario, blue and red lines show scenarios of habitat improvement (multiplier  $< 1$ ) and degradation (multiplier  $> 1$ ) respectively. The grey points and dotted line highlight changes in  $MSY/F_{MSY}$  according to simulations.

#### Combined habitat scenarios

The value of steepness changes gradually with the quality multiplier, without effect of surface area scenario (Fig. 3.1.3). The carrying capacity is modified by both surface and quality multiplier, but with a higher sensitivity to the quality multiplier, most of the gradient in values of  $K$  being induced by changes in this multiplier (Fig. 3.1.3), which is a direct consequence of the fact that carrying capacity is an exponential function of the habitat multiplier (eq. 8) when it is a linear function of the surface multiplier (eq. 7) (but see also Supp. Mat. 3.1.4).

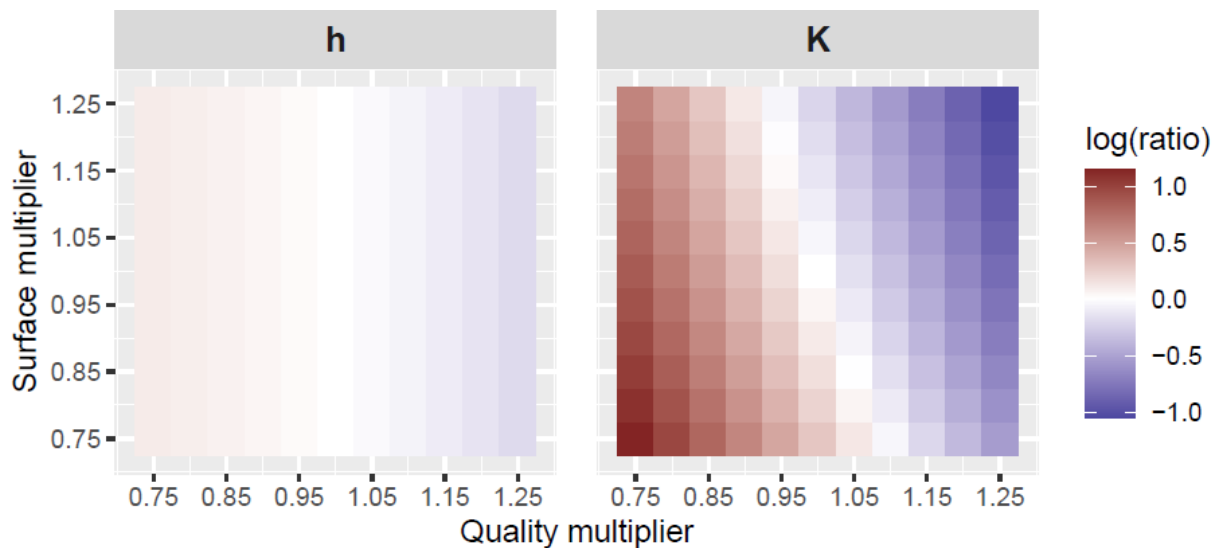


Figure 3.1.3: Effect of juvenile habitat scenario combining quality and surface area modifications on the value of  $h$  and  $K$  parameters for the European plaice. Habitat multiplier  $>1$  (resp.  $<1$ ) correspond to a habitat degradation (resp. improvement). The colour indicates intensity of gain (red) or loss (blue).

As expected,  $F_{MSY}$  only depends on steepness  $h$  and hence is only affected by changes in habitat quality, but not by changes in the surface area (Fig. 3.1.4). By contrast, biomass and yield at MSY depend upon both  $h$  and  $K$ , hence are affected by both changes in habitats quality and quantity (Fig. 3.1.4), with a higher sensitivity to the quality multiplier that logically follows the response of  $K$  (Fig. 3.1.3).

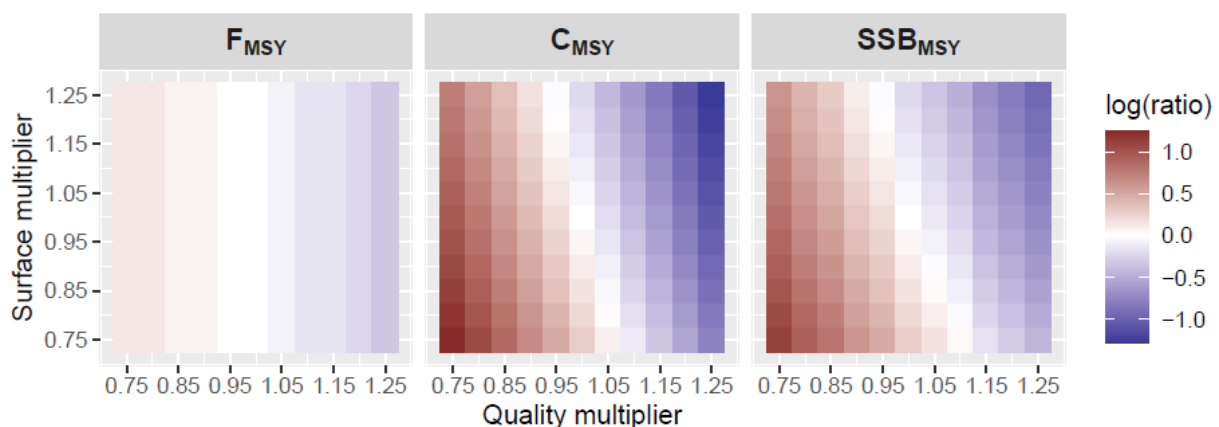


Figure 3.1.4: Effect of juvenile habitat scenario combining quality and surface area modifications on the value of  $F_{MSY}$ ,  $C_{MSY}$  and  $SSB_{MSY}$  for the European plaice. Habitat multiplier  $>1$  (resp.  $<1$ ) correspond to a habitat degradation (resp. improvement). The colour indicates intensity of gain (red) or loss (blue).

### 3.1.3.2 Comparing the response across contrasted life histories

As for plaice, modifying the surface area of nursery habitat only affects carrying capacity but not steepness, and the influence of the surface multiplier on  $K$  is identical across the species (Fig. 3.1.5). Again, this response was expected as the partial derivative of  $K$  relative to the surface multiplier is proportional to  $K$  (eq. S4.4 in Supp. Mat.3.1.4).

As already observed for plaice, scenarios affecting the quality of nursery habitat induce modifications of both steepness and carrying capacity. The sensitivity to quality multiplier depends upon the species-specific life history parameters (Fig. 3.1.5; but see also equations in Supp. Mat. 3.1.4). Steepness sensitivity depends on  $M_{DI}$ , larval mortality and the number of eggs produced on average by a recruit during its lifetime (eq. S4.5 in Supp. Mat.3.1.4). Steepness of cuckoo ray is the most sensitive, while plaice and anchovy are less sensitive to change in habitat quality. The steepness sensitivity relative to the quality multiplier as a function of life history traits value (Fig. S3.1.4.1) emphasises the very low sensitivity of anchovy, in relation to the low value of  $M_{DI}$  (lowest of the three species, Table 3.1.1). Low sensitivity of plaice steepness is related to a high value of the product  $\bar{W} \times e^{-M_{larvae}}$  (highest of the three species, Table 3.1.1). The carrying capacity sensitivity relative to the quality multiplier displays two groups of species. Anchovy and cuckoo ray, with a much lower sensitivity, as a direct consequence of lower value of  $M_{DI}$ , and higher value of  $M_{DD}$  for these two species. On the opposite, plaice is more sensitive because of higher value of  $M_{DI}$  and lower value of  $M_{DD}$  (eq. S4.6 in Supp. Mat.3.1.4 and Fig. S3.1.4.2).

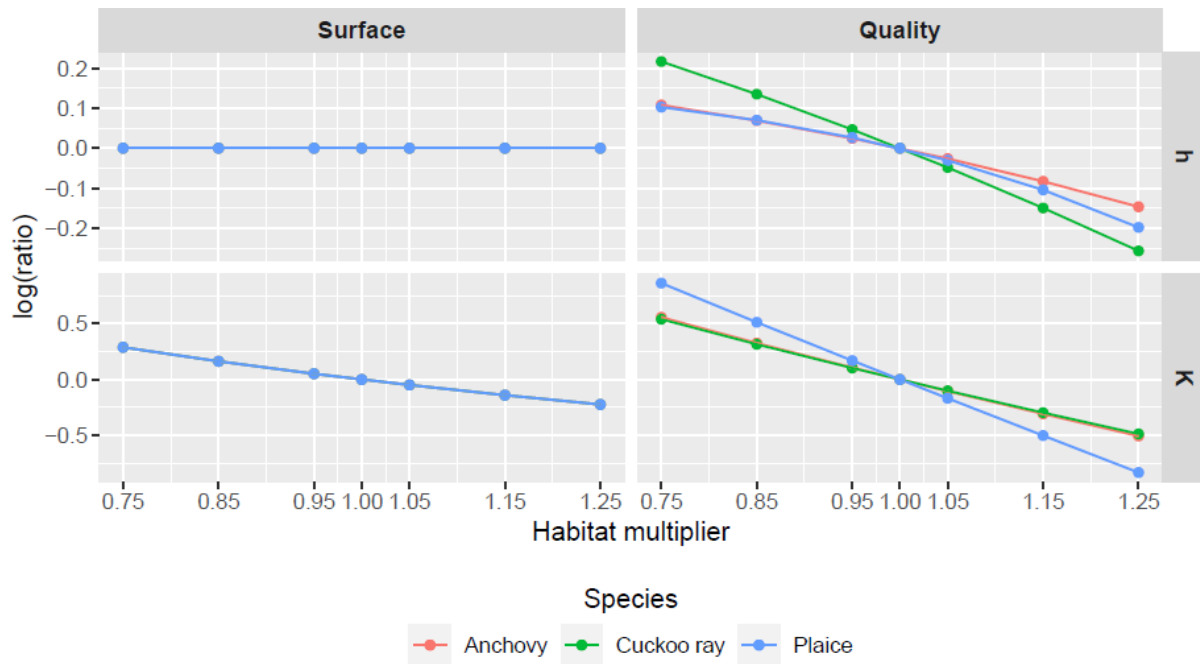


Figure 3.1.5: Effect of modifying the surface area (left panel) and the quality (right panel) of juvenile nursery habitat on the value of  $h$  and  $K$  parameters for three species. Habitat multiplier  $>1$  (resp.  $<1$ ) correspond to a habitat degradation (resp. improvement).

As for plaice (Fig. 3.1.2), modifying the surface area of nursery habitat has a direct scaling effect on  $C_{MSY}$  and  $SSB_{MSY}$  and no consequences on  $F_{MSY}$ . As mentioned above, there is no differences among species in  $K$  response leading to identical responses of population dynamics.

Overall, the group of species identified in the response of stock-recruitment parameters also emerged in the MSY indicators (Fig. 3.1.6). Loss/gain in  $F_{MSY}$  could be anticipated from the sensitivity of the steepness relative to the quality multiplier (eq. S4.7 in Supp. Mat.3.1.4 and Fig. S3.1.4.3): cuckoo ray reveals the most sensitive, plaice has an intermediary value, and the value for anchovy remains nearly unchanged, in accordance with the low sensitivity of its steepness. It is worth noting that  $F_{MSY}$  response for plaice is stronger for degradation (multiplier  $>1$ ) than for restoration (multiplier  $<1$ ). Responses of  $SSB_{MSY}$  are driven by the carrying capacity sensitivity, thus exhibit contrasts between anchovy which is less sensitive and plaice which is more sensitive (eq. S4.6 in Supp. Mat.3.1.4 and Fig. S3.1.4.2). For cuckoo ray,  $SSB_{MSY}$  responses depend upon the multiplier value; with less sensitivity for restoration (comparable to anchovy) and higher one for degradation (comparable to plaice). The sensitivity of  $C_{MSY}$  results from a combination of the stock size ( $SSB_{MSY}$ ) and fishing level ( $F_{MSY}$ ). Consequently, cuckoo ray and plaice display the highest (mix of strong and intermediary responses in  $SSB_{MSY}$  and  $F_{MSY}$ ), and anchovy has the weakest response (weak responses in  $SSB_{MSY}$  and  $F_{MSY}$ ).



Differences between restauration and degradation appear again with similar response for ray and plaice for restauration and stronger response of ray for degradation (Fig. 3.1.6).

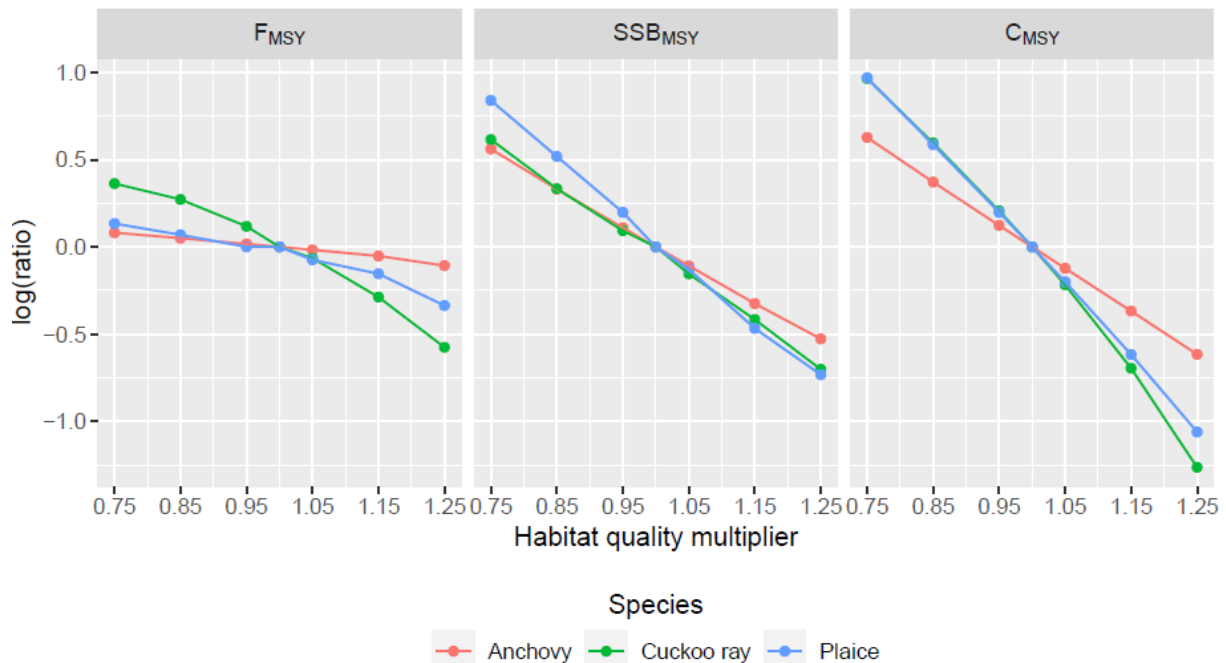


Figure 3.1.6: Effect of juvenile habitat quality scenarios on the value of  $F_{MSY}$  (left panel),  $SSB_{MSY}$  (central panel) and  $C_{MSY}$  (right panel) for three species.

### 3.1.4 Discussion

Our approach combined an age and stage-structured model with a steepness-based stock-recruitment relationship designed to assess the consequences of nursery habitat degradation/restoration on the productivity of exploited marine fish populations. Both quality and surface area scenarios led to modification in population size and yield at MSY, with different magnitudes. Quality scenarios also changed the shape of the productivity curve determining the level of fishing mortality at MSY. When combining quality and surface area scenarios, the overall responses were mainly driven by changes in habitat quality. Sensitivity of indicators to changes in surface area was identical across species, while response to quality scenario dramatically depended on the species life histories. Overall, the results were sensible with gradient of life history traits. Ray population (large body size, long-living, low steepness) exhibited the highest sensitivity of  $F_{MSY}$  to habitat quality degradation and anchovy population (small body size, short living, high steepness) the lowest.

#### 3.1.4.1 *The need for a generic model integrating habitat in exploited marine fish population dynamics*

Previous studies have already investigated the effect of habitat surface area and/or quality scenarios based on modification of stock-recruitment parameters. (Moussalli and Hilborn, 1986) assigned new values to stage specific survival and capacities. Other authors expressed those parameters as function of habitat attributes, such as temperature (Honea et al., 2009; Scheuerell et al., 2006; Stelzenmüller et al., 2010), river flows (Ruiz et al., 2009; Scheuerell et al., 2006), sediment or habitat structure (Honea et al., 2009; Mizerek et al., 2011; Scheuerell et al., 2006), habitat size (Camp et al., 2020), oxygen (Rose et al., 2018), pollutions (Ono et al., 2019), or a combination of environmental factors (Rahikainen et al., 2017). (Rochette et al., 2013), then (Archambault et al., 2018) and (Champagnat et al., 2021) used a spatially structured life cycle model to simulate scenarios regarding surface area (empiric estimations from historical habitat suitability maps) and quality (stock-recruitment parameters substitution for degraded area with values from a less impacted zone). However, these population models remained strongly case-specific, were highly data demanding to be parameterised, at the cost of genericity and transferability (Lipcius et al., 2019). Our work provides a substantive contribution by using a comprehensive steepness-based parameterization of the stock-recruitment relationship that directly depends upon habitat quality and surface area of nursery habitats. This stock-recruitment model was incorporated into a standard age- and stage-structured population model to simulate population dynamics under combined scenarios of nursery degradation or restoration.

Our approach could potentially be applied to any population for which key life history traits (natural mortality, maximum age, age at maturity, growth, weight and fecundity) and stock-recruitment parameters (steepness, larval survival) are available. Those can be extracted from the literature (e.g., global database like FishBase, (Froese and Pauly, 2022); meta-analyses like Fishlife package, (Thorson, 2020)) and/or from analytical stock assessment models. Hence, given that analytical stock assessment models exist for more than a thousand stocks worldwide (1359 assessed stocks in the RAM database; (Myers et al., 1995), in February 2023) and for 43% of the 256 evaluated stocks in the Northeast Atlantic (Scientific, Technical and Economic Committee for Fisheries (STECF), 2022), our method has a great potential of application.

#### 3.1.4.2 *Effect of nursery habitat size and quality on population production*

Juvenile habitat impacted population dynamics through direct effects on stock-recruitment parameters (steepness and juvenile carrying capacity). Carrying capacity directly depends upon

habitat surface area and both density-dependent and density-independent mortality, whereas steepness is a function of density-independent mortality rate only. Thus, population response differed according to the scenarios.

Surface area scenarios proportionally affected carrying capacity (the larger the surface area, the higher  $K$ , (Ma et al., 2022; Sundblad & Bergström, 2014) without any effects on steepness. Consequently, surface area scenarios did not affect the relative productivity of the stock nor the level of fishing mortality at MSY (Moussalli & Hilborn, 1986), but impacted the magnitude of the spawning biomass and catches for a given level of fishing mortality (Archambault et al., 2018; Champagnat et al., 2021). Biomass and catch at MSY were proportional to surface multiplier (Camp et al., 2020).

Quality scenario had a more complex influence. The carrying capacity that set the population size is affected (van Poorten et al., 2018) and thus the number of individuals available for harvest. But quality scenarios also impacted steepness (Munyandorero, 2020; Thorson, 2020) which drives the productivity of the stock, thus modified the response to exploitation, hence the  $F_{MSY}$  (Horbowy and Hommik, 2022) and the related biomass and catches at MSY (Moussalli & Hilborn, 1986). Both effects were cumulated for  $C_{MSY}$ , resulting in high sensitivity of this indicator to quality scenario.

When surface and quality are combined (Champagnat et al., 2021), both parameters' modification are at play, leading to cumulative results when transferred to the population.

#### 3.1.4.3 Limitations

Our approach however had some limitations. First, we parameterised archetypes from the literature and we arbitrarily set the baseline population size to  $10^6$ , without embedding our model within a full statistical approach to estimate all parameters. As a consequence, MSY related indicators may have different values than the one estimated from data-driven stock assessment models. For instance, baseline scenario led to a  $F_{MSY}$  value of 0.14 for plaice while estimation for North Sea and Skagerrak plaice stocks reached 0.19 (ICES, 2021b). No  $F_{MSY}$  estimations from stock assessment were available for comparison for cuckoo ray and anchovy. The ratio  $\frac{C_{MSY}}{SSB_{MSY}}$  is supposed to be proportional to  $r$ , the intrinsic rate of population increase (Winker et al., 2018), leading to lower values for species characterised by low fecundity and thus lower resiliency to fishing. This ratio reached values of 0.13, 0.15 and 0.39 for plaice, cuckoo ray and anchovy respectively, apart from plaice having a lower value than cuckoo ray,

the ranking matched our expectations in relation with intrinsic rate of population increase value for each species ( $r$  value in Table 3.1.1).

Our quality scenarios assumed a unique multiplier that modifies both the density-dependent and -independent mortality rate. This is a strong assumption because both mortality terms could be associated with different mechanisms. The density-dependent mortality rate refers to interactions with congeners of the same cohort, mostly competition for food or space (Maunder, 2022). It is generally attributed to density-dependent growth, reproduction and movement affecting survival (Craig et al., 2007; Le Pape & Bonhommeau, 2015; Stige et al., 2019). Density-independent mortality may involve other mortality processes linked to a large panel of environmental stresses (e.g. pollutant, Ono et al., 2019; Rose et al., 2003). However, no previous knowledge nor experimental studies were available to build sensible quantification of how  $M_{DI}$  and  $M_{DD}$  should be impacted separately. While many in-laboratory studies have shown the adverse impact of anthropogenic stressors to the fitness of individuals, evidences of the direct influence of stressors on marine fish demography are dramatically lacking (Ono et al., 2019; Schneeweiss et al., 2023). The lack of information on vital rates at population scale was evidenced for a large panel of meta-analyses (Brown et al., 2018; Champagnat et al., 2021; Rabalais, 2015; Vasconcelos et al., 2014), hampering to estimate and separate out the influence of stressors on  $M_{DI}$  and  $M_{DD}$  (Johnson, 2007). For example, xenobiotics or oxygen depletion would affect individual (density-independent) mortality, but their impact at community scale could also alter prey and competition for food, thus, density-dependent mortality (Rose et al., 2018). Our simplifying hypothesis of a single multiplier systematically applied to both  $M_{DI}$  and  $M_{DD}$  may have led to overestimate the impact of quality scenarios.

Consequently, care should be taken when comparing surface area and quality scenarios. In addition, the processes modified by each multiplier (mortality rates and surface area) are at completely different scale, thus a change of +/-25% had dramatically different impacts in terms of value range. Thus, our comparison between these scenarios aimed to emphasise qualitative differences in responses between species and not quantitative ones. It also prevented us from analysing cumulative responses in the combined scenarios because of the stronger weight of quality in the response. This scale issue would have to be considered thoroughly when adapting the model to realistic scenarios.

Our model ignored all sources of uncertainty and stochasticity. Parameters were fixed and population dynamic was described as a deterministic process, whereas inter-individual

variability (demographic stochasticity; Koons et al., 2016; Plard et al., 2019) and multiple sources of environmental variations (environmental stochasticity; Engen et al., 1998; Pfister & Stevens, 2003; Rose et al., 2001) exist in the wild. This is particularly true for the strongly stochastic recruitment processes (Cury et al., 2014; Houde, 2008; Szuwalski et al., 2015), for which the level of stochasticity depends upon life history traits (Archambault et al., 2014). However, the present approach is based on a simplified population dynamic model easily parameterised from the literature, and scaling parameters uncertainty would therefore have been difficult. As already demonstrated (Archambault et al., 2018), integrating both parameters uncertainty and environmental stochasticity through classical hypothesis (random variations without trend or shift) would not change the qualitative results as the expectation (grand mean) of the population dynamics would behave similarly to the deterministic one.

The model considered juvenile habitat as one block, although coastal and estuary areas are marked by high spatial heterogeneity (Fodrie et al., 2009; Nagelkerken et al., 2015; Rochette et al., 2013; Wennhage & Pihl, 2001). Considering nursery habitat as a mosaic of habitat of different quality raises multiple questions about stock-recruitment parameters (White, 2010), strength of the density dependence in each area (Rochette et al., 2013) and population connectivity (Archambault et al., 2016). Diffusion of the outcomes of local nursery restoration at a metapopulation scale highly depends on the level of connectivity at different stage of the life cycle (Archambault et al., 2018). Including these spatial aspects would considerably enrich the model but would also multiply its complexity, making its parameterization and scenarios design difficult. Exploring the role of spatial structure and how it interacts with habitats scenarios would however constitute rich research avenues.

#### 3.1.4.4 *Population responses differ between life histories*

Our modelling approach highlighted difference in species responses to habitat quality, according to their life history traits. Indeed, the steepness (Horbowy & Hommik, 2022; Miller & Brooks, 2021) combined with other life history traits (i.e., life duration and mortality, Thorson, 2020) is the main driver of the relative productivity of a population.  $F_{MSY}$  sensitivity depended upon density-independent mortality rate and number of larvae reaching nursery stage produced on average by an egg. Strong responses were obtained for species with high  $M_{DI}$  values and low fecundity, here cuckoo ray (equation S4.7 and Fig. S3.1.4.3).

Several frameworks have been conceptualised to analyse species-specific population dynamics in relation to their life history parameters. (Langangen et al., 2023) and (White et al., 2022)

explored the consequences of early-life mass mortality events (also denominated as pulse disturbances) on population along a gradient of life histories. (Kindsvater et al., 2016b) focused on interspecific patterns in compensatory capacity, describing population's ability to withstand mortality (especially fishing mortality). They suggested to order species along two axes, fecundity and adult mortality, and identified four extreme strategies: Precocial, Opportunist, Survivor and Episodic (POSE). Regarding (Kindsvater et al., 2016b), we can characterise cuckoo ray as a survivor (long lifetime, large body size, low adult mortality and low fecundity) and anchovy as an opportunist (short lifetime, short body length, high fecundity, high adult mortality). Indeed, because of its low steepness (i.e., low compensation in recruitment dynamic), ray revealed very sensitive to habitat scenario, while anchovy, with a larger compensatory value, was less sensitive. Plaice was more difficult to analyse within the POSE framework. Indeed, some of its life history traits matched with episodic (long lifetime, low mortality and high fecundity), but this strategy is also characterised by a high recruitment variability (Winemiller, 2005) which does not apply for plaice (compared to other species; (Archambault et al., 2014; Iles and Beverton, 2000).

Studies of habitat restoration on anadromous fish population also indicated importance of life histories in the control of patterns and rates of re-colonization (Pess et al., 2014), but those life history traits were related to migration behavior.

#### *3.1.4.5 Management implications*

High importance of coastal and estuarine nursery grounds for many marine exploited species, as high levels of degradations of these habitats and related impacts on coastal nursery dependent species are well established (Brown et al., 2018). Several simulation studies have focused on the impacts of local restoration scenarios on global population (Camp et al., 2020; Fodrie et al., 2009; Ono et al., 2019; Ruiz et al., 2009), and some have shown that restoring coastal nurseries may be even more beneficial than regulating fishing pressure (Hughes et al., 2015; Levin and Stunz, 2005; van de Wolfshaar et al., 2015). The present study quantified consequences of both surface area loss and quality degradation of coastal habitat on population dynamics in a generic approach enabling transferability to multiple case studies. However, the direct application of our framework to enhance stock assessment models remains limited. Indeed, the time scale of habitat restoration is far beyond (few years to decades, (Duarte et al., 2020; Jokinen et al., 2016; Moreno-Mateos et al., 2012; Orth et al., 2020) the annual time scale of fisheries advice process and short term management objectives. Similarly to studies focusing on global change (Cheung

et al., 2010; Free et al., 2019; Rijnsdorp et al., 2010; Yeung and Yang, 2018), our study rather aimed to highlight mid to long term trends and not interannual changes, because of the extended time scale of processes at play.

Quantification of the effect of habitat restoration in the real world are rather rare, although some examples exist (Benayas et al., 2009; Buelow et al., 2022; Duarte et al., 2020; Schmitz, 2012). Habitat restorations have a longer history in freshwater ecosystems, implying higher hindsight to estimate population effect. Dam removal is a typical example of these habitat restoration actions and several examples showed the positive effect on anadromous fish population (Pess et al., 2014). Habitat enhancing in lakes has also proven efficacy to increase fish production (Radinger et al., 2023).

According to the requirement of the UN decade on ecosystem restoration, there is an urgent need to specifically consider the protection and restoration (Duarte et al., 2020; Radinger et al., 2023) of essential fish habitat to sustain marine fish and the related fisheries in conservation plans (Horwood et al., 1998), thereby integrating fisheries and ecosystem-based management (Kraufvelin et al., 2018).

#### Authors contributions

JC, ER and OLP conceived the ideas, designed methodology and analysed the results; JC executed the simulations, prepared the figures and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### Acknowledgements

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#### Data availability statement

Authors confirm that all the data underlying this study are fully available. Life history data used to parametrise the simulation model are either extracted from FishLife package (Thorson, 2017); either fully presented in SuppMat3. Scripts and data used to perform the analysis are available at <https://github.com/jchampag/GenericLifeCycle>.

## 3.2 Potential impacts of coastal and estuarine habitats restoration on the dynamics of nurseries dependent fisheries resources, a case study in the Eastern Channel

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Gernez M.<sup>1\*</sup>, Champagnat J.<sup>1</sup>, Rivot E.<sup>1</sup>, Le Pape O.<sup>1</sup>

<sup>1</sup>DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, IFREMER, INRAE, 35042 Rennes, France

Corresponding author: [mael.gernez@ifremer.fr](mailto:mael.gernez@ifremer.fr)

### Highlights

- Effects of restoration of nursery habitat common to four Eastern Channel species were assessed.
- Species with the higher concentration in shallow nurseries were the most sensitive to habitat restoration.
- Differences in life histories traits lead to species-specific responses: a lower steepness induces a stronger response to restoration of habitat quality.

### Abstract

Coastal and estuarine (CE) areas are essential fish habitats; they act as nurseries for a large proportion of species of fisheries interest but face high levels of cumulated anthropogenic pressures. A comprehensive analysis of the impacts of CE nursery habitat degradation at population scale for exploited fish species is still lacking. Our study aims at assessing the effects of restoration of CE nursery habitats for four species of main fisheries interest in the Eastern English Channel (EEC): sole, plaice, whiting and seabass. A generic age- and stage-based population model representing the dynamics of exploited populations and integrating the dependence of the recruitment on juvenile habitats is used to evaluate the combined effect of nursery degradation and fishing pressure on stocks dynamics. The model is parameterised for each of the four species, based on stock assessments outputs in the EEC and literature, then used to simulate equilibrium states under different scenarios of habitat quality. Scenarios of restoration are built using previous estimates of both surface loss and decrease in marine juvenile fish density in CE habitats facing anthropogenic pressures. Surface and quality restoration both enhance biomass and sustainable catch levels for the four species in the EEC.



The species with the higher level of concentration on shallow nursery areas were the most sensitive to habitat restoration. The response also depends on life history traits; i.e., species with lower steepness exhibit a stronger response to habitat quality scenarios.

**Keywords:** Coastal degradation; Nursery; Population dynamics; Maximum Sustainable Yield; Eastern English Channel.

### 3.2.1 Introduction

Coastal and estuarine (CE) areas are essential habitats for many fish species (Seitz et al., 2014). CE ecosystems act as nurseries for a large proportion of fish resources (Beck et al., 2001; Miller et al., 1984; Minello, 1999), play a major role in the renewal of nursery-dependent species (Gibson, 1994; Rijnsdorp et al., 1992) thus are of great importance to fisheries. For instance, two-thirds of commercial landings in the North-East Atlantic come from species using CE systems as nursery habitat (Brown et al., 2018).

However, the concentration of juveniles in CE areas renders them particularly vulnerable to human activities (Airoldi and Beck, 2007; Lotze, 2006). These pressures can impact both areas and suitability of these nursery habitats (Johnson et al., 1998; Peterson et al., 2000). Surface losses in CE areas lead to dramatic decrease of nursery habitat capacity (Rochette et al. 2010). Toxic effects of exposure to pollutants at juvenile stage impact growth and survival (Davoodi and Claireaux, 2007; Foekema et al., 2008; Wessel et al., 2010) but also future reproductive success (Daouk et al., 2011; Fonds et al., 1995; Horri et al., 2018). 92% of species that use coastal habitats are impacted by human pressures, which can be related to pollutants, eutrophication, anoxia, invasive species and physical development of the coastline (Brown et al., 2018).

However, if the impacts of local anthropogenic disturbance on juveniles of nearshore nursery-dependent species are well documented (Brown et al., 2018), their consequences for population renewal remain poorly quantified (Lotze, 2006; Sundblad and Bergström, 2014; Vasconcelos et al., 2014) and even largely unknown (Boyd et al., 2018; Hamilton et al., 2016; Rose et al., 2003). Few studies have quantified the impact of nursery habitat degradation at population scale from age- and stage-based models (Camp et al., 2020; Champagnat et al., 2021; Ono et al., 2019; Rose et al., 2018). These models were very case-specific, especially regarding the large amount of data and knowledge required for parameterization (Lipcius et al., 2019). Consequently, their application to other case studies is difficult or even not realistic, although

such approaches are required for management purpose (Hayes et al., 2009; Kraufvelin et al., 2018).

In this work, we used a generic age- and stage-structured population model for nursery-dependent exploited species (Champagnat et al. sub.) to quantify the importance of nursery restoration on population dynamics and productivity. This model describes density dependent survival in nursery area (hereafter called stock-recruitment relationship) with a Beverton and Holt (1957) relationship parametrised in terms of steepness (Mace and Doonan, 1988; Punt and Dorn, 2014) and carrying capacity. Parameterization of a stock specific stock-recruitment relationship between the spawning biomass and the number of recruits is spurious (Myers et al., 1999; Rose et al., 2001; Zhou, 2007). The steepness is a dimensionless proxy of the resilience of a stock to fishing pressure (Mangel et al., 2013; Munyandorero, 2020; Myers et al., 1999). Hierarchical meta-analyses have been conducted to provide relationships between steepness and life history traits that can be used to provide reliable estimates of steepness for a wide range of species (Hilborn, 2003; Myers and Mertz, 1998; Myers et al., 1999; Thorson, 2020). Formulating our model in terms of steepness hence provides a sensible way to parametrise stock-recruitment relationships for different species of fisheries interest. In addition, following Champagnat et al. (sub), the steepness-based parameterization of the stock-recruitment relationship is extended and directly depends upon habitat quality and surface of nursery habitats and allows for simulating habitat restoration scenarios.

The model was applied to nursery-dependent species of fisheries interest at the stock level/management unit in the Eastern English Channel (EEC). The EEC (ICES division 7.d; Fig. 3.2.1) is a fishery area of main interest (Ulrich et al., 2002). CE areas of the EEC face high levels of anthropogenic pressures (Champagnat et al., 2021; Le Pape et al., 2007). They experienced important morphological changes from land reclamation, channel dredging, and the building of dikes and harbors (Ducrotoy and Dauvin, 2008; Stamp et al., 2022), with a resulting substantial reduction in suitable nursery areas (Rochette et al., 2010). In addition, land-sea interfaces have been facing high levels of chemical contamination for decades in the EEC (Barjhoux et al., 2018; Meybeck et al., 2007; Tappin and Millward, 2015), causing reductions in habitat quality for marine juvenile fish (Amara et al., 2007; Courrat et al., 2009; Gilliers et al., 2006). Four species of high fisheries interest were accounted for this analysis: sole (*Solea solea*), plaice (*Pleuronectes platessa*), whiting (*Merlangius merlangus*) and seabass (*Dicentrarchus labrax*). These species have similar life cycle with juveniles concentrated in CE habitats but wider adult's distribution (Day et al., 2021; Leakey et al., 2008; Riou et al., 2001).

The study aims to quantify the effects of human disturbance on nurseries in the EEC and assess their consequences on the four populations of interest. We first parameterised the generic stage-based population model of Champagnat et al. (sub.) for the four populations of interest. Then, the model was used to simulate the response of populations to nursery habitat restoration scenarios. For this purpose, the loss of nursery habitat area in EEC since 1870 was quantified, and the effects of quality degradation on marine juvenile density were also estimated. Then, the potential effects of the restoration of both surface and quality of these habitats on population dynamics and fishery productivity were assessed and compared between species.

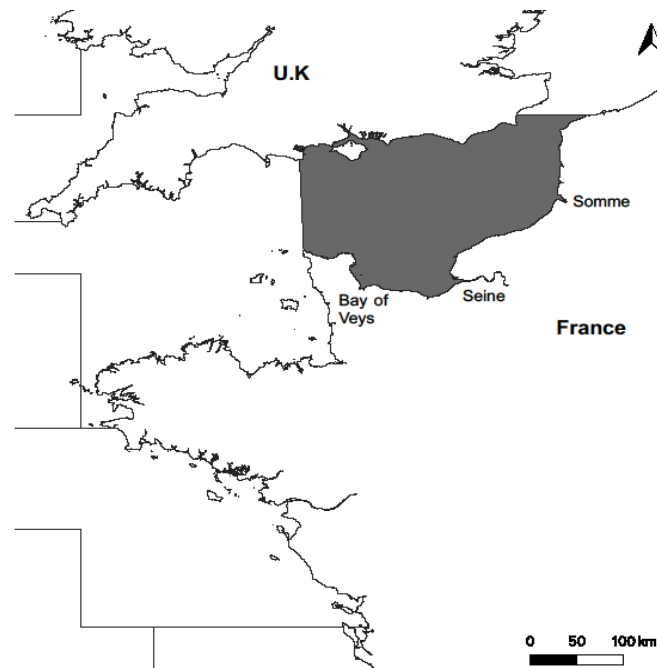


Figure 3.2.1. Location of the Eastern English Channel (ICES division 7.d)

### 3.2.2 Materials and Methods

#### 3.2.2.1 *Population dynamic model*

The impact of the degradation of nursery areas on stock productivity was simulated with a deterministic life cycle model, structured by stage and age (Champagnat et al. sub). This model considers a single closed population and a unique nursery area. After recruitment age ( $a_{rec}$ ), fish undergo both natural and fishing mortality. Population abundance ( $N_{a,y}$ ) at age  $a$  for year  $y$  is described by the classical population dynamics (equation 1):

$$N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y}+F_{a,y})} \quad (1)$$

with  $M$  and  $F$  the natural and fishing mortality rates, respectively.

For the last age group  $a_{max}$ , the population abundance is described as:

$$N_{a_{max},y+1} = N_{a_{max},y} \times e^{-(M_{a_{max},y}+F_{a_{max},y})} + N_{a_{max}-1,y} \times e^{-(M_{a_{max}-1,y}+F_{a_{max}-1,y})} \quad (2)$$

Recruitment, defined as the number of juveniles produced in nurseries, accounts for the habitat-mediated mortalities during juvenile stage and is the critical component of this model.

The recruitment  $N_{a_{rec},y}$  is computed from eggs numbers produced in a year,  $\omega_y$  (equation 3):

$$\omega_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times Mat_a \times pf_a \times Fec_a \quad (3)$$

with,  $Mat_a$  the probability of being mature at age  $a$ ,  $pf_a$  the female proportion at age  $a$ , and  $Fec_a$  the fecundity at age  $a$ , all considered constant in time.

The mortality from eggs to recruited juveniles follows a compensatory density dependent mortality process resulting from intra-cohort competition for trophic resources and/or space (Beverton and Holt, 1957). Recruitment ( $N_{a_{rec},y}$ ) is modelled by a Beverton-Holt relationship parametrised in terms of its asymptote,  $K$ , interpreted as the carrying capacity of the nursery, and steepness ( $h$ ) (equation 4):

$$N_{a_{rec},y} = \frac{4 \times h \times \omega_{y-1}}{\bar{W} \times (1-h) + \frac{4 \times h \times \omega_{y-1}}{K}} \quad (4)$$

$h$  is the steepness. It is defined as the proportion of unfished equilibrium recruitment produced when the spawning stock biomass is reduced to 20% of its unfished level (Mace and Doonan, 1988). It characterises the drop off in recruitment when the reproductive potential is reduced. It varies in theory from 0.2, for a linear stock-recruitment relationship, to 1, for a constant recruitment above 20% of pristine biomass (Mangel et al., 2013; Myers et al., 1999; Rindorf et al., 2022).

$K$  is the carrying capacity (Daily and Ehrlich, 1992), defined as the maximal number of juveniles that a nursery area can produce.

$\bar{W}$  is the average number of eggs produced by a recruit during its lifetime in the absence of fishing (equation in Supp. Mat 3.2.1).

Once parameterised for each species (see next section), this simulation model is used to simulate equilibrium states under a wide range of fishing mortality rate ( $F$ , from 0 to 1) to

empirically construct equilibrium curves for Catch (C) and Spawning Stock Biomass (SSB), enabling the estimation of management reference points such as  $SSB_{MSY}$ ,  $C_{MSY}$  and  $F_{MSY}$  (MSY, Maximum Sustainable Yield). Equations for computation of catch and SSB are available in appendix A.  $F_{MSY}$  and the ratio  $\frac{SSB_{MSY}}{SSB_0}$  will be used as indicators to be compared with stock assessment outputs and with empirical results of (Froese et al., 2016), respectively.

### 3.2.2.2 *Parameterization of the case studies*

For each of the four case studies, all stock-specific parameters were extracted from both stock assessments outputs and literature (Table 3.2.1), except for the carrying capacity ( $K$ ) which was calibrated.

#### *Parameters from stock assessment and literature*

Recruitment age, maximum age, weights at ages, maturity ogive and natural mortality were taken from the assessment reports for the four studied stocks (ICES, 2021a, 2021b). Fecundity equations, larvae mortality, and length at ages were collated from literature (Supp. Mat 3.2.2).

The Fishlife package (Thorson, 2020) was used to parameterise steepness for the baseline scenarios. This package analysed stock-recruitment series from the RAM database (Myers et al., 1995), in relation to life-histories data extracted from Fishbase (Froese and Pauly, 2022) using a multivariate hierarchical Bayesian model with taxonomic structure. Steepness values were extracted at the taxonomic level of the Order to obtain a robust estimate (Thorson, 2020).

#### *Calibration of carrying capacity for the baseline habitat scenario*

Only the parameter  $K$ , the carrying capacity of the nursery areas, which ultimately determines the population size, requires calibration. For each of the four case-study, the carrying capacity  $K$  representative of the current state (baseline habitat scenario) was estimated by minimising the difference between the SSB and catches simulated by our model with thus of the stock assessment outputs (i.e., by minimising the objective function in equation 5):

$$\sum_{y=y_{min}}^{y_{max}} (\log(SSB_{pred,y}) - \log(SSB_{ICES,y}))^2 + (\log(C_{pred,y}) - \log(C_{ICES,y}))^2 \quad (5)$$

with  $y_{min}$  and  $y_{max}$  the first and the last year of the stock assessments respectively,  $SSB_{pred}$  the model predictions of SSB,  $SSB_{ICES}$  the SSB provided by the stock specific assessment (ICES, 2021a, 2021b),  $C_{pred}$  the model predictions of catches and  $C_{ICES}$  the catches.

For sole and plaice, spawning stock biomass and catches were directly taken from the stock assessments (ICES, 2021a). For whiting (ICES, 2021a) and seabass(ICES, 2021b), SSB and catches were derived from stock assessments covering a wider area. They were scaled to the EEC proportionally to the average proportion of landings in division 7.d with respect to total landings (in Supp. Mat 3.2.3).

Table 3.2.1. Species-specific model parameterization for the baseline habitat scenario.

	<b>Recruitment age (<math>a_{rec}</math>)</b>	<b>Maximum age (<math>a_{max}</math>)</b>	<b>Steepness (<math>h</math>)</b> (Thorson, 2019)	<b>Natural mortality rate (<math>M</math>)</b>	<b>Larvae mortality rate (<math>M_{larvae}</math>)</b> (Le Pape and Bonhommeau, 2015)	<b>Carrying capacity (<math>K</math>)</b> (calibrated)
<b>Sole</b>	<b>1</b> (ICES, 2021a)	<b>11</b> (ICES, 2021a)	<b>0.771</b>	<b>0.1</b> (ICES, 2021a)	<b>3×log(10)</b>	<b>4.0 × 10<sup>7</sup></b>
<b>Plaice</b>	<b>1</b> (ICES, 2021a)	<b>7</b> (ICES, 2021a)	<b>0.771</b>	Age 1: <b>0.3531</b> ; Age 2: <b>0.3132</b> ; Age 3: <b>0.292</b> ; Age 4: <b>0.2749</b> ; Age 5: <b>0.2594</b> ; Age 6: <b>0.2474</b> ; Age 7: <b>0.2329</b> (ICES, 2021a)	<b>3×log(10)</b>	<b>7.1 × 10<sup>7</sup></b>
<b>Whiting</b>	<b>0</b> (ICES, 2021a)	<b>8</b> (ICES, 2021a)	<b>0.626</b>	Age 0: <b>2.0057</b> ; Age 1: <b>1.1510</b> ; Age 2: <b>0.6560</b> ; Age 3: <b>0.5107</b> ; Age 4: <b>0.4690</b> ; Age 5: <b>0.4477</b> ; Age 6: <b>0.3387</b> ; Age 7: <b>0.2797</b> ; Age 8: <b>0.2610</b> (ICES, 2021a)	<b>3×log(10)</b>	<b>5.3 × 10<sup>9</sup></b>
<b>Seabass</b>	<b>0</b> (ICES, 2021b)	<b>16</b> (ICES, 2021b)	<b>0.736</b>	<b>0.24</b> (ICES, 2021b)	<b>3×log(10)</b>	<b>1.1 × 10<sup>7</sup></b>

### 3.2.2.3 Parameterization of scenarios for CE nursery habitat

Scenarios of habitat restoration were parameterised by modifying both the surface and the quality of nursery habitat (Champagnat et al. sub), that will impact the two key parameters  $h$  and  $K$  in the stock-recruitment relationship in equation (4).

Modelling scenarios of surface modification is straightforward. The carrying capacity  $K$  depends directly on the surface  $S$  of the nursery habitats (equation 6). Writing the carrying capacity  $K$  as the product of a carrying capacity per unit of surface  $K^*$  and the surface  $S$ , we parameterised surface scenarios using a multiplier ( $\lambda_{surface}$ ) as follows:

$$K = K_{baseline}^* \times \frac{S_{baseline}}{\lambda_{surface}} \quad (6)$$

so as  $\lambda_{surface} = 1$  corresponds to the baseline situation and a value of  $\lambda_{surface} < 1$  denote an increase of surface area.

To model scenarios of habitat quality alteration/restoration, we rely on a parameterization developed by Champagnat et al. (sub) that used a parameterization of the stock-recruitment relationship (equation 4) in terms of instantaneous density-independent ( $M^{di}$ ) and density-dependent ( $M^{dd}$ ) mortality rates between larvae and juveniles (Quinn and Deriso, 1999). Relationships between classical ( $h$ ,  $K$ ) and new parameters ( $M^{di}$ ,  $M^{dd}$ ) can be written as (see Champagnat et al. (sub), and in Supp. Mat 3.2.1 for more details):

$$h = \frac{e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}{4 + e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}} \quad (7)$$

$$K = \frac{M^{di}}{M^{dd}} \times \frac{1}{e^{M^{di} \times a_{rec}} - 1} \times S \quad (8)$$

with  $M_{larvae}$  the density independent mortality occurring during larvae drift and  $S$  the surface of the nursery. Hence, looking at equation (6), the carrying capacity per unit of surface writes as a function of  $M^{di}$  and  $M^{dd}$  ( $K^* = \frac{M^{di}}{M^{dd}} \times \frac{1}{e^{M^{di} \times a_{rec}} - 1}$ ).

This alternative formulation allows us to parameterise the restoration (resp. alteration) of the quality of juvenile habitats in terms of a decrease (resp. increase) in both density-independent and density-dependent mortality rates,  $M^{di}$  and  $M^{dd}$  (Champagnat et al., sub.). A common multiplier ( $\lambda_{quality}$ ) is applied to  $M^{dd}$  and  $M^{di}$  which in turns modifies the values of  $h$  and  $K^*$ .

Finally, the combination of scenarios of surface alteration/restoration (playing with  $\lambda_{surface}$ ) and quality alteration/restoration (playing with  $\lambda_{quality}$ ) modifies stock-recruitment parameters ( $h, K$ ) as:

$$h = \frac{e^{-\lambda_{quality} \times M^{di} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}{4 + e^{-\lambda_{quality} \times M^{di} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}} \quad (9)$$

$$K = \frac{M^{di}}{M^{dd}} \times \frac{1}{e^{\lambda_{quality} \times M^{di} \times a_{rec} - 1}} \times \frac{S_{baseline}}{\lambda_{surface}} \quad (10)$$

### Parameterization of surface losses

The habitat surface scenarios were based on estimation of surface losses since 1870, derived from bathymetry data in three coastal sectors of the French EEC coastline in 1870 (Bay of Veys, Seine Estuary, Somme and Canche) available on the EMODnet website. The maps in 1870 were compared with the 2020 bathymetry map (in Supp. Mat 3.2.4). The loss of habitats above a bathymetry of 5 meters, including intertidal area, was estimated in each sector. This limit was chosen because it integrates almost all of surfaces loss in CE nursery areas (Rochette et al., 2010; Stamp et al., 2022). The proportion of habitat loss ( $S_{loss}$ ) was estimated as the mean of the areas lost in each French sector between 1870 and 2020:  $S_{loss} = 37.6\%$  (in Supp. Mat 3.2.4).

In scenarios,  $S_{loss}$  was considered as a proxy of the surface loss at the EEC scale. Indeed, (i) these sectors represent major nursery areas for the four studied species (Carpentier et al., 2009; Riou et al., 2001); (ii) to our best knowledge, no similar data were available for the English coast. However, English intertidal habitats have lost surface during the same period with similar levels of loss (Stamp et al., 2022). A surface restoration multiplier ( $\lambda_{restoration}$ ) was calculated as follow:

$$\lambda_{restoration} = \frac{1}{1 - S_{loss}} \quad (11)$$

### Species-specific bathymetric distribution of juveniles

The juveniles of the four studied species have different bathymetric distributions (Carpentier et al., 2009; Ellis et al., 2012; Riou et al., 2001), hence different concentration in shallow areas (<5m). Those different concentrations determine the proportion of juveniles impacted by surface loss in these shallow areas. The species-specific proportion of juveniles present in habitats above 5 meters ( $Prop$ ) was estimated from both bathymetric and nursery maps (Supp.



Mat. 3.2.5;  $Prop = 49.7, 16.7, 4.1$  and  $80.2$  for sole, plaice, whiting and seabass, respectively).

The nursery surface loss factor was only applied to the proportion of juveniles present in this area. So, a species-specific surface restoration factor ( $\lambda_{surface}$ ) was calculated to simulate a restoration of the nursery area as in 1870 (equation 12; Table 3.2.2):

$$\lambda_{surface} = \frac{1}{1+(Prop \times \lambda_{restoration})-Prop} \quad (12)$$

### Parameterization of quality effects

We relied on Courrat et al. (2009), who quantified the impact of the chemical quality of EEC estuaries on the density of marine juvenile fish to estimate the ecological status of estuarine waters for the European water framework directive (Delpéch et al., 2010). Courrat et al. (2009) found that estuaries with a medium ecological status had densities of juveniles 20% lower than estuaries of good quality. We assumed that this loss of density was directly reflecting a loss in carrying capacity per unit of surface ( $K^*$ ) due to degradation of habitat quality only (without loss of surface area). We denote  $K_{scenario}^*$  the new carrying capacity under habitat scenario.

Based on equation (10) (but see also details in Appendix F), we back-calculated the habitat quality multiplier  $\lambda_{quality}$  to be applied to  $M^{di}$  and  $M^{dd}$  that corresponds to change from the baseline carrying capacity  $K^*$  to  $K_{scenario}^*$ :

$$\lambda_{quality} = \frac{\log\left(\frac{M^{di}}{K_{scenario}^*} + 1\right)}{\frac{M^{dd}}{M^{di}}} \quad (13)$$

The quality scenarios have been constructed by considering a homogeneous quality status of the nursery areas for all the nursery sectors (i.e., a single parameter  $\lambda_{quality}$  for the whole EEC). Then, an additional assumption of the ecological status of CE areas in the EEC has been made: on average, all estuaries are considered in average quality and our scenarios will simulate the restoration of these estuaries to a good ecological status.

The sensitivity of juveniles to change in habitat quality could depend upon their dependency/concentration on shallow habitat (<5m), which varies greatly among species (Table 3.2.2; parameter  $Prop$ ). One can indeed argue that the higher the concentration in shallow areas, the higher the sensitivity to change in habitat quality. To assess the sensitivity of the response to habitat quality to the concentration in shallow areas, we tested two different scenarios for habitat quality restoration.

A first scenario considers the restoration applied to all juveniles (*quality all*). This restoration scenario was based on a new carrying capacity ( $K_{scenario\ all}^*$ ) calculated to simulate a restoration of the 20% lost:

$$K_{scenario\ all}^* = K^* \times 1.25 \quad (14)$$

A second one considers the restoration applied only to the proportion of juveniles located above the 5m bathymetry (*quality band*). This assumption was made to differentiate juveniles present in very coastal areas, sensitive to high levels of contamination, from those located in deeper waters, considered as not impacted. In this second scenario,  $K_{scenario\ band}^*$ :

$$K_{scenario\ band}^* = (K^* \times Prop \times 1.25) + (K^* \times (1 - Prop)) \quad (15)$$

### 3.2.2.3.1 Summary of scenarios

The estimates of surface losses and quality effects (Table 3.2.2) were used to simulate four species-specific scenarios: (i) surface restoration (ii) quality restoration applied to all juveniles (*quality all*) (iii) quality restoration applied to the most coastal juveniles (*quality band*) and finally (iv) a scenario that combines surface and *quality band* restoration.

Table 3.2.2. Percentage of juveniles present in habitats above 5m and associated restoration factor.

	Sole	Plaice	Whiting	Seabass
Percentage of juveniles in shallow nurseries ( <i>Prop</i> )	49.71	16.72	4.10	80.23
Surface restoration factor ( $\lambda_{surface}$ )	0.7703	0.9088	0.9760	0.6750
Quality restoration factor <i>Quality all</i> ( $\lambda_{quality}$ )	0.9453	0.9330	0.8574	0.9367
Quality restoration factor <i>Quality band</i> ( $\lambda_{quality}$ )	0.9712	0.9877	0.9932	0.9481

In a first step, the results will be illustrated only with the second quality scenario (impact on inshore juveniles, *quality band*). Finally, a sensitivity analysis will compare the two quality scenarios.

### 3.2.3 Results

A detailed interpretation of both calibration and results of the habitat scenarios is presented for seabass, before interspecific comparisons.

#### 3.2.3.1 Seabass case study

The results are expressed as a percentage of seabass SSB or catch reallocated to area 7.d (in Supp. Mat 3.2.3) and not in relation to the actual management unit (ICES, 2021b).

#### Calibration of the carrying capacity to stock assessment outputs

$K$  is estimated at  $1.1 \times 10^7$  juveniles. Results highlight discrepancies between model predictions and catches and SSB reported by ICES (in Supp. Mat 3.2.7). But the average SSB values estimated by ICES and the average SSB values predicted by our model are quite similar ( $5.8 \times 10^6$  and  $5.6 \times 10^6$  Kg respectively). The same conclusion holds for catches (average ICES values at  $1.4 \times 10^6$  Kg and model predictions at  $1.2 \times 10^6$ , in Supp. Mat 3.2.8). Model behavior at equilibrium is realistic: a  $F_{MSY}$  of 0.15 without habitat restoration scenario (Figure 3.2.2B), while the  $F_{MSY}$  from ICES (2021a) was 0.17, and a  $\frac{SSB_{MSY}}{SSB_0}$  of 0.28.

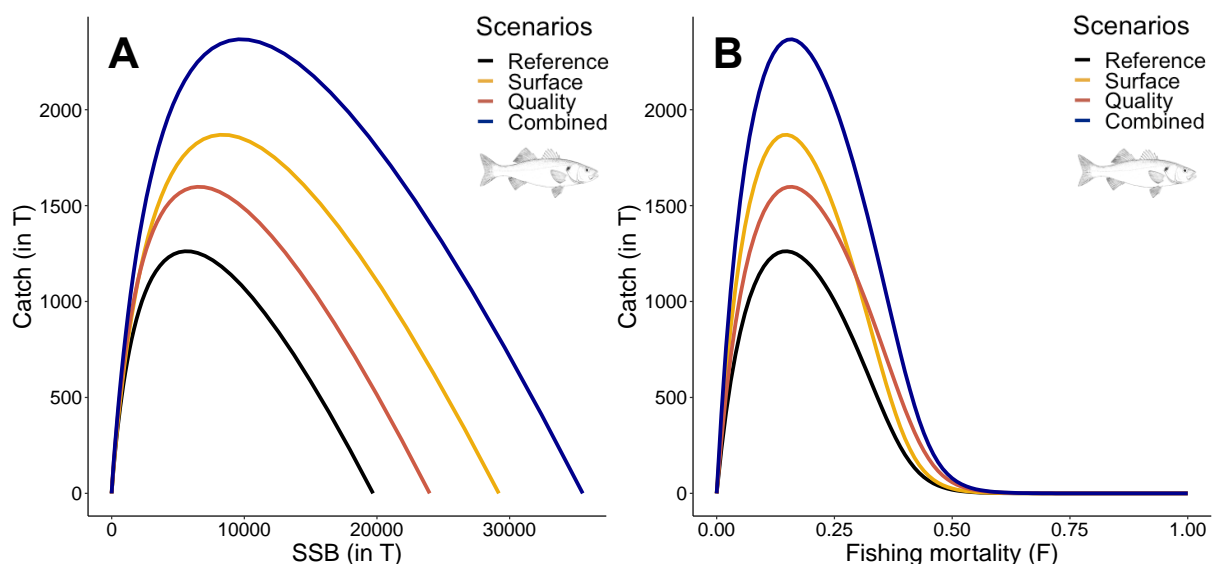


Figure 3.2.2. Production curves according to habitat scenarios as function of SSB (A) or fishing mortality (B) for seabass in ICES division 7.d. Quality and combined effect use the quality band hypothesis.

### Equilibrium production curves under habitat restoration scenarios

Restoring the surface of juvenile habitat only impacts  $K$  (equation 10), hence the scale of the productivity curve, with increased catches, and increased level of biomass at MSY (Fig.3.2.2A), but  $F_{MSY}$  remains unchanged (Fig. 3.2.2B). By contrast, restoring habitat quality (*quality band* scenario) affects both  $K$  and  $h$  parameters (equation 9 and 10), hence increases catches,  $SSB_{MSY}$  and also  $F_{MSY}$  (Fig. 3.2.2).

#### 3.2.3.2 Comparison between species

##### Population model fit

As for the seabass, the calibration of the model led to predictions of catches and SSB that do not fit perfectly with annual ICES data (in Supp. Mat 3.2.7). However, the average SSB and catches estimated by ICES and predicted by our model were almost similar. Overall, models' outputs at equilibrium,  $F_{MSY}$  and ratio  $\frac{SSB_{MSY}}{SSB_0}$  fit within the expected range (in Supp. Mat 3.2.8).

##### Maximum sustainable yield indicators under habitat restoration scenarios

Impacts of habitat restoration scenarios were compared across species, by estimating relative gains in SSB and catches at MSY equilibrium states (Fig. 3.2.3). The surface scenario has the largest impact on SSB with gains ranging from 2.5% for whiting to 48.1% for seabass (Fig.3.2.3A). This interspecific pattern also concerned the gains linked to the restoration of quality with an increase in SSB ranging from 0.4% for plaice to 17.1% for seabass. When combining the surface/quality restoration scenarios, the effects are multiplicative (i.e. greater than the sum of both effects), and two groups of species emerge: whiting and plaice, for which the combined restoration has the lowest effect, with gains of 3.9% and 10.5%, respectively, whereas sole and seabass gained 39.8% and 73.4% of SSB, respectively. Catch increase at MSY almost followed those of the SSB (Fig.3.2.3B). In volume, the restoration of both habitat surface and quality represents an increase in catches of 435, 1290, 2727 and 1104 tons for whiting, plaice, sole and seabass, respectively.

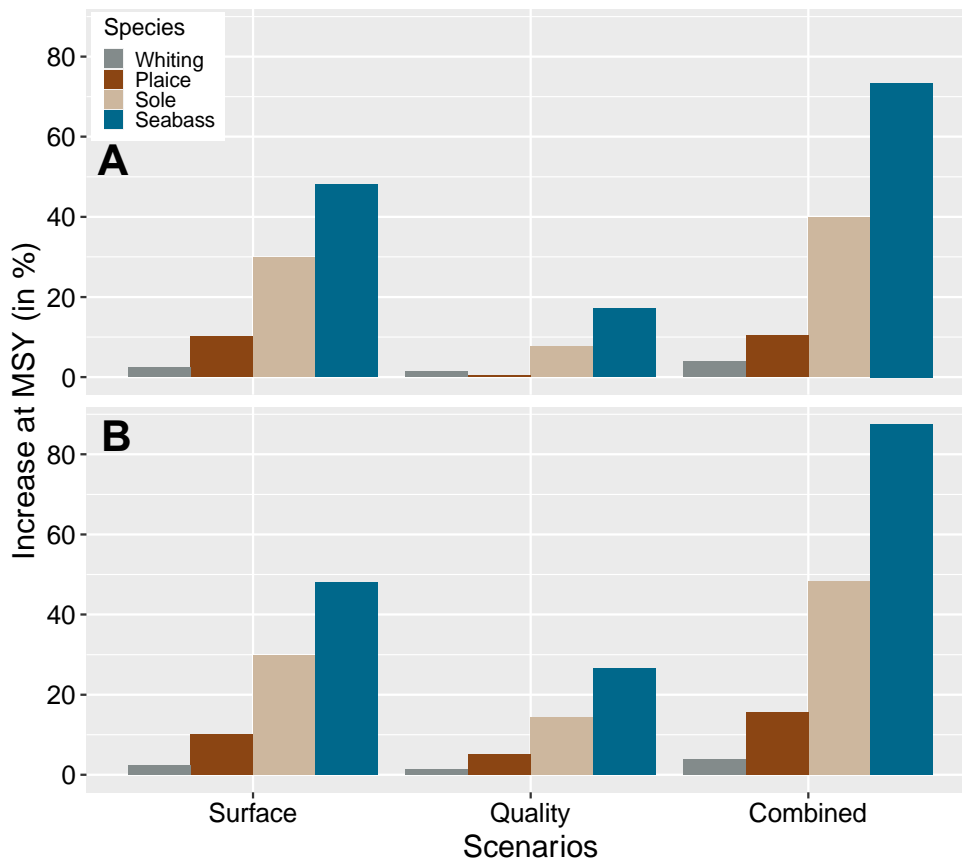


Figure 3.2.3. Effects of habitat scenarios on SSB (A) and Catch (B) gain at MSY by species. Quality and combined scenarios use the quality band hypothesis.

#### Sensitivity to quality scenario hypothesis

Large differences emerge across the two scenarios for quality restoration (*quality band* = impacts only the juveniles located in shallow (<5m) habitat / *quality all* = impacts all juveniles in the EEC). The restoration of quality for all juveniles in the EEC leads to a greater homogeneity in the gains than when the restoration is carried out according to the bathymetric distribution of juveniles (Fig.3.2.4). Under the *quality all* scenario, interspecific patterns depended on demographic parameters only, and especially on steepness and fecundity, which differ between species. Results show that the sensitivity to quality restoration is higher for species with lower steepness (whiting; Fig.3.2.4). Moreover, all species have greater catch gains in this “global” restoration scenario due to a larger quantity of juveniles impacted by the restoration (an increase of 32, 26, 15 and 7 %, compared to the “partial” scenario, for whiting, plaice, sole and seabass respectively; Fig. 3.2.4).

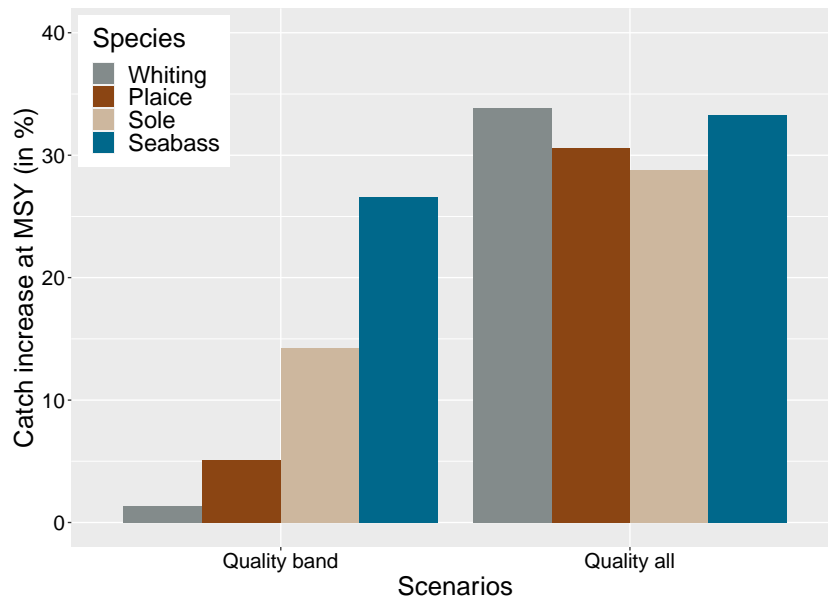


Figure 3.2.4. Difference in catch gains per species according to the assumption made for quality scenarios. Quality band is the restoration scenario applied only to the juveniles in shallow habitats (<5m) and quality all is the restoration scenario applied to all the juveniles.

### 3.2.4 Discussion

#### 3.2.4.1 Main findings

We assessed the consequences of CE nursery restoration through a generic age- and stage-structured model with a stock-recruitment relationship that directly depends upon the quality and surface of nursery habitat (Champagnat et al. sub). The model was applied to four nursery-dependent species, i.e., sole, plaice, whiting and seabass, characterised by various life history traits and various degrees of concentration on the same coastal nursery habitats in the EEC. For the four species, models were parameterised from the literature and stock assessments outputs (ICES, 2021a, 2021b), except for the carrying capacity, calibrated on stock assessments outputs to achieve realistic population size.

The model was used to simulate equilibrium catch curves obtained under different scenarios of nursery quality and surface restoration for the four species. Surface restoration increased the catches and biomass at MSY. The restoration of quality lead to an increase in catches and biomass at MSY, but also in fishing mortality at MSY. Overall, the species with the higher level of concentration on shallow nursery areas were the most sensitive to the habitat restoration scenarios. Thus, seabass was the species for which habitat restoration had the greatest positive impact, while whiting was the least affected. However, the response also depends upon species-

specific life history traits: lower steepness lead to a stronger response to habitat quality scenarios.

#### 3.2.4.2 *Limitations in model assumptions and scenarios*

##### *A generic model to simulate population dynamics without stochastic recruitment variability*

In this generic model, only one parameter, the carrying capacity ( $K$ ), needed to be calibrated from stock assessment outputs. This makes it very easy to apply for several case studies, i.e. four stocks here. However, the calibration of  $K$  implies two ecological assumptions, the first being that the carrying capacity of the nursery habitat is limiting the recruitment (Beverton and Iles, 1992; Le Pape and Bonhommeau, 2015). The second assumption is that this carrying capacity does not vary over time.

Considering the carrying capacity as constant over time certainly induces a strong limitation. Indeed, fluctuations were previously evidenced (Le Pape et al., 2003; Luo et al., 2001), for instance as a response to the supply of nutrients and organic matter that support food provisioning (Day et al., 2021; Kostecki et al., 2010). Environmental variability dramatically impacts population dynamics, especially regarding the recruitment process (Pfister and Stevens, 2003).

Considering a deterministic population dynamic is another limitation. This has led to poor predictions of annual variations in SSB and catches. However, the objective was not to reproduce these annual fluctuations but to simulate realistic average population dynamics. The calibration led to an average estimate of SSB and catches close to the average estimate of the ICES over the same period, for all species. In addition, population indicators ( $F_{MSY}$  and ratio  $\frac{SSB_{MSY}}{SSB_0}$ ) confirmed the realism of the dynamics.

##### *A model without spatial structure in metapopulation*

The model considered juvenile habitat as a single homogeneous block whereas CE areas are composed of a multitude of habitats with high heterogeneity that can vary over time («shifting habitat mosaic», (Nagelkerken et al., 2015; Peterson, 2003; Wimberly, 2006). Considering the nursery areas as a single block is limiting, especially for the construction of quality restoration scenarios. However, considering spatial heterogeneity would require parameterising specific Beverton-Holt relationships for each nursery area (Rochette et al., 2013), which is inaccessible. Moreover, considering different nursery sectors in the EEC would greatly complicate our model and the elaboration of restoration scenarios by raising questions about steepness estimation for

the different nursery sectors (White, 2010) and population connectivity (Archambault et al., 2016). Diffusion of the outcomes of local nursery restoration at a metapopulation scale highly depends on the level of connectivity at different stage of the life cycle (Archambault et al., 2018; Ma et al., 2022; Randon et al., 2021). Results therefore provide global estimates at stock scale, with caution on the interpretations on both internal and external spatial structure, especially when based on an MSY approach (Ying et al., 2011).

### *Realistic but simplified scenarios*

The estimation of surface losses was based on historical data available on three CE nursery areas of the French side of the EEC in 1870. Accounting for these three CE areas losses was an innovative step forward, as previous studies in the EEC have focused on the single Seine Estuary (Archambault et al., 2018; Champagnat et al., 2021; Rochette et al., 2010). No similar data were available for the English coasts, where nurseries have however suffered surface losses over the same period (Stamp et al., 2022). This proxy of French surface loss was considered as the best available knowledge for the EEC.

To fit with available information on CE surface loss, the concentration of juvenile in shallow nursery habitat was considered as dependent on depth only. Depth is a main driver of juvenile fish distribution for the studied species in the EEC (Carpentier et al., 2009; Ellis et al., 2012; Riou et al., 2001) but defining an ecological niche by a single variable is a very simplifying assumption (Grinnell, 1917; Hutchinson, 1957). CE nursery areas can be defined by other parameters, e.g. salinity and hydrodynamics (Kelley, 1988; Kennedy and Fitzmaurice, 1972; Le Pape et al., 2003), sediment structure (Riou et al., 2001; Rochette et al., 2010), coastal shelter (Trimoreau et al., 2013). The estimation of species-specific surface losses was therefore oversimplified and likely underestimated. Moreover, the proportion of juvenile above 5 meters was calculated on maps representing present habitats. When shallow habitats were of larger surface, as in 1870, the proportion of juveniles present in this shallow fringe was likely greater.

The scenarios of quality degradation were based on a global estimate of juvenile density loss in nursery areas (Courrat et al., 2009). This proxy was used due to the lack of knowledge on the species-specific impact of nursery habitat quality degradation on the demographic parameters of juvenile fish. Indeed, despite the well-documented impacts of local anthropogenic disturbances on the juveniles of CE nursery-dependent species (Brown et al., 2018), the consequences of these impacts on demographic rates are still poorly understood and need to be quantified to infer impacts at population scale (Lipcius et al., 2019; Vasconcelos et al., 2014). Given this lack of knowledge, two strong hypotheses were made. First, the parameterization of



the quality scenario assumed a common multiplier on density-dependent and density independent mortality rate. This is a strong assumption as different processes are associated to these mortality rates (Johnson, 2007; Juanes, 2007). Density-dependent mortality refers to interactions between juveniles of the same cohort, mostly competition for food or space (Craig et al., 2007; Gibson, 1994; Le Pape and Bonhommeau, 2015). Density-independent mortality involves other mortality processes linked to a large panel of stressors (e.g. pollutant, (Rose et al., 2003); oxygen, (Gibson, 1994) and/or predation (Gibson, 1994; Hilborn and Walters, 2021). Second, the simulation results were very sensitive to the assumptions made on which specific sectors of the nursery habitat are affected by habitat restoration/degradation (i.e. the whole nursery area or the <5m band only). The lack of knowledge on the gradient of land-sea impact on marine juvenile fish in CE nurseries prevent to develop more accurate scenarios.

Because survival rates are very low at young stage, the sensitivity of population dynamics to minor changes of mortality rate is high (Hilborn and Walters, 2021; Levin and Stunz, 2005) and would require attention in future studies to design more accurate scenarios.

#### *3.2.4.3 Effects of nursery restoration and comparison between species*

To our best knowledge, our study is the first that assess the effect of restoration of CE nursery areas for a group of species at the scale of a management unit.

Surface restoration, which leads to an increase in the carrying capacity of the nursery, enhances the catches and biomass at MSY. The restoration of quality increases both the carrying capacity and the steepness, thus catches, biomass and also fishing mortality at MSY (Champagnat et al. sub). For a combined restoration, the effects are multiplicative, i.e. higher than the single addition of the marginal restoration effects.

The difference in gains between species due to surface restoration is mainly due to a different degree of concentration of juveniles in shallow nursery habitat. The differences in quality restoration are also related to these patterns of concentration in shallow areas, with high sensitivity to assumptions regarding the proportion of juvenile impacted by restoration. But impacts of quality restoration are also related to species-specific demographic parameters (Champagnat et al. sub). Thus, an interesting result of this study is that life history traits, and especially steepness, not only drive the sensitivity of marine fish to fishing pressure (Froese et al., 2016; Horbowy and Hommik, 2022; Miller and Brooks, 2021) but also their response to essential fish habitat degradation.

Previous studies, focusing on sole, have already examined the effect of areas and/or habitat quality scenarios in the EEC with more complex and species-specific life cycle models. Archambault et al. (2018) and Champagnat et al. (2021) demonstrated the effects of quality degradation and surface loss of CE nursery areas in EEC, considering the restoration of the surface and the quality of the Seine estuary only. The present model provided outputs consistent with these species-specific approaches; but its main interest was its generic formulation, allowing to consider four species. This generic steepness-based approach requires limited tuning (i.e., carrying capacity parameter) to parametrise the stock-specific population dynamic as far as an age-structured stock assessment is available. Such tool to infer consequences of habitat degradation at population and fisheries scale is highly needed (Rabalais, 2015), and this model could easily be applied for other study area and fish species in the future. However, the accuracy of the scenarios relies on the existing knowledge on both the fraction of juvenile concentrated in impacted CE nurseries, and the level of impact (surface loss and drop in demographic rates or density in response to lower quality), with high sensitivity to even moderate levels of change (Hilborn and Walters, 2021; Levin and Stunz, 2005; Zimmermann et al., 2021).

#### *3.2.4.4 Management implications*

The present approach evidences that the gains from fisheries management could be greatly increased if nursery areas were restored in the EEC. This restoration could lead to an annual catch gain of 3.9%, 15.6%, 48.3% and 87.5% for whiting, plaice, sole and seabass respectively, which represents a gain of 435, 1290, 2727 and 1104 tons, respectively. In addition to catch gains, the spawning stock biomass would also be increased, which could have beneficial consequences for the whole ecosystem (Froese et al., 2016, 2008). Ongoing management measures to restore the surface area (in the Seine estuary, (Ducrotoy and Dauvin, 2008) and quality of CE habitats (decreases in pollutant levels; (Meybeck et al., 2007; Tappin and Millward, 2015) in the EEC should therefore be continued to enhance fish and fisheries production (Katara et al., 2021).

This study supports the need to consider essential fish habitat in the management of fishing resources (Brown et al., 2018; E. J. Brown et al., 2019; Kraufvelin et al., 2018). The high level of surface loss and anthropogenic disturbances of remaining quality of CE ecosystems (Halpern et al., 2008) impact their nursery function (Jokinen et al., 2016) worldwide (Barbier et al., 2011). Substantial recovery of the function of habitats essential to marine life could be achieved

(Duarte et al., 2020). Restoring coastal nurseries (Buelow et al., 2022; Troast et al., 2022), may be even more beneficial than regulating fishing pressure (Levin and Stunz, 2005; van de Wolfshaar et al., 2011).

Authors contributions

**Gernez Maël:** Conceptualization, Methodology, Software, Investigation, Writing - Original Draft, Editing.

**Champagnat Juliette:** Conceptualization, Methodology, Software, Investigation, Writing - Original Draft.

**Rivot Etienne:** Conceptualization, Methodology, Writing - Original Draft.

**Le Pape Olivier:** Conceptualization, Methodology, Writing - Original Draft, Funding acquisition.

Declaration of Competing Interest

None.

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## Conclusion du chapitre 3

Dans ce chapitre, nous avons développé une approche générique permettant d'évaluer l'impact des pressions anthropiques affectant la surface et la qualité des nourriceries sur la dynamique de populations aux histoires de vie contrastées. L'expression de la relation SR en fonction des attributs de la nourricerie a permis de construire des scénarios de dégradation/restauration de la surface et de la qualité des nourriceries. Ces scénarios ont été simulés jusqu'à un état d'équilibre pour construire les courbes de biomasse féconde et de captures à l'équilibre et calculer les gains ou pertes d'indicateurs au rendement maximum durable (RMD) par rapport à une simulation de référence (sans modification de l'habitat).

La première étude (chapitre 3.1) a développé un modèle générique s'appuyant sur une formalisation des processus « *process driven* » (cf. 1.4.2.5), basé sur une relation SR exprimée en fonction de la steepness. Elle a permis de comparer, pour des espèces modèles aux histoires de vie contrastées, l'impact de scénarios théoriques portant sur la surface et la qualité des nourriceries simulés à l'aide de multiplicateurs de dégradation et restauration.

Les résultats mettent en évidence que certains motifs généraux de réponse sont similaires entre les trois espèces. Notamment, les deux types de scénarios (surface et qualité) ont un effet sur l'échelle des courbes de production, et donc sur la biomasse féconde et la capture au RMD (effet positif pour la restauration, et négatif pour la dégradation). La surface agit comme un facteur d'échelle et l'impact des scénarios de surface sur les indicateurs de biomasse et de captures au RMD est proportionnel au multiplicateur utilisé (Camp et al., 2020; Ma et al., 2022). Les scénarios de qualité modifient non seulement l'échelle, mais aussi la forme de la courbe, et donc la mortalité par pêche au RMD (Moussalli and Hilborn, 1986). Cette réponse est induite par la modification de la steepness qui détermine la productivité de la population et donc le niveau d'effort de pêche au RMD (Horbowy and Hommik, 2022). Lorsque les scénarios sont combinés, les réponses sont fortement déterminées par les changements de qualité.

A l'inverse de scénarios de surface, les scénarios de qualité mettent en exergue des différences dans l'intensité des réponses en fonction des THV. La sensibilité de la mortalité par pêche au RMD est la plus forte pour la raie (grande taille, vie longue, faible steepness) et la plus faible pour l'anchois (petite taille, vie courte et forte steepness). Cette différence de sensibilité coïncide avec le gradient de capacité compensatoire (i.e. capacité d'une population à supporter

la mortalité, Kindsvater et al. 2016) : valeur faible pour la raie, espèce à la stratégie « survivant » ; élevée pour l'anchois à la stratégie « opportuniste » et intermédiaire pour la plie.

La seconde étude (chapitre 3.2) évalue quel est le potentiel de la restauration de nourriceries communes à quatre espèces de la Manche Est sur leur dynamique de population et leur potentiel d'exploitation durable. Le même modèle est appliqué, mais une phase additionnelle de calibration permet d'ajuster les niveaux de biomasses et de captures aux données disponibles pour chaque espèce, à partir des évaluations de stock sur la zone. De plus, les multiplicateurs appliqués pour chaque scénario sont quantifiés à partir de données sur les pertes de qualité et de surface des nourriceries observées en Manche Est. Ces multiplicateurs sont modulés par la concentration de chaque espèce sur les habitats les plus côtiers, pour prendre en compte les contrastes de répartition entre espèces et leur degré de dépendance à des ZFHI restreintes. Cette répartition détermine fortement la réponse des indicateurs de biomasse féconde et de captures au RMD pour chaque espèce : le bar et la sole, fortement concentrés sur les habitats peu profonds ont une sensibilité bien plus forte que la plie et le merlan à la surface et la qualité des habitats côtiers et estuariens. Enfin les résultats montrent aussi que la combinaison des scénarios de surface et qualité induit une réponse non additive : les réponses cumulées sont synergiques, i.e., elles ont des effets plus forts que la somme des impacts séparés.

**4. Modélisation de l'impact de pressions anthropiques au niveau des nourriceries et des frayères sur la dynamique de populations d'espèces marines aux histoires de vie contrastées**

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*Illustration : Sylvie Champagnat*

## Introduction du chapitre 4

Le chapitre 3 a permis de développer une approche générique permettant d'évaluer l'impact des pressions anthropiques impactant la surface et la qualité des nourriceries sur la dynamique de plusieurs populations aux histoires de vie contrastées. Dans le chapitre 4, nous généralisons cette approche pour modéliser l'effet de pressions anthropiques au niveau plusieurs ZHFI associées à plusieurs stades de vie différents, les habitats de nourricerie et les habitats de frayère.

Pour ancrer l'étude dans un contexte concret, nous nous intéressons notamment à la modélisation des impacts de l'hypoxie sur ces deux ZHFI. Au sein des nourriceries, l'impact de l'hypoxie est modélisé au travers de la modulation de la « qualité » de façon analogue au chapitre précédent, c'est-à-dire via un multiplicateur appliqué sur les processus de mortalité juvénile. L'impact de l'hypoxie au niveau des frayères est modélisé en contrastant deux hypothèses de réponse individuelle : l'évitement ou la persistance (Behrens et al., 2018; Petersen and Pihl, 1995; Skjæraasen et al., 2008). Chaque hypothèse a des conséquences distinctes à l'échelle de la population (une plus forte mortalité des œufs qui sont pondus dans un habitat moins favorable ou une plus forte mortalité des adultes participant à la reproduction, respectivement).

L'approche est appliquée à trois populations de Baltique (morue, plie et hareng) qui subissent des conditions hypoxiques au moment de leur ponte et dans leurs nourriceries côtières. En l'absence de données pour quantifier le lien pression-impact, nous avons utilisé des multiplicateurs théoriques pour comparer les impacts des trois scénarios mentionnés ci-dessus, c'est-à-dire évaluer les effets respectifs de perturbations à différents stades de vie (i.e. œuf, juvénile et adulte mature). À cette fin, l'approche développée au chapitre 3.1 a été adaptée afin de rendre comparable l'effet de multiplicateurs appliqués sur des transitions aux taux de mortalité instantanée et durées différentes. Les impacts sont simulés de façon marginale sur chaque habitat puis combinés pour évaluer les impacts de l'accroissement/mitigation de l'hypoxie au niveau des ZFHI (i.e. dégradation/restauration) sur la productivité des populations, et les captures associées. Une comparaison inter-espèce est aussi menée pour explorer comment les réponses varient pour le gradient d'histoires de vie couvert.

# Impact of hypoxia on essential fish habitats throughout the life cycle of exploited marine species

Cet article est en cours de préparation pour une soumission à l'ICES Journal of Marine Science.

Champagnat J.<sup>1\*</sup>, Brown E.<sup>2.</sup>, Rivot E.<sup>1</sup>, Le Pape O.<sup>1</sup>.

<sup>1</sup>DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, IFREMER, INRAE, 35042 Rennes, France

<sup>2</sup> National Institute of Aquatic Resources, The Technical University of Denmark, 2800 Kgs. Lyngby, Denmark

\*Corresponding author: [juliette.champagnat@institut-agro.fr](mailto:juliette.champagnat@institut-agro.fr)

## Abstract

Spawning grounds and juvenile habitats are critical Essential Fish Habitats (EFH) that support key phases where fish aggregate on restricted area. These EFH face anthropogenic pressures that impact fish population dynamics, yet these impacts are poorly quantified. In this study we consider the impact of hypoxia a very widespread pressure which may impact fish both inside juvenile and spawning habitats. Specifically, we assess the consequences of hypoxia increase/mitigation inside EFH on the productivity of exploited marine fish populations. Our approach combines an age- and stage-structured simulation model with a habitat-enhanced stock-recruitment relationship to integrate hypoxia impact on juvenile habitats. For the impacts of hypoxia on spawning grounds, two hypotheses were tested: a higher mortality of eggs that are spawned in less favourable habitats or a higher mortality of spawners. We applied this framework in the Baltic to explore population responses of cod, plaice and herring; which face hypoxic conditions in their juvenile habitats and spawning grounds. All scenarios lead to modifications in sustainable fishing pressures  $F_{MSY}$ , and population size and yield at MSY, with different magnitudes. Population responses were consistent across the three species. Perturbations to spawning habitats that result in higher mortality of eggs had the least impact while the more direct effect of habitat on spawners themselves had the largest impact. Within each scenario, the responses depended upon species and life history traits, with contrast in steepness and lifespan that explain most of the differences between species. Cumulative impacts of pressures at both life stages were also investigated and revealed nonlinear responses for a



majority of indicators and scenarios. Our framework is a generic tool, transferable to a large panel of case studies, to quantify the relative impact of EFH degradation/restoration for the dynamics of marine exploited populations.

## 4.1 Introduction

Coastal and estuarine ecosystems are highly productive areas (Costanza et al., 1997) serving as spawning grounds, juvenile habitats, foraging areas and migration corridors for numerous fish and invertebrates (Beck et al., 2001; Elliott and Hemingway, 2002). They host areas that can be considered as Essential Fish Habitat (EFH, (Magnuson-Stevens Fishery Act, 2007)). Coastal and estuarine areas are used in at least one life-history stage by 44% of the commercially important species for which advice is provided by the International Council for the Exploration of the Sea (ICES) in the Northeast Atlantic (Seitz et al., 2014). A similar level of dependence is acknowledged worldwide (C. J. Brown et al., 2019; Fodrie and Mendoza, 2006; Lellis-Dibble et al., 2008; Peterson, 2003).

EFH located in coastal and estuarine areas face pressures from multiple human activities (Batista et al., 2014; Brown et al., 2018; Halpern et al., 2008). The most current pressures are: contamination by xenobiotics, nutrient excess, biological invasion and surface area losses. Moreover, those pressures may interact, which leads to cumulative impacts on coastal ecosystems (Halpern et al., 2009) and related EFH (Brown et al., 2018). The interactions between these various pressures can be simply additive, synergistic (magnitude is greater than the sum of independent pressures) or antagonistic (magnitude of combined impact is less than the sum of independent pressures) (Crain et al., 2008). This high level of anthropogenic pressure induced a widespread degradation and destruction of native nearshore ecosystems worldwide (Bulleri and Chapman, 2010; Halpern et al., 2008) and related loss in their function as EFH (Barbier et al., 2011; Worm et al., 2006).

The impact of local anthropogenic pressures on fish individuals has been widely documented (Brown et al., 2018), but quantitative estimations of the consequences of these pressures at the population scale remain scarce (Lotze, 2006; Sundblad & Bergström, 2014; Vasconcelos et al., 2014). Understanding the effects of these pressures on fish population is essential for guiding effective management actions in a context where trade-offs must be made between various human activities (Lipcius et al., 2019; Rönnbäck et al., 2007; Rose et al., 2018; Sundblad & Bergström, 2014).

Approaches assessing how anthropogenic pressures, acting via EFH, impact fish population dynamics and fisheries yield exist (Archambault et al., 2018; Eero et al., 2011; Camp et al., 2020; Mizerek et al., 2011; Rose et al., 2018; Scheuerell et al., 2006). However, they often remain strongly case-specific, highly data-demanding and quite complex, which prevent broader applications of these approaches. A comprehensive framework has recently been developed for analysing the impacts of anthropogenic pressures on juvenile habitat (Champagnat et al., sub.). However, anthropogenic pressures affecting spawning habitats, together with their combined effect with pressure on juvenile habitats have not been addressed yet.

Hypoxia and anoxia are important human induced pressures that may potentially affect both juveniles and spawning habitats. In the Baltic Sea, hypoxia and anoxia in the deeper basin areas is a naturally occurring phenomenon that has been exacerbated in both severity and scale by human activities, such that the volumes of hypoxic water are larger, cover broader areas and persist for longer across the seasons (Eero et al., 2011; Piehl et al., 2022; Rahikainen et al., 2017; Uusitalo et al., 2016). In particular, basin scale hypoxia has become a routine feature in various known spawning habitats. Atlantic cod (*Gadus morhua*), and European plaice (*Pleuronectes platessa*) both spawn in these basins (Eero et al., 2011; Petereit et al., 2014; Rahikainen et al., 2017; Receveur et al., 2022), where autumn hypoxia is extending into wintertime, during spawning. With the expansion of hypoxia, the risk of coastal hypoxia increases and is likely to occur in concert with coastal marine heatwaves (Rolff et al., 2022). Indeed, both of these phenomena have been observed in Danish coastal waters but not yet reported in primary literature (Frausing et al., 2022; Payne, 2020; Støttrup et al., 2018). Persistent warming in coastal marine habitats has already excluded adult cod from these areas (Dinesen et al., 2019). In the western Baltic, Atlantic herring (*Clupea harengus*) spawn in these shallower waters on macroalgae and gravels, which are becoming more exposed to pulses of hypoxia and thermal stress (Moyano et al., 2022), which may overlap with different stocks' spawning times in late summer/autumn. Moreover, juvenile cod, plaice and herring are also located in coastal areas (Seitz et al., 2014), where they face hypoxic conditions, especially intense during their summer growth period.

Hypoxic and anoxic areas can have multiple direct and indirect effects on aquatic organisms, modifying their metabolism, ecology and life-history traits (Chabot and Dutil, 1999; Domenici et al., 2007; Herbert and Steffensen, 2005; Pichavant et al., 2001), up to entire ecosystem functioning (Breitburg, 2002; Diaz and Rosenberg, 2008; Wu, 2002). At an individual level,

fish experiencing detrimental environmental conditions (e.g. hypoxia) can try to either avoid or tolerate the stressor (McKenzie, 2011). In order to avoid, fish can increase locomotion (speed or turning frequency), at a cost of increasing oxygen demand which is limiting in both hypoxic and high temperatures (Herbert et al., 2011). A strategy to tolerate and wait-out the stressor, relies on the down-regulation of energy demanding activities such as locomotion and digestion (Cook et al., 2014). The strategy taken depends on the species' tolerances, the magnitude of the stressor and the individuals' past exposure (Cook and Herbert, 2012; Ferrari et al., 2016). When investigating the impacts of these stressors on populations, we cannot determine which proportion of the population will behave in any given way, so we must understand the potential outcomes for the various possible strategies and the mechanisms of action of the stressor on the population in these different strategies. In addition to species-specific levels of exposure and sensitivity to oxygen depletion along the life cycle, population responses to habitat quality differ between life histories and demographic traits (Champagnat et al., sub.; Langangen et al., 2023; White et al., 2022). Similar levels of exposure could lead to various levels of demographic response among different species.

In this paper, we developed a population model to test for the impact of hypoxia on both juvenile and spawning grounds habitat on several species of fisheries interest. The approach is based on a generic age- and stage-structured population model designed to be easily parameterised for different species with contrasted life histories and to assess the impact of scenarios modifying juvenile and spawning habitats on population dynamics and productivity. The model was applied to test the effect of anoxia and hypoxia on three different species of particular interest to fisheries in the western Baltic Sea and with contrasting life histories: cod, plaice and herring. We ran simulations to explore the responses of population productivity and fisheries yield to different scenarios of increase/mitigation of hypoxia (i.e. degradation/restoration) inside both juvenile and spawning habitats. We compared the population responses under different hypotheses regarding the direct impact of hypoxia on the spawning grounds. Both marginal and cumulative effects of habitat degradation on juvenile and spawning habitats were evaluated on a species-specific basis, and we explored how these responses vary across the various life histories.

## 4.2 Materials & methods

### 4.2.1 Population dynamic model

Impact of EFH degradation on population dynamics and productivity was assessed with a deterministic life cycle model, structured by stage and age based on Champagnat et al. (sub.) and fully described in Supp. Mat.4.1. This model considers a single closed population with unique but distinct spawning and juvenile habitat areas.

The evolution of population abundance from year  $y$  and age class  $a$  ( $N_{a,y}$ ) to year  $y+1$  and age class  $a+1$  ( $N_{a+1,y+1}$ ) is described by the classical population dynamics (equation 1):

$$N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y}+F_{a,y})} \quad (1)$$

with  $M$  and  $F$  the natural and fishing mortality rates, respectively. The natural and fishing mortality depend upon the life stages and associated habitat and are further detailed below.

Recruitment, defined as the number of juveniles produced in juvenile habitats, accounts for the habitat-mediated mortalities during the early-life stages. The recruitment  $N_{a_{rec},y}$  is computed from density-dependent mortality process from eggs to recruited juveniles. Eggs numbers produced in a year,  $\omega_y$  (equation 2):

$$\omega_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times e^{-ts(M_{a,y}+F_{a,y})} \times Mat_a \times pf_a \times Fec_a \quad (2)$$

with  $Mat_a$  the probability of being mature at age  $a$ ,  $pf_a$  the female proportion at age  $a$ , and  $Fec_a$  the fecundity at age  $a$ , all considered constant in time.  $ts$  is a time scaling factor considering the mortality happening before spawning, it was set at 0.27 for all species.

Following Archambault et al., (2014) and Champagnat et al., (sub), the model incorporates a comprehensive parameterization of the recruitment process. We assumed that the mortality from eggs to recruited juveniles follows a two-stage process:

- (i) first a density-independent mortality during the eggs and larval drift, with resulting survival  $e^{-M_{larvae}}$ ;
- (ii) then a combination of density independent and compensatory density-dependent mortality processes with mortality rates  $M_{DI}$  and  $M_{DD}$ , respectively. The compensatory mortality is resulting from intra-cohort competition for trophic resources and/or space (Beverton and Holt, 1957).

Note that to simplify the notations, the duration of these two stages (larval drift and juvenile stage) is implicit in the rates  $M_{DI}$  and  $M_{larvae}$  and does not appear anymore in the equations. The resulting recruitment ( $N_{a_{rec},y}$ ) can be expressed as (equation 3, Brooks et al., 2019):

$$N_{a_{rec},y} = \frac{e^{-M_{DI} \times e^{-M_{larvae} \times \omega_y}}}{1 + \frac{1}{S} \times \frac{M_{DD}}{M_{DI}} \times (e^{M_{DI}-1}) \times e^{-M_{DI} \times e^{-M_{larvae} \times \omega_y}}} \quad (3)$$

Equation 3 is known as a Beverton-Holt relationship (Quinn & Deriso, 1999). It can be easily reparametrised in terms of its asymptote,  $K$ , interpreted as the carrying capacity of the juvenile habitat, and steepness  $h$  (equation 4, see Champagnat et al., (sub) for more details on the derivations).

$$N_{a_{rec},y} = \frac{4 \times h \times \omega_y}{\bar{W} \times (1-h) + \frac{4 \times h \times \omega_y}{K}} \quad (4)$$

The carrying capacity  $K$  is defined as the maximum number of juveniles that a juvenile habitat area can produce (Del Monte-Luna et al., 2004). Under the hypothesis that habitat quality is homogeneous in space, the asymptote  $K$  can itself be written as the product of a carrying capacity per unit of surface, that denotes the quality of habitat, and  $S$  the surface of the juvenile habitat (equation 5):

$$K = K^* \times S \quad (5)$$

The carrying capacity per unit of surface can be derived from equation 3 and fundamentally depends upon the balance between  $M_{DD}$  and  $M_{DI}$  as (equation 6):

$$K^* = \frac{M_{DI}}{M_{DD}} \times \frac{1}{(e^{M_{DI}-1})} \quad (6)$$

The steepness  $h$  is defined as the proportion of unfished equilibrium recruitment produced when the spawning stock biomass is reduced to 20% of its unfished level (Mace and Doonan, 1988). It characterises the drop-off in recruitment when the reproductive potential is reduced. It varies in theory from 0.2, for a linear stock-recruitment relationship, to 1, for a constant recruitment above 20% of pristine biomass (Mangel et al., 2013; Myers et al., 1999; Rindorf et al., 2022). Steepness can be expressed as a function of density-independent eggs and juvenile mortality and  $\bar{W}$  (equation 7):

$$h = \frac{e^{-M_{DI} \times e^{-M_{larvae} \times \bar{W}}}}{4 + e^{-M_{DI} \times e^{-M_{larvae} \times \bar{W}}}} \quad (7)$$

$\bar{W}$  is the mean number of eggs produced by a recruit during its lifetime in the absence of fishing (Mangel et al., 2010), expressed as the product of survival, maturity, proportion of female and fecundity for each age summed over ages (equation 8):

$$\bar{W} = \sum_{a=a_{rec}}^{a_{max}} S_a \times Mat_a \times pf_a \times Fec_a \quad (8)$$

with  $S_a$  the cumulative survival until age  $a$  in the absence fishing, defined as (equation 9):

$$S_a = \prod_{i=a_{rec}}^{a-1} e^{-M_i} \quad (9)$$

#### 4.2.2 Modelling the effect of hypoxia on EFH

Using the population model, we simulate scenarios that consider the modification of habitat quality induced by hypoxia on two types of EFH: juvenile habitats and spawning grounds. Both impacts rely on different hypotheses regarding the mechanisms.

##### 4.2.2.1 *Impact on juvenile habitats*

Regarding the low capacity of migration of juvenile fish (Le Pape and Cognez, 2016), we consider that juvenile cannot avoid anoxic areas. Therefore, juvenile habitat scenarios will consider that the surface of available juvenile habitat is not affected by change in hypoxia conditions, but that the quality of habitat is affected. As the direct consequence of changes in the habitat quality, we consider that the juvenile survival rates are affected by hypoxia conditions, and in turn affect the steepness  $h$  and the carrying capacity per unit of surface  $K^*$  (Champagnat et al., sub.).

The density-independent survival of juveniles in equation 3 is  $e^{-M_{DI}}$ . We hence applied a multiplier  $\alpha_J$  to this resulting survival (equation 10):

$$\alpha_J \times e^{-M_{DI}} \quad (10)$$

Because no information is available to define how hypoxia would impact differently the density-independent ( $M_{DI}$ ) and dependent mortality rates ( $M_{DD}$ ), we assume a common multiplier for as a default hypothesis (see (Champagnat et al., sub.) for more details and discussion this hypothesis). Hence, the new values of steepness and carrying capacity per unit of surface given the juvenile habitat multiplier  $\alpha_J$  are (equations 11 and 12):

$$h(\alpha_J) = \frac{\alpha_J \times e^{-M_{DI}} \times e^{-M_{larvae}} \times \bar{W}}{4 + \alpha_J \times e^{-M_{DI}} \times e^{-M_{larvae}} \times \bar{W}} \quad (11)$$

$$K^*(\alpha_J) = \frac{M_{DI}}{M_{DD}} \times \frac{1}{e^{M_{DI} - \log(\alpha_J)} - 1} \quad (12)$$

#### 4.2.2.2 Impact on spawning grounds

To model the impacts of hypoxia on spawning grounds, we conceptualised different hypotheses based on expected individual fish response (Fig. 4.1):

- (i) Hyp. 1. Fish avoid the hypoxic area and spawn in a less suitable area, which leads to an increase in egg mortality but without affecting the future life of spawners;
- (ii) Hyp. 2. Spawners don't avoid hypoxic areas and are directly affected by the hypoxia conditions through an increase of their mortality.

Note that for both hypotheses, scenarios of restoration (i.e. mitigation of hypoxia) would lead to a decrease in the mortality of eggs (Hyp. 1) and spawners (Hyp.2).

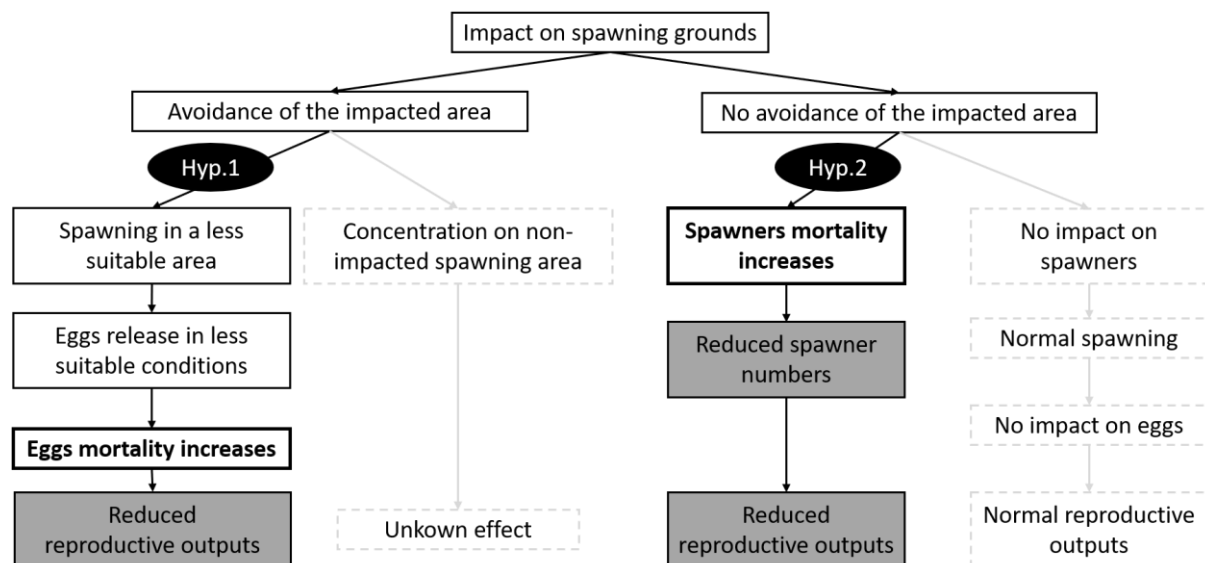


Figure 4.1: Diagram of the hypothetical consequences of impacts of hypoxia on spawning grounds. Black and solid line emphasise the two hypothesised mechanisms of action. Bold text indicates the model parameters modified by the scenario. Grey shaded shapes highlight the consequences at the population scale. Shapes outlined in grey dashed lines display less likely mechanisms of action, with unclear consequences, not investigated in this study.

For the first hypothesis implying change in egg mortality (Fig. 4.1), we follow the same logic as for scenarios on juvenile habitats. The density-independent survival of eggs in equation 3 is  $e^{-M_{larvae}}$ . We hence applied a multiplier  $\alpha_\omega$  to this resulting survival.

It is straightforward to see that the new steepness value given the multiplier  $\alpha_\omega$  is (equation 13):

$$h(\alpha_\omega) = \frac{\alpha_\omega \times e^{-M_{DI} \times e^{-M_{larvae} \times \bar{W}}}}{4 + \alpha_\omega \times e^{-M_{DI} \times e^{-M_{larvae} \times \bar{W}}}} \quad (13)$$

For spawner mortality (Hyp. 2, Fig. 4.1) we modify the population equation with a spawner survival multiplier ( $\alpha_S$ ) that is applied for all ages after the maturation age, that is for all age  $a \geq a_{mat}$  (with  $a_{mat} \geq a_{rec}$ )(equation 14):

$$N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y} + F_{a,y})} \times \alpha_S \quad (14)$$

It is worth noting that because we suppose the mortality are affected at all ages starting at the age at first reproduction, then  $\alpha_S = 1$  for all ages  $\leq a_{mat}$ . Then, the survival until age  $a$  is modified as follows (equation 15):

$$S_a(\alpha_S) = \prod_{i=a_{rec}}^{a-1} \alpha_S \times e^{-M_i} = \alpha_S^{(a-1-a_{mat})} \times \prod_{i=a_{rec}}^{a-1} e^{-M_i} = \alpha_S^{(a-1-a_{mat})} \times S_a \quad (15)$$

In turn, such a scenario has a great impact on the mean number of eggs produced by a recruit during its lifetime in the absence of fishing (equation 16).

$$\bar{W}(\alpha_S) = \sum_{a=a_{rec}}^{a_{max}} \alpha_S^{(a-1-a_{mat})} \times S_a \times Mat_a \times pf_a \times Fec_a \quad (16)$$

#### 4.2.2.3 Impact on both EFH

We also assessed the impacts of cumulative pressure on both juvenile and spawning habitats. Based on our hypothesis we build two combined scenarios:

- (i) Impact of hypoxia on both juveniles and spawning habitat, with hypoxia impacting eggs survival (Juveniles + eggs)
- (ii) Impact of hypoxia on both juvenile and spawning habitat, with hypoxia impacting spawners survival (Juveniles + spawners).

Juveniles + eggs scenarios imply the combinations of  $\alpha_J$  and  $\alpha_\omega$  in the steepness expression as follow (equation 17):

$$h(\alpha_J, \alpha_\omega) = \frac{\alpha_J \times \alpha_\omega \times e^{-M_{DI} \times e^{-M_{larvae} \times \bar{W}}}}{4 + \alpha_J \times \alpha_\omega \times e^{-M_{DI} \times e^{-M_{larvae} \times \bar{W}}}} \quad (\text{equation 17})$$

The carrying capacity per unit of surface is only impacted by  $\alpha_J$  so its expression remains as defined in equation 12.



In juveniles + spawners scenario,  $\alpha_J$  and  $\alpha_\omega$  will modify values of steepness, carrying capacity per unit of surface, population abundance and  $\bar{W}$  through equations 11, 12, 14 and 16.

#### 4.2.3 Literature-based parametrization

Model parametrization requires both Life History Traits (LHT: natural mortality, maximum age, age at maturity, weight at age and fecundity) and stock-recruit (steepness, carrying capacity) parameters. Most of them can be extracted from the package Fishlife (Thorson, 2020; Thorson et al., 2017) which applies a multivariate hierarchical model with a taxonomic structure to fish records from Fishbase (Froese & Pauly, 2022) and stock-recruitment series from the RAM database (Myers et al., 1995). In addition to FishLife parameters (Table 4.1 and Table S4.2.1), other parameters (weight-length relationship, fecundity...) needed to complete the model were drawn from the literature (Table S4.2.1). The carrying capacity of the juvenile habitat is a scaling factor of population size which writes as the product of carrying capacity per unit of surface and the nursery habitat surface area (Champagnat et al., sub.); they were arbitrarily set to  $K = 10^6$  (number of individuals), with  $K^* = 1$  and the surface used as the scaling factor for the population size fixed to  $S = 10^6$  for all species (note that the unit of surface is arbitrary as only the product  $K^* \times S$  matters). The mortality rate of eggs and larval drift ( $M_{larvae}$ ) is also needed and was set so that the resulting survival is  $10^{-3}$  for plaice and anchovy and  $10^{-5}$  for cod (Le Pape and Bonhommeau, 2015). Baseline values of  $M_{DI}$  and  $M_{DD}$  were derived from the LHT and based on equations 6 and 7.  $M_{DI}$  is derived from steepness, larval mortality and mean number of eggs produced by a recruit during its lifetime ( $\bar{W}$ ) while  $M_{DD}$  is totally determined by the values of  $M_{DI}$  and  $K^* = 1$  (Table 4.1).

Table 4.1: Life history parameters data for the three-example species in the baseline configuration (all habitat multipliers = 1).  $a_{mat}$  and  $a_{max}$  refers to maturity and maximum age,  $M$  is the natural mortality,  $h$  is the steepness,  $r$  is the intrinsic rate of population increase (all extracted from FishLife, Thorson, 2020).  $e^{-M_{larvae}}$  is the survival from eggs to the larvae just before their arrival on juvenile habitat (Le Pape and Bonhommeau, 2015).  $\bar{W}$  is the mean number of eggs produced by a recruit during its lifetime in the absence of fishing, computed based on species LHT. Density-independent mortality  $M_{DI}$  parameter is derived from species data (equation 7) and density-dependent mortality  $M_{DD}$  is deduced from  $M_{DI}$  and  $K^* = 1$  (equation 6).

Species	$a_{mat}$	$a_{max}$	$M$	$h$	$r$	$e^{-M_{larvae}}$	$\bar{W}$	$M_{DI}$	$M_{DD}$
Atlantic cod	3	15	0.27	0.79	0.35	$10^{-5}$	$2.6 \cdot 10^6$	0.54	0.75
Atlantic herring	5	12	0.24	0.58	1.2	$10^{-3}$	$3.7 \cdot 10^4$	1.92	0.33
European plaice	4	28	0.14	0.82	0.25	$10^{-3}$	$4.5 \cdot 10^5$	3.23	0.13

#### 4.2.4 Simulations

Once parameterised for each species, the model was used to simulate population dynamics under various habitat scenarios (i.e., combinations of  $\alpha_J$ ,  $\alpha_\omega$  and  $\alpha_S$ ). Habitat scenarios were run by setting survival multipliers to values between 0.8 (lower habitat quality) and 1.2 (higher habitat quality). First marginal effects were investigated by varying only one multiplier, while the others were fixed to one. Then cumulative effects were evaluated by exploring the impact of both nursery and spawning grounds impacts (Table 4.2).

Table 4.2: Summary table of scenarios, the habitat they target, the modified parameters and corresponding multiplier.

Scenario	Target habitat	Modified parameters	Multiplier
Juveniles	Juvenile habitats	Juvenile mortalities	$\alpha_J$
Eggs	Spawning grounds	Eggs mortality (Hyp. 1)	$\alpha_\omega$
Spawners	Spawning grounds	Adult mortality (Hyp. 2)	$\alpha_S$
Eggs + Juveniles	Nurseries & spawning grounds	Juvenile & eggs mortalities (Hyp. 1)	$\alpha_J$ & $\alpha_\omega$
Spawners + Juveniles	Nurseries & spawning grounds	Juvenile & adult mortalities (Hyp. 2)	$\alpha_J$ & $\alpha_S$

For each simulation, the effect of fishing pressure combined with habitat impact was assessed by exploring a wide range of fishing mortality rate ( $F$  from 0 to 1.5). The population was simulated with constant conditions ( $F$  and all parameters) for 500 years to ensure an equilibrium state is reached. Results were used to empirically construct the equilibrium curve relating Catch ( $C$ ) and Spawning Stock Biomass ( $SSB$ ) at equilibrium, therefore enabling the estimation of management reference points such as  $SSB_{MSY}$ ,  $F_{MSY}$  and  $C_{MSY}$  (i.e., at the Maximum Sustainable Yield (MSY); widely used key indicators of the stock status and management reference points; Hilborn & Walters, 1992).

Consequences of each habitat scenario were investigated through the gain/loss relative to the baseline scenario, calculated as (equation 18):

$$\%gain/loss = \frac{indicator_{scenario} - indicator_{baseline}}{indicator_{baseline}} \times 100$$

with indicator being  $F_{MSY}$ ,  $SSB_{MSY}$  or  $C_{MSY}$ .

For the evaluation of cumulative effects, we limited complexity by using only one scenario of combined degradation (0.9) and one restoration (1.1). The cumulative habitat impact scenarios were evaluated by comparing the sum of the two marginal effects with the effect measured from the scenario resulting from the combination of effects. Based on the comparison of these two values, we can characterise three types of effects (Côté et al., 2016; Crain et al., 2008):

- Additive effects: when the effect measured from the scenario resulting from the combination of effects equals the sum of the two marginal effects;
- Synergistic effects (positive or negative depending on the sign of the effect): when the scenario resulting from the combination of effects has a greater effect than the sum of the two marginal effects;
- Antagonistic effects (positive or negative depending on the sign of the effect): when the scenario resulting from the combination of effects has a lower effect than the sum of the two marginal effects.

### 4.3 Results

First, a detailed interpretation of the results on Atlantic cod is presented, with details on the consequences of changes in both juvenile and spawning ground habitats. Then the differences between species are highlighted to illustrate the sensitivity to life history.

### 4.3.1 Atlantic cod

Habitat scenarios affect population dynamics and productivity. Equilibrium productivity curves are modified with important differences between the three scenarios (Fig. 4.2).

Modifying the egg survival on spawning grounds has the lowest effects on productivity curve and level of fishing mortality at MSY. By contrast, modifying the quality of juvenile habitat (Juveniles) has a larger impact, which is the direct consequence of the effects of scenarios on the carrying capacity of the stock (equation 12) which sets the size of the population.  $F_{MSY}$  exhibits a monotonous response to juveniles and eggs scenarios with a slight increase when habitat is getting better. The sign and magnitude of changes in  $F_{MSY}$  are the same for these two scenarios because the survival multipliers act in the same way in the steepness equation (equation 11 and 13). The spawners scenario has the strongest impact on the productivity curve: the shape of the curve is deeply modified across multiplier with a contraction when restoring and a spreading when degrading. This is a direct consequence of the changes in spawners survival that cumulates over the whole life duration of spawners. These major modifications of the curve shape result in strong modification of MSY.  $F_{MSY}$  is affected too but in a lesser extent, and with a non-monotonous response marked by a decrease of  $F_{MSY}$  when restoring habitat and an increase when degrading.

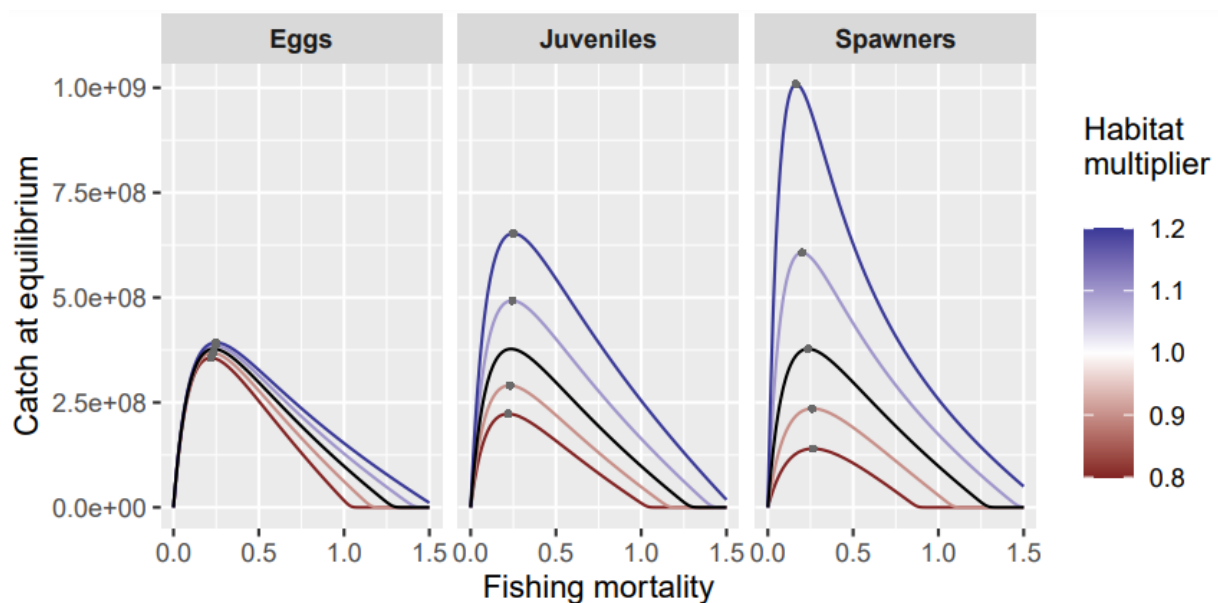


Figure 4.2: Marginal effects of modifying spawning ground habitat with hypothesis 1 (Eggs, left panel) or 2 (Spawners, right panel), or juvenile habitat quality (Juveniles, middle panel) on equilibrium productivity curves of the Atlantic Cod. Black line is the baseline scenario, blue and red lines show scenarios of restoration (multiplier  $>1$ ) and degradation (multiplier  $<1$ ) respectively. The grey points highlight changes in  $MSY/F_{MSY}$  according to simulations.

### 4.3.2 Comparing the response across species and life histories

#### 4.3.2.1 *Marginal effects*

As noticed for cod, the eggs scenario globally has the least effect on the three indicators, while the spawners scenario was the most impacting for the three species (Fig. 4.3). Effects of restoration and degradation scenarios on juvenile habitat and eggs survival are symmetric, while spawners restoration has a higher impact than degradation.

Juveniles and eggs scenarios exhibit identical changes in  $F_{MSY}$ . Herring is the most impacted species which is expected as it has the lowest baseline values of steepness and hence the highest dependency to the amount of eggs.  $SSB_{MSY}$  is rather insensitive to eggs scenarios, but is impacted by juvenile scenarios with cod exhibiting the strongest response because  $M_{DI}$  of cod is the lowest among all species tested and hence the effect on  $K$  the highest (equation 12).

For scenarios impacting the spawners, plaice is the most impacted, and herring the least. This response is related to the lifespan and age at maturity characteristics. Indeed, plaice live the longest with a moderate age at maturity (28 and 4 years, respectively, Table 4.1). Hence, any increase in spawners' mortality cumulates over the entire lifespan and mechanically affects this species more than herring which is more short-lived and later maturing (12 and 5 years, respectively, Table 4.1).

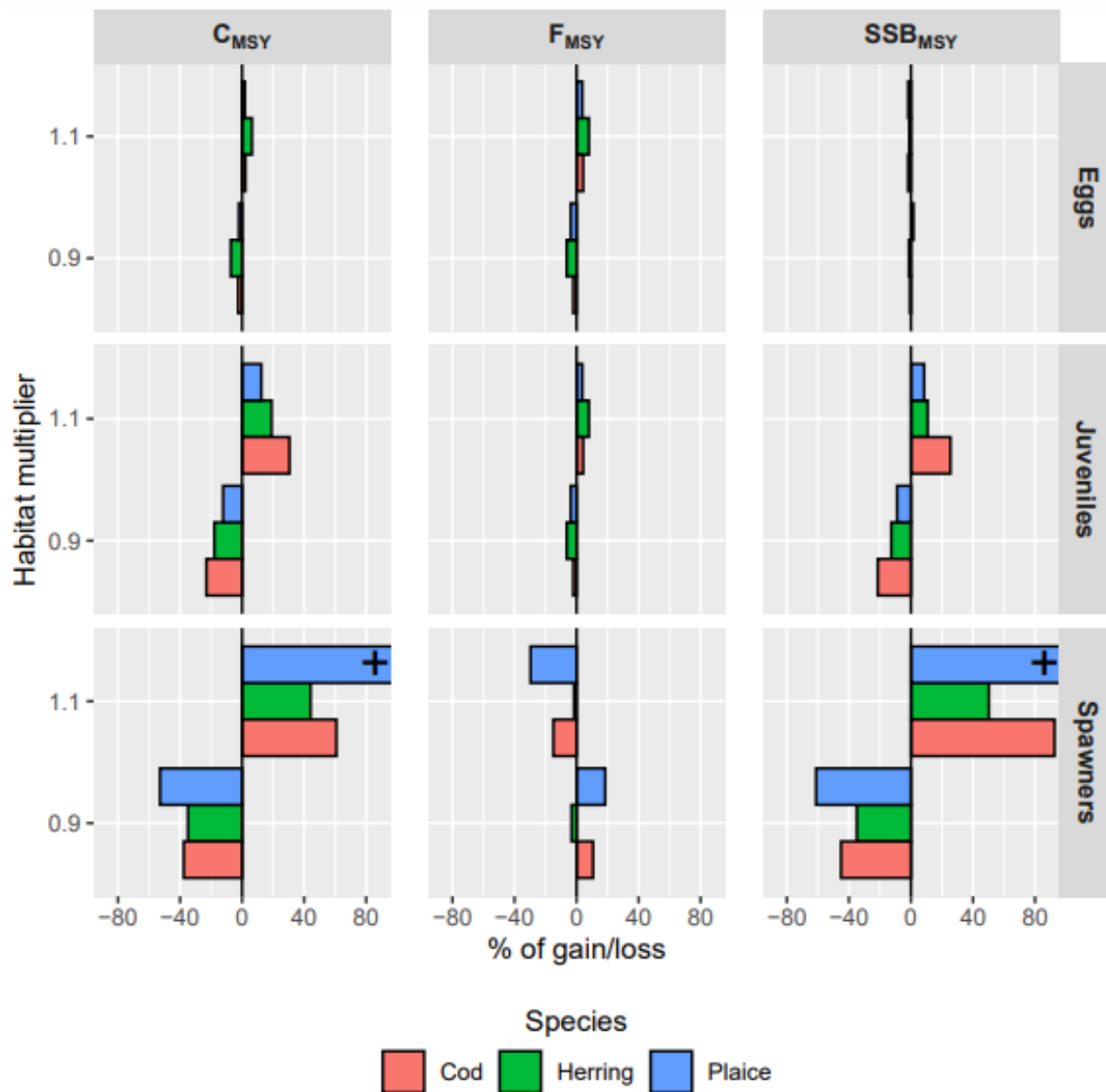


Figure 4.3: Marginal effects of the three habitat scenarios (rows) on the value of  $C_{MSY}$  (left column),  $F_{MSY}$  (middle column), and  $SSB_{MSY}$  (right column) for the three-example species (European plaice: Blue, Atlantic cod: Green, and Atlantic herring: Orange). The stars indicate out of the graph high values obtained for plaice in spawners scenario (140% for left panel, 246% for the right one).

#### 4.3.2.2 Combined scenarios

Scenarios combining impacts on eggs and juveniles leads to slightly non-additive effects (Fig. 4.4, upper row) but with only slight difference between species. For restoration scenarios, effects on  $F_{MSY}$  are antagonistic, for the three species, while changes in  $SSB_{MSY}$  are slightly synergistic. Consequently, changes in  $C_{MSY}$  are simply additive. For degradation scenarios, plaice, the less sensitive species to eggs and juveniles marginal scenarios, exhibits only additive effects. Cod and herring show opposite effects compared to restoration scenarios with light synergy for  $F_{MSY}$  and light antagonism for  $SSB_{MSY}$ .

Scenarios combining spawners' and juveniles' impacts lead to stronger non-additive responses and stronger contrasts between species (Fig. 4.4, bottom row). For  $SSB_{MSY}$ , effects are antagonistic for degradation scenarios and synergistic for restoration (except for plaice with an antagonistic effect, not visible on Fig.4.4). Effects on  $C_{MSY}$  are very similar to those on  $SSB_{MSY}$ . Effects on  $F_{MSY}$  are more mitigated. Cod and plaice responses are antagonistic under the degradation scenario and synergistic for restoration.  $F_{MSY}$  responses for herring are opposite to cod and plaice, exhibiting a synergistic effect under degradation and an antagonistic effect under restoration.

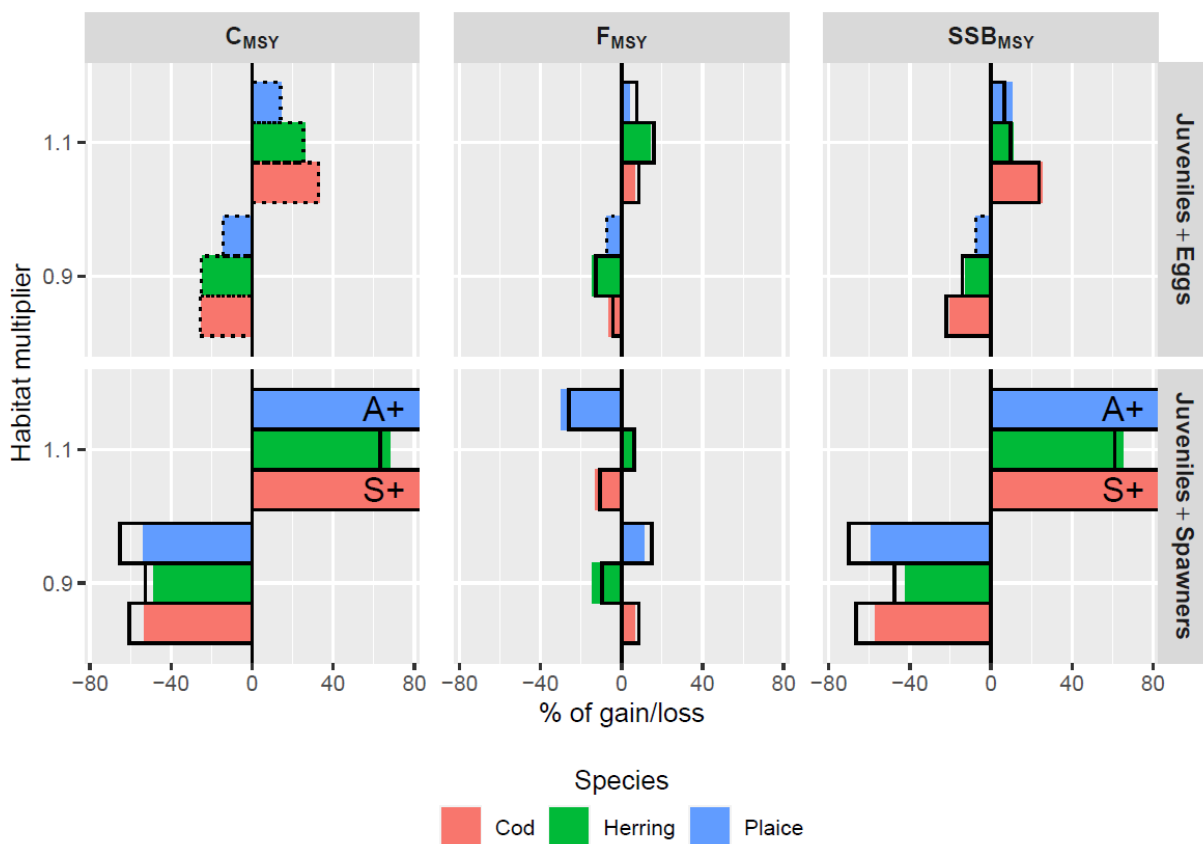


Figure 4.4: Effect of the two combined habitat scenarios (rows) as compared with the sum of marginal effects. Effects are shown on the values of  $C_{MSY}$  (left column),  $F_{MSY}$  (middle column), and  $SSB_{MSY}$  (right column) for the three-example species (European plaice: Blue, Atlantic cod: Green, and Atlantic herring: Orange). The colour filling indicates the effects of the combined scenario and the black borders shows the value of the sum of marginal effects. Dotted borders are used when there is no significant difference (difference between combined and summed values is less than 5%). The text labels indicate what is the type of cumulative effect observed for out of scale high values of effects obtained in spawners scenario (“A+” for positive antagonism and “S+” for positive synergism).

## 4.4 Discussion

We developed a modelling approach that combines an age- and stage-structured simulation model with a sensible parameterization of habitat quality on both juvenile and spawning habitat to assess the consequences of habitat degradation/restoration on the productivity of exploited marine fish populations. The model is built and parameterised to acknowledge a wide range of species with variable life histories. Our framework is applied in the Baltic to explore population responses when mitigating/increasing hypoxia within two EFH: juvenile habitats and spawning grounds. Scenarios were applied on three species with contrasted life cycles (plaice, cod and herring), out of the large number species impacted by anoxia in the Baltic at both juvenile and spawning stages (Jokinen et al., 2016; Kraufvelin et al., 2018). We developed different hypotheses relative to the way hypoxia affects eggs or spawners themselves on the spawning grounds, and proposed parameterization for each of them. The model can be used to simulate marginal effects of habitat scenarios on either juvenile habitat or spawning grounds, but also to simulate cumulative effects of pressures affecting populations simultaneously on juvenile and spawning habitats.

Our global aim is to simulate scenarios impacting transitions (survival) at different life stages. To do so we modified the use of multipliers in scenarios compared to Champagnat et al. (sub.). Because the different stages (egg, juvenile and spawner) have different mortality rates and duration that are raised at the exponential scale to get survival expressed as a proportion of individuals that survive, parameterising scenarios using multipliers in the scale of mortality rates mechanically lead to higher influence of multipliers applied to transitions with the higher mortality rates and duration (Levin and Stunz, 2005). As a direct consequence, the multipliers applied to mortality rates on adults would mechanically have a lower influence than those applied to eggs and to juveniles. To overcome this scaling issue, we parameterised scenarios by applying multipliers directly on the resulting survival rates at life stage (i.e., applied to survival expressed as the proportion of eggs/individuals that survive).

The tested scenarios lead to modifications in level of sustainable fishing pressure  $F_{MSY}$ , and population size and yield at MSY, but with different magnitudes among species depending on their life history traits. Marginal effects of the habitat scenarios were consistent across the three species. Perturbations of spawning habitats resulting in increased eggs mortality had the least impact while the more direct effect on spawners survival exhibited the largest impact. Those results were consistent with our expectation. Indeed, increasing eggs mortality is numerically



equivalent to decreasing spawners fecundity, which has already been associated with light population response (Champagnat et al., 2021). In contrast, increasing spawners mortality cumulates over the entire lifespan and hence has a much stronger impact long-term reproductive potential, and thus stronger impacts on  $SSB_{MSY}$ ,  $C_{MSY}$  and  $F_{MSY}$ . Within each scenario, population responses depended upon species and life history traits, with contrasts among species mainly driven by differences in steepness and lifespan.

#### 4.4.1 Limitations

The two hypotheses of impacts of hypoxia on spawning ground, led to dramatically different population responses. These hypotheses directly rely on different mechanistic hypotheses of individual fish response (Fig. 4.1): avoidance, which results in fewer eggs spawned or that survive; or persistence that results in increasing spawners mortality (Behrens et al., 2018; Petersen and Pihl, 1995; Skjæraasen et al., 2008). Both mechanisms are likely in the wild and may even occur simultaneously in a population for different individuals. Those two hypotheses regarding the individual consequences of hypoxia during spawning were contrasted and combined with the effect of habitat perturbations in juvenile habitats, where persistence appears as the realistic option (Le Pape and Cognez, 2016).

Because of the multiple potential impacts of hypoxia and the complexity of fish life histories, predicting/quantifying the effect of hypoxia on wild fish populations remain challenging (Rose et al., 2009; Eero et al., 2011). While we focus on the direct impacts of habitat perturbations, other processes induced by hypoxia probably interact with population dynamics, for example: massive food deprivation all along the lifespan, increase in catchability, or reduced fecundity (Rose et al., 2018). Our simulations of hypoxia impact on populations remain theoretical because no information was available to parametrise realistic effects. Indeed, while many in-laboratory experiments/studies evidenced direct influence of hypoxia on fishes (see Thomas et al., (2019) for a review), quantification of impacts in the wild is still lacking (Rose et al., 2018). Although life stage is an important determinant of the relative sensitivity of an organism to environmental stressors (Thomas et al., 2019), the lack of realistic estimates leads us to test the same multiplier for the three stages of life impacted (egg, juvenile and adult).

Population dynamics also remained theoretical because we parametrised the three studied species from the literature and arbitrarily set the baseline population size to  $10^6$ . We did not embed our model within a full statistical approach to estimate all parameters but rather assess the realism of baseline population dynamics (i.e., under no habitat modification) by looking at

the values of  $F_{MSY}$  and  $\frac{C_{MSY}}{SSB_{MSY}}$ . Baseline scenarios lead to a  $F_{MSY}$  value of 0.14, 0.24 and 0.32 for plaice, cod and herring respectively. While cod and herring  $F_{MSY}$  values were close to the estimated value in stock assessments (0.26 for cod and 0.31 for herring ICES, 2022), the  $F_{MSY}$  value for plaice appears a bit low. The values reported in the assessment for the stock that includes plaice in the SW Baltic (0.31, ICES, 2022) and estimations for the North Sea and Skagerrak (0.19, ICES, 2021b) stocks.

The model itself had two main limitations, which have been thoroughly discussed in Champagnat et al., (sub). First the model is deterministic thus demographic (Koons et al., 2016; Plard et al., 2019) and environmental (Engen et al., 1998; Pfister and Stevens, 2003) stochasticity are not considered. Second, juvenile and spawning habitat are considered as one block although those areas are marked by high spatial heterogeneities (Fodrie et al., 2009; Nagelkerken et al., 2015). Including spatial aspects would multiply the complexity of the model and make the parametrisation more data demanding (Champagnat et al., 2021; Ono et al., 2019) and scenarios design more difficult. In addition, including stochasticity would add another source of complexity to explore population trajectories and equilibrium. Exploring the role of spatial structure and stochasticity and how they interact with habitat scenarios would, however, constitute rich research avenues and important considerations for management (Punt, 2019; White, 2010).

#### 4.4.2 Life histories shape population responses

Our modelling approach highlighted that the life history stage impacted by anoxia (egg, juvenile or spawner) induced differential and species-specific responses.

As observed Champagnat et al., (sub), scenarios modifying steepness (e.g. eggs and juveniles scenarios) resulted in strong sensitivity of  $F_{MSY}$  for species with low steepness value, here herring. Indeed, the steepness (Horbowy & Hommik, 2022; Miller & Brooks, 2021) combined with other life history traits (i.e., life duration and mortality, Thorson (2020) is the main driver of the relative productivity of a population, i.e. the lower the steepness, the less the recruitment is dampened and the higher the sensitivity to lower amount of spawning products.

Spawners' scenarios were simulated through change in spawners' mortality. The sensitivity to these scenarios were mechanically driven by adult natural mortality value and the number of age class affected (determined by lifespan and age at maturity). Therefore, plaice (long-living, medium age at maturity) exhibits very strong responses while herring (medium living and late

maturing) was least impacted. Here, the species with the shorter lifespan also matures the later (i.e., herring, Table 4.1), which further reduces the proportion of adults in the population being affected in the spawning phase and thus the strength of the response. However, these characteristics are quite species-specific. Indeed, longevity, maximum size, adult mortality and age at maturity are usually positively correlated traits among marine fish populations (Kindsvater et al., 2016a, 2016b; Thorson et al., 2017). Because of these trade-offs between LHT, the proportion of impacted year class in the population would likely be more balanced between long- and short-living species. Therefore, enlarging the range of life histories in our analysis might lead to less contrasted population results.

#### 4.4.3 Cumulative pressure on multiple EFH and life stages

Our study differed from classical multi-stressor studies (for instance, Teichert et al., (2016) assessing different stressors, or Archambault et al. (2018) assessing couples of stressor-life stage) because we did not consider different types of stressors but rather one stressor acting at different life stages (with different consequences) as discussed in Brown et al., (2018).

The simulations of combined pressure on juvenile and spawning habitats led to various cumulative effects depending on the scenario (juveniles+eggs or juveniles+spawners), the indicator ( $F_{MSY}$ ,  $SSB_{MSY}$  and  $C_{MSY}$ ) and the species. But as mentioned in other studies (Crain et al., 2008; Darling and Côté, 2008; Teichert et al., 2016), cumulative effects were more prevalent than simple additive effects in our results (observed in 28 simulations out of 36). However, they were rather limited as cumulated effects rarely strongly depart from the sum of marginal effects, and no general patterns emerge from their analysis.

For eggs+juveniles scenarios, cumulative effects in  $F_{MSY}$  and  $SSB_{MSY}$  counterbalanced themselves and led to no cumulative effects in  $C_{MSY}$  (simple additive effects). By contrast, the strong response of  $SSB_{MSY}$  for spawners+juveniles scenarios overwrote  $F_{MSY}$  responses, leading to an identical type of cumulative effect for  $C_{MSY}$  and  $SSB_{MSY}$ . Cumulative effects on  $SSB_{MSY}$  for restoration scenarios revealed synergetic for almost all cases, underlining the high interest of mitigating habitat perturbations such as hypoxia at different life stages (Rahikainen et al., 2017), even if we are not sure about the individual mechanism associated with spawning grounds.

#### 4.4.4 Management implications

Mitigation of hypoxia, among other pressures, has already been described as a potential lever to increase fish populations (Champagnat et al., 2021, sub.; Fodrie et al., 2009; Ono et al., 2019; Ruiz et al., 2009). Here, the magnitude of gains in response to a proportional improvement in theoretical “habitat quality” indicates that there is a greater scope for habitat restoration to improve stock productivity.

Our framework could be easily adapted to consider other pressures which might affect spawning grounds. For instance, habitat losses caused by human activity affecting coastal spawners (e.g., herring vegetated spawning beds; Kanstinger et al., 2018 or contamination by xenobiotics, Ono et al., 2019).

#### 4.4.5 Need for further research work

Adapting this framework to provide for more tactical level evidence-based advice would require a better knowledge of the relationships between pressures and demographic rates at various life-history stages. Investigating the impacts of hypoxia and other pressures on different life history stages should therefore be a priority to inform both the framework presented here as well as attempts to utilise habitat and spatial management tools to support the exploitation of fish populations (Brown et al., 2018; Vasconcelos et al., 2014).

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## Conclusion du chapitre 4

Dans ce chapitre nous avons étendu l'approche pour modéliser l'effet de pressions anthropiques agissant sur plusieurs ZHFI associés à plusieurs stades de vie différents : les habitats de nourricerie et les habitats de frayère. L'étude s'est intéressée au cas de la Baltique où plusieurs populations d'intérêt commercial subissent des conditions hypoxiques au sein des ZFHI associées à la ponte et au stade juvénile. Bien que l'analyse soit restée théorique (pas de calibration à l'échelle des stocks, ni de données ou d'informations pour paramétrer les scénarios), elle permet de comparer les effets de l'hypoxie à différents stades de vie (i.e., œuf, juvénile et adulte reproducteur) et d'analyser comment les gradients d'histoires de vie impactent les réponses des populations.

Les trois scénarios (i.e., impact de l'hypoxie sur la mortalité des œufs, des adultes reproducteurs, ou des juvéniles) impactent les biomasses, les captures et la pression de pêche au rendement maximal durable. Mais l'échelle des réponses dépend du scénario : les effets induits par une variation de la mortalité des œufs sont très limités, tandis que ceux induits par une variation de la mortalité des adultes reproducteurs sont très forts, et ce pour les trois espèces. En effet, l'augmentation de la mortalité des adultes reproducteurs se cumule au cours du temps et impacte la biomasse ainsi que le potentiel reproducteur de la population, ce qui explique les fortes réponses. Au contraire, l'augmentation de la mortalité des œufs engendre les mêmes effets qu'une baisse de la fécondité qui sur le long terme, pour une population non surexploitée (ici on estime les effets au RMD), n'a pas un fort impact sur la dynamique de population (Champagnat et al., 2021).

Au sein de chaque scénario, la sensibilité des indicateurs dépend de l'espèce et de ses THV. Comme observé au chapitre précédent pour les scénarios de qualité des nourriceries, la sensibilité de la pression de pêche au RMD en réponse aux scénarios impactant la mortalité des œufs et des juvéniles dépend de la steepness (Horbowy and Hommik, 2022). Parmi les trois espèces comparées, le hareng qui a la plus faible steepness est donc l'espèce la plus impactée. Pour les scénarios impactant les adultes reproducteurs, la sensibilité est déterminée le nombre de classes d'âge matures affectées (i.e. déterminée par le nombre de cohortes entre l'âge à maturité et l'âge maximal). La plie vit longtemps et mature relativement tôt, elle est donc plus fortement impactée par ce scénario que le hareng à la vie plus courte et à la maturité plus tardive.

Le cumul des scénarios (mortalité des œufs + des juvéniles ; mortalité des adultes reproducteurs + des juvéniles) simule l'impact d'une pression intervenant à différents stades de vie et donc dans différents ZFHI. Ces cumuls engendrent des effets non additifs (valeur de l'effet cumulé différent de la simple somme des effets marginaux) pour une majorité de configurations (28 sur 36), ce qui concorde avec les résultats de nombreuses autres études (Crain et al., 2008; Darling and Côté, 2008; Teichert et al., 2016). Pour autant, les effets cumulés sont en général peu différents en valeur de la somme des effets marginaux, et aucun motif général n'émerge de l'analyse. On peut toutefois noter que pour presque tous les scénarios de restauration, les effets cumulés sur la biomasse des adultes reproducteurs au RMD sont synergiques, ce qui indique que l'atténuation de l'hypoxie sur les frayères et nourriceries pourrait aboutir à des effets forts sur le niveau des populations.



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## **5. Discussion générale**

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*Illustration: Sylvie Champagnat*



## 5.1 Synthèse des résultats de la thèse

Ce travail de thèse apporte une contribution à l'étude de l'impact de la dégradation des ZFHI sur la dynamique des populations marines exploitées. Nous avons (i) développé des modèles de population pour explorer les conséquences des pressions anthropiques s'exerçant *via* l'habitat à différents stades de vie sur le renouvellement des populations et leur potentiel d'exploitation ; (ii) appliqué ces modèles pour des espèces avec des cycles de vie et des caractéristiques démographiques contrastées pour explorer la variation des réponses dans un gradient d'histoires de vie.

Le chapitre 2 s'est concentré sur un cas d'étude précis : l'impact de la dégradation de la nourricerie de l'estuaire de Seine sur la métapopulation de sole de Manche Est. La dynamique des trois sous-populations de ce stock est simulée grâce à un modèle de cycle de vie structuré en âge, en stades et spatialement. Le modèle intègre l'exploitation par la pêche, la dépendance des juvéniles aux habitats de nourricerie ainsi que le fonctionnement spatial de la métapopulation en lien avec le processus de recrutement spatialisé au niveau de cinq nourriceries côtières. En amont de la thèse, ce modèle a été ajusté sur des séries de données (captures commerciales, indices d'abondances de la fraction adulte et de la fraction juvénile de la population) grâce à une approche de modélisation statistique intégrée mobilisant un cadre hiérarchique bayésien. Le modèle est ensuite utilisé pour simuler des scénarios de restauration de l'habitat construits à partir de données et d'expertise multidisciplinaires portant sur la surface et la qualité de la nourricerie de l'estuaire de Seine. Ces scénarios révèlent le fort potentiel de la restauration de l'estuaire de Seine pour augmenter la biomasse et les captures en Manche Est. Les effets sont les plus forts dans la zone adjacente au secteur de nourricerie de la Seine, mais se diffuse à l'ensemble de la Manche Est au travers de la dynamique de métapopulation. Cependant la complexité de l'approche liée à l'articulation entre modélisation et inférence statistique et à la quantité d'informations et de données nécessaire à sa paramétrisation souligne sa grande spécificité et met en exergue sa faible transférabilité à d'autres cas d'étude.

Le chapitre 3 s'est attaché à développer un modèle de simulation capable d'intégrer l'impact de l'habitat juvénile sur la dynamique d'une population tout en s'appuyant sur une paramétrisation générique pouvant être adaptée à différentes populations afin (i) d'explorer comment les réponses des populations varient pour un gradient d'histoires de vie, et (ii) de pouvoir appliquer l'approche à un assemblage d'espèces exploitées à l'échelle d'une façade maritime. Pour ce faire, on combine un modèle structuré en âge et stades et une relation stock-recrutement

paramétrée en fonction de la steepness et qui dépend directement de la qualité et de la surface d'habitat juvénile. Des multiplicateurs de surface et de qualité sont appliqués pour construire des scénarios et réaliser des simulations jusqu'à un état d'équilibre. Puis des indicateurs de la productivité de la population au RMD sont calculés (biomasse féconde, captures, mortalité par pêche).

Une première application du modèle à trois espèces choisies pour les contrastes dans leurs THV (raie fleurie, anchois, plie ; chapitre 3.1) permet d'explorer les réponses induites par les différents scénarios (dégradation/restauration de surface ou de qualité des nourriceries) mais aussi d'analyser comment les réponses varient entre espèces en fonction de leurs THV. Les scénarios de surface ont un simple effet de taille sur la population et les captures, identiques pour les trois espèces ; alors que la qualité induit aussi un changement de productivité, pour lequel une steepness faible accroît la sensibilité de la population (e.g., raie réponse forte, anchois réponse faible).

Le modèle est ensuite appliqué à quatre stocks exploités de Manche Est (sole, plie, bar et merlan ; chapitre 3.2) qui dépendent de zones de nourricerie communes, pour étudier l'impact de la restauration de ces nourriceries sur les quatre populations. Le modèle est calibré pour chaque espèce à partir de données issues des évaluations de stock et de la littérature. Des scénarios réalistes de restauration de la surface et de la qualité des nourriceries côtières communes aux quatre stocks sont construits et simulés. Les résultats de cette étude pointent à la fois le fort potentiel de la restauration des habitats côtiers pour augmenter la taille des populations et les captures associées, mais aussi la sensibilité des réponses aux caractéristiques des espèces. Les populations fortement concentrées sur les habitats peu profonds (e.g., le bar et la sole) ont une réponse bien plus forte que la plie et le merlan, et ce quel que soit le scénario.

Dans le chapitre 4, le modèle générique est étendu pour considérer l'impact de pressions s'exerçant au niveau des frayères et donc sur les adultes lors de la reproduction. Plus précisément l'analyse se concentre sur l'impact de l'hypoxie dans les frayères et les nourriceries. Deux scénarios sont formulés à partir d'hypothèses sur la réponse des individus exposés à l'hypoxie au sein d'une zone de ponte : augmentation de la mortalité des adultes reproducteurs (persistance) ou augmentation de la mortalité des œufs pondus dans un habitat moins favorable (évitement). L'impact sur les juvéniles dans leurs nourriceries est modélisé via une augmentation des mortalités du stade juvéniles (même formulation que les scénarios de qualité du chapitre 3). Le modèle est appliqué à trois espèces de poissons exploités en Baltique (morue, plie et hareng) qui peuvent subir des évènements hypoxiques dans leurs ZFHI.

L'impact marginal de chaque scénario est évalué. Pour les trois espèces, une forte réponse émerge du scénario qui touche les adultes reproducteurs alors que l'hypothèse d'une hausse de mortalité des œufs impacte peu la population. Les réponses dépendent aussi des THV des espèces. Une faible steepness (e.g., hareng) engendre une plus forte sensibilité aux scénarios touchant la mortalité des œufs et des juvéniles tandis qu'un nombre élevé de cohortes matures (e.g., la plie) accroît l'intensité de la réponse aux scénarios touchant la mortalité des adultes reproducteurs.

## 5.2 Compromis entre généralité et précision

Bien que reposant sur un socle de modélisation commun (i.e., modèle de dynamique de population structuré en âge et stades), les stratégies de modélisation déployées au cours de la thèse se positionnent différemment sur un gradient « data-driven » vs « process-driven ».

### 5.2.1 Un modèle paramétré précisément à partir d'une approche statistique intégrée

La première approche (chapitre 2) s'appuie sur un modèle de cycle de vie pour représenter la dynamique de métapopulation de la sole de Manche Est. Elle mobilise une grande quantité de données et de connaissances expertes couvrant presque intégralement le cycle de vie de la sole : matrice de survie et de répartition des larves dans les différents secteurs de nourricerie (sorties d'un modèle IBM biophysique, Rochette et al., 2012; Savina et al., 2016), indices d'abondance juvéniles (sorties d'un modèle d'habitat basé sur des séries temporelles issues de campagnes scientifiques côtières, Rochette et al. 2010), captures et indices d'abondances des adultes détaillés par âges (données du CIEM et hypothèses de répartition spatiale des données), structure spatiale de la population et connectivité entre chaque stade et région (analyse de paramètres biologiques, morphométrie des otolithes, génétique (Randon et al., 2020) et modèle de capture-marque-recapture (Lecomte et al., 2020)).

*In fine*, le modèle est très consommateur en données et les sorties produites sont fortement conditionnées par ces données (« data driven »). Cette caractéristique se retrouve dans de nombreux modèles visant à quantifier l'impact de l'habitat sur une population (voir la méta-analyse de Lipcius et al. 2019, mais aussi Camp et al. (2020) et Rose et al. (2018)). La plupart nécessitent une grande quantité de données et un effort de paramétrisation important ce qui compromet leur transférabilité à d'autres cas d'étude.

Plus généralement, le modèle spécifique au cas d'étude de la sole en Manche Est et les approches de modélisation développées ensuite dans cette thèse font écho à la nécessité d'accepter un compromis entre les trois pôles de la modélisation théorisés par Levins (1966) dans « The strategy of Model Building in Population Biology » : la précision, le réalisme et la généralité. Levins (1966) postule que le fonctionnement global d'un système naturel est trop complexe pour que l'on puisse en faire une description totalement fidèle par des équations mathématiques, et qu'il est vain de chercher à développer une approche de modélisation permettant de maximiser ces trois pôles simultanément. Ainsi, dans la pratique, toute approche devra faire un compromis entre ces trois pôles, en cherchant par exemple à maximiser deux d'entre eux au dépend du troisième (Fig. 5.1). Notre première approche (chapitre 2) est indubitablement précise et réaliste au détriment de la généralité.

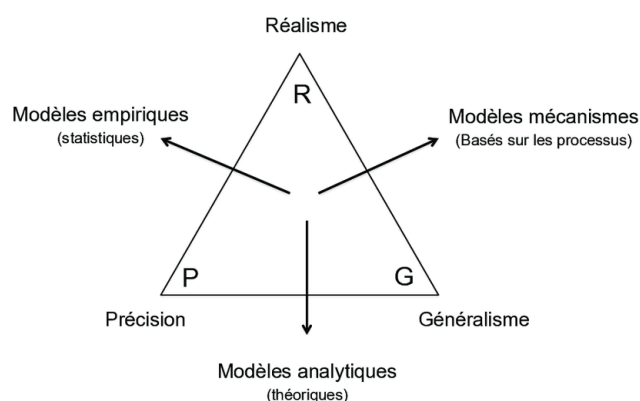


Figure 5.1 : Triangle de Levins représentant les trois propriétés d'un modèle et les stratégies de modélisation qui en découlent (Levins, 1966).

### 5.2.2 Vers un modèle plus générique

Le constat ci-dessus a motivé le développement d'un modèle capable de quantifier l'impact de l'habitat juvénile sur la dynamique de population tout en gardant une paramétrisation parcimonieuse et accessible à partir de la littérature (chapitre 3). Cette stratégie sacrifie donc la précision au profit de la généralité et du réalisme.

Dans les chapitres 3.1 et 4, les populations simulées sont « théoriques » c'est-à-dire qu'elles reposent sur une paramétrisation issue de la littérature et ne font pas l'objet de calibration. Elles représentent une dynamique basée sur les THV de l'espèce. Le réalisme est assuré par le fait que cette paramétrisation s'appuie sur des connaissances solides issues de la littérature pour l'essentiel des THV (Thorson, 2020; Thorson et al., 2017), mais aussi le calcul d'indicateurs de

la dynamique de population qui sont évalués comparativement à des références. La mortalité par pêche au RMD a été confrontée à des valeurs issues d'évaluations de stock lorsqu'elles étaient disponibles et le ratio captures/biomasse au RMD a été comparé entre espèces (Winker et al., 2018). Ces diagnostics sont assez simples et probablement réducteurs. Ils permettent néanmoins de s'assurer d'un niveau acceptable de réalisme des approches menées.

Dans l'étude décrite dans le chapitre 3.2, l'application à des cas d'étude spécifiques implique une étape de calibration. Cependant, cette calibration a uniquement porté sur le paramètre de capacité d'accueil des nourriceries ( $K$ ), qui détermine le nombre maximal de juvéniles parvenant au stade adulte et donc *in fine* la taille du stock. La plupart des paramètres utilisés restent issus de la littérature et la calibration se base sur des résultats d'évaluation de stock (séries temporelles de biomasse et de captures), issus de modèles qui s'appuient sur des méthodes statistiques permettant d'intégrer l'ensemble des données disponibles.

## 5.3 Hypothèses structurantes et limites

### 5.3.1 La relation stock-recrutement (SR)

La relation SR est une composante clef des modèles de population. Elle permet de « boucler » le cycle de vie et donc de simuler des états d'équilibre et d'en déduire des points de référence biologiques, afin de contribuer à l'aide à la décision pour la gestion (Hilborn et Walters 1992 ; Punt, Smith, et Cui 2001). La forme de la courbe SR détermine la résilience d'une espèce à l'exploitation et aux perturbations environnementales (Keith & Hutchings, 2012 ; Lee et al., 2012 ; Mangel et al., 2010). Dans les approches développées dans ce travail de thèse, elle est essentielle car le stade de recrutement englobe les processus de mortalité intervenant dans les habitats des juvéniles, directement liés à la surface et la qualité de ces habitats.

#### 5.3.1.1 *Paramétrisation des relations SR*

La paramétrisation des relations SR est difficile. Le processus de recrutement, en particulier chez les poissons, est éminemment stochastique, et la part de variabilité résiduelle non expliquée par les modèles SR est toujours très dominante par rapport à la variabilité expliquée (Chambers et Trippel 1997 ; Hinrichsen 2001 ; Houde 1997, 2008 ; Myers et Barrowman 1996). À cela se rajoute que les séries temporelles de stock (généralement la biomasse féconde) et de recrutement (généralement l'abondance de recrues) utilisées comme données d'entrée sont souvent courtes et de surcroît elles-mêmes empreintes d'incertitude (Burrow, Horwood, et Pitchford 2013 ; Hinrichsen 2001 ; Le Pape et al. 2020). Elles sont donc peu informatives pour

estimer des valeurs de paramètres SR (Conn, Williams, et Shertzer 2010 ; Myers, Bowen, et Barrowman 1999 ; Zhou 2007). Malgré la grande quantité de données mobilisées, le modèle de cycle de vie de la sole de Manche Est n'y fait pas exception. En effet, les valeurs estimées pour la survie à faible densité dans les relations stock-recrutement au sein des nourriceries (pente à l'origine de la courbe SR) sont très discutables. Pour toutes les nourriceries cette survie maximale est estimée autour de 0,9 , ce qui paraît irréaliste, ce taux de survie étant probablement très inférieur (Le Pape and Bonhommeau, 2015). La surestimation de ces paramètres provient probablement de l'hypothèse forte formulée sur la mortalité journalière lors de la dérive larvaire (stade non observé) ; mais aussi des faibles contrastes dans les séries SR (peu voire pas d'observations d'un stock très dépeuplé où les mécanismes densité-dépendants sont fortement réduits). Les conséquences potentielles de cette surestimation sur les résultats de la simulation nous interrogent. En effet, des taux de survie trop élevés peuvent générer des dynamiques de population irréalistes. Elles peuvent notamment conduire à des estimations de rendement maximal durable obtenues pour des mortalités par pêche très élevées lorsque la sélectivité est dirigée uniquement vers les adultes.

Une pratique courante pour dépasser ces problèmes d'estimation est l'usage d'approches par méta-analyse : le faible signal existant entre la variation du stock et du recrutement est cumulé sur de multiples populations (Britten, Dowd, et Worm 2016 ; Myers, Bowen, et Barrowman 1999 ; Hilborn et Liermann, 1998) et/ou entre taxons (Archambault et al. 2014 ; Thorson 2020). Ces approches hiérarchiques permettent d'estimer de façon plus robuste les paramètres des relations SR et d'établir des relations entre ces paramètres et les traits d'histoire de vie ou les façades géographiques (Myers et Mertz, 1998). Par exemple, la steepness a été estimée conjointement à d'autres THV (âge maximum, âge à maturité, taux de croissance de Von Bertalanfy, longueur et poids maximum...) pour un très large panel d'espèces de poissons par une approche de méta-analyse (Thorson, 2020).

Au vu (i) de la difficulté d'estimer des paramètres SR fiables et informatifs à partir de données d'une seule population, (ii) de l'existence de valeurs par taxons estimées de façon robuste par métanalyses hiérarchiques, le choix a été fait de paramétrer la relation SR du modèle générique en fonction de la steepness. Une paramétrisation originale de la relation SR en fonction des taux de mortalité instantanée densité-dépendants et densité-indépendants sur lesquels sont modélisés directement les effets de l'habitat nous a permis de relier indirectement les effets de l'habitat à la steepness. De plus, les estimations des THV ont servi de base d'information unique pour de

nombreux paramètres (chapitres 3 et 4), ce qui permet d'intégrer la corrélation de la plupart de ces traits (Thorson et al., 2017).

### 5.3.1.2 *Stochasticité vs déterminisme*

Le modèle générique développé au chapitre 2 est déterministe. Cela représente une hypothèse très forte au vu de la stochasticité observée dans la dynamique des populations de poissons, notamment en lien avec la stochasticité du processus de recrutement. En effet, d'une année à l'autre la survie de l'œuf au juvénile est très fluctuante et dépend du succès de la reproduction et de la survie des jeunes stades, en lien avec les conditions environnementales (Bakun 1997 ; Houde 2008). Pour de nombreux poissons, la phase de dérive des œufs et des larves est sous contraintes hydrologiques (Bakun 1997 ; Cushing 1995), climatiques (développement conditionné par la température, Gerber et al. 2014), trophiques (disponibilité en nourriture (Beaugrand et al., 2003) et prédation (Vanderveer et al., 2000)). Cette phase est la principale cause de la variabilité du recrutement. En effet, bien que soumise à des fluctuations environnementales, la seconde phase du recrutement (phase juvénile au sein des nourriceries) est en comparaison bien moins variable (Houde 2008 ; Le Pape et Bonhommeau, 2015).

En utilisant la variabilité résiduelle autour de modèles SR comme proxy de la variabilité du processus de recrutement, certaines études ont montré des différences entre ordres de poissons marins exploités. Archambault et al. (2014), par exemple, ont estimé que la stochasticité du recrutement des Clupéiformes et Gadiformes est significativement plus élevée que celle des Perciformes et des Pleuronectiformes. La phase juvénile nourricerie-dépendante des Pleuronectiformes agit comme un tampon sur la variabilité du recrutement, ce qui explique les différences observées avec les Gadiformes (bentho-demersaux) et les Clupeiformes (pélagiques) moins dépendants d'habitats juvéniles restreints spatialement (hypothèse de concentration, Iles et Beverton 2000). Plus généralement, Rose et al. (2001) mettent en lien la stochasticité du recrutement et les traits d'histoire de vie des populations, à partir des stratégies décrites par Winemiller et Rose (1992). Les espèces à stratégie opportuniste ont une variabilité plus forte que celles à stratégie périodique ou équilibrée (Fig. 5.2). Par exemple, les Clupéiformes peuvent être considérés comme des opportunistes (petit, maturation rapide, vie courte et recrutement très fluctuant) et les pleuronectiformes comme équilibrés (vie longue et recrutement relativement stable). Pour les autres ordres, les stratégies varient entre espèces et sont plus difficiles à établir.

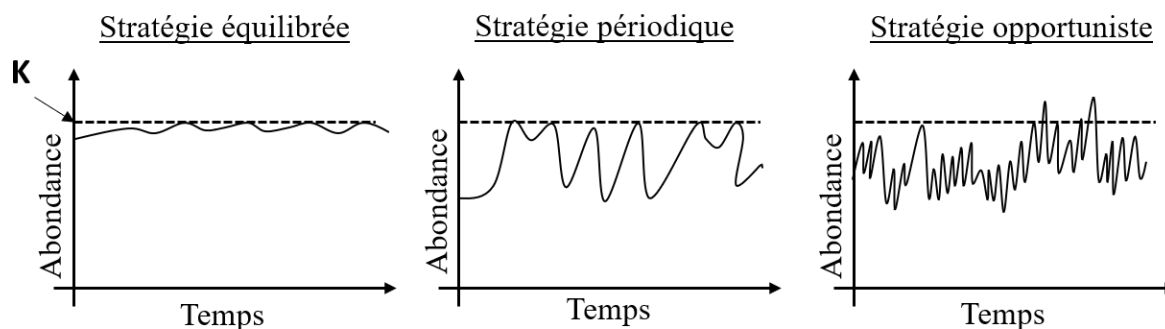


Figure 5.2 : Dynamiques de population prédites pour différentes stratégies d'histoire de vie à partir de la force et de la fréquence relative de la densité dépendance en lien avec une capacité d'accueil  $K$  hypothétique (figure redessinée à partir de Winemiller, 2005).

Ainsi, intégrer la stochasticité dans la dynamique de population constitue une piste majeure de développement de notre approche. Cela permettrait notamment d'explorer d'autres types d'indicateurs comme les temps de reconstitution (Langangen et al., 2023; White et al., 2022) ou les risques d'effondrement. D'autre part, cela augmenterait le réalisme et la généralité de l'approche, notamment parce que pour certaines espèces la stochasticité peut être considérée comme un facteur majeur de la régulation des populations (Canales et al., 2020). Cela permettrait aussi de la rendre plus compatible avec l'essentiel des modèles développés en évaluation des stocks, qui considèrent la stochasticité, notamment (mais pas que) au niveau du processus de recrutement. Enfin, la variabilité du recrutement aurait pu être intégrée comme pseudo trait d'histoire de vie dans l'étude de nos populations contrastées (chapitre 3.1). A cet effet, des estimations de la variance du recrutement pour différents taxons disponibles dans le package FishLife (Thorson, 2020) auraient pu être utilisées.

### 5.3.1.3 Une mortalité compensatoire limitée à une classe d'âge

Au-delà de la stochasticité, des hypothèses fortes ont également été faites sur la modélisation de la mortalité densité-indépendante et densité-dépendante pendant le recrutement. En effet, la relation SR utilisée dans nos approches sépare les processus de l'œuf aux recrues en deux phases :

- (i) Une première pendant la dérive des œufs puis des larves où la mortalité est exclusivement densité-indépendante ;
- (ii) Une seconde, qui se déroule au sein des habitats de nurserie et combine une mortalité densité-indépendante et une mortalité densité-dépendante de type compensatoire. Cette mortalité compensatoire est supposée résulter de processus de compétition intra-cohorte liés à l'espace et aux ressources trophiques (Beverton 1995 ; Beverton et Holt 1957).



Cette écriture du processus induit que le phénomène de mortalité compensatoire lié à la compétition est uniquement subi dans les premiers mois qui suivent l'arrivée des juvéniles dans les nourriceries. Cela suppose que les stades précédents (larves) et suivants (juvéniles plus âgés et adultes) ne subissent pas d'effets densité-dépendants.

Pour les stades précédant l'arrivée des juvéniles dans les nourriceries (œufs et larves), l'hypothèse est réaliste car pour une très forte proportion d'espèces marines de poissons, les œufs sont libérés en pleine eau et les larves sont pélagiques. On peut s'interroger sur le cas particulier des espèces qui pondent dans les milieux benthiques dont les œufs sont déposés sur un substrat, qui peut être limitant. C'est le cas du hareng de Baltique pour lequel des expériences en laboratoire ont montré une mortalité densité-dépendante des œufs (Finke et al., 2022).

Pour les stades suivants, l'hypothèse est plus discutable. En effet, les juvéniles de certaines espèces résident plusieurs années dans les nourriceries (e.g., sole 2 ans, bar 4 ans voire plus) et plusieurs cohortes peuvent être en compétition pour un espace et des ressources trophiques limitées, même si des migrations ontogéniques limitent cette compétition (Dorel et al., 1991). Prendre en compte ces processus nécessiterait d'utiliser une relation SR multi-stades telle que proposée par Brooks et al. (2019). Par ailleurs, l'extension de la mortalité densité-dépendante à d'autres âges questionne aussi sur les interactions entre espèces cohabitant dans la même nourricerie (Day et al., 2021; Nishikawa et al., 2022).

L'intégration de processus densité-dépendants supplémentaires (lors de la ponte ou au stade juvénile dans le cadre d'une compétition inter-cohortes et/ou inter-espèces) serait intéressante car ces mécanismes (i) déterminent le recrutement et donc *in fine* la dynamique de population, (ii) seraient susceptibles d'être modifiés par des scénarios de surface et de qualité d'habitat, (iii) pourraient conditionner les contrastes entre espèces (e.g., durée de résidence dans la nourricerie, stratégie de ponte). Cependant, les données disponibles sont généralement bien trop limitées pour établir de telles relations, et donc pour les intégrer à la dynamique de population.

#### 5.3.1.4 Stationnarité des paramètres SR

Notre représentation du recrutement suppose aussi que les paramètres SR sont stationnaires au cours du temps. La relation stock-recrutement résultant des hypothèses énoncées plus haut est une courbe de saturation dont l'asymptote s'interprète comme le nombre maximal de juvéniles pouvant être produits, soit la capacité d'accueil de la nourricerie (Del Monte-Luna et al., 2004). Dans le modèle hiérarchique bayésien (chapitre 2), les capacités d'accueil des cinq secteurs de nourricerie ne sont pas explicitement variables dans le temps, mais la stochasticité des relations

SR permet de capturer une part des variations interannuelles de la capacité d'accueil. En revanche, notre modèle générique (chapitre 3 et 4) est déterministe et fait l'hypothèse de paramètres constants au cours du temps. Or plusieurs auteurs indiquent que la capacité d'accueil peut fluctuer à des échelles annuelles ou saisonnières (Le Pape et al. 2003 ; Luo et al. 2001), par exemple en réponse à des variations des disponibilités nutritives. Cette variabilité de la capacité des nourriceries mériterait d'être prise en compte.

#### 5.3.1.5 *Homogénéité spatiale de l'habitat*

Les modèles développés supposent une séparabilité entre la qualité et la surface des habitats. En effet, ils font l'hypothèse que la capacité d'accueil peut s'écrire sous la forme du produit d'une capacité d'accueil par unité de surface et de la surface de la nourricerie. On considère donc implicitement que la capacité d'accueil par unité de surface est homogène sur toute la surface de la nourricerie et que la répartition des juvéniles dans l'espace est aussi homogène. Or les zones côtières et estuariennes sont marquées par une forte hétérogénéité spatiale (Fodrie et al., 2009 ; Nagelkerken et al., 2015 ; Rochette et al., 2013 ; Wennhage & Pihl, 2001). On parle notamment de « mosaïque d'habitats » connectés entre eux (Peterson, 2003; Sheaves et al., 2015). Cette notion s'observe dans la distribution non homogène des juvéniles dans l'espace en fonction des caractéristiques de l'habitat (Rochette et al. 2010 ; Trimoreau et al. 2013). Cette variabilité spatiale interroge la construction de nos scénarios de surface car selon la qualité de la zone impactée pour les juvéniles, les conséquences de sa dégradation/restauration seront différentes. Bien que pertinente, affiner la représentation spatiale de l'habitat implique une grande quantité de données, à la résolution spatiale fine, non disponibles pour une très large majorité de stocks.

#### 5.3.2 Structure spatiale, connectivité et métapopulation

Dans nos approches, l'espace est toujours pris en compte de manière implicite (sensu Beissinger et Westphal (1998)) en tant que patches (ou blocs) discrets d'habitat. Mais les deux approches mises en œuvre au cours de cette thèse représentent des niveaux distincts de prise en compte de la structure spatiale et du fonctionnement en métapopulation qui en résulte.

Le modèle hiérarchique bayésien développé au chapitre 2 permet une représentation précise de la structure spatiale de la métapopulation de sole de Manche Est : trois sous-populations qui alimentent cinq secteurs de nourricerie avec une faible connectivité entre les sous-populations. Chaque secteur de nourricerie possède des caractéristiques propres (surface, qualité, intensité de la densité-dépendance) ce qui nécessite d'estimer des paramètres stock-recrutement pour

chaque secteur de nourricerie. Cela suppose aussi de modéliser l'imbrication de ces relations à l'échelle de la population globale (Punt, 2019 ; White, 2010), donc de faire intervenir des taux d'échange entre les sous-populations alimentées par chaque secteur de nourricerie. Les taux d'échange entre populations sont gouvernés par des matrices de connectivité, paramétrées à partir de sorties de modèles de dérive Lagrangienne de particules dans des modèles physiques de champs de courants et de température (Rochette et al., 2012). La résolution du fonctionnement spatial de la métapopulation a requis de nombreuses données et analyses : modèle multi-décennal de capture-marquage-recapture (Lecomte et al., 2020), analyse de croissance et de taux démographiques (Randon et al., 2018), de marqueurs individuels (génétiques et otolithes, Randon et al. 2020), puis analyse holistique combinant toutes ces méthodes (Randon et al., 2021). En l'absence de toutes ces données, Archambault et al. (2018) avaient utilisé deux hypothèses extrêmes pour simuler des scénarios de restauration d'une des cinq nourriceries : isolement vs mélange total des sous-populations. La dynamique de la métapopulation était logiquement très sensible à ces hypothèses extrêmes tout comme les résultats de la restauration à diverses échelles spatiales.

Dans le modèle générique développé aux chapitres 3 et 4, la structure de métapopulation a été simplifiée pour ne représenter qu'une population unique alimentée par une zone de nourricerie unique (chapitre 3) et une frayère unique (chapitre 4). Considérer une multiplicité de ZFHI, voire une structure en métapopulation, complexifierait grandement le modèle, sa paramétrisation et le design des scénarios (homogénéité vs hétérogénéité des paramètres, *cf.* 5.3.1, et hypothèses sur la connectivité).

Étudier le rôle de la structure spatiale et son interaction avec des scénarios d'habitat propose des perspectives de recherche riches et enthousiasmantes. Elles convoquent des concepts théoriques d'écologie spatiale, de dynamique des métapopulations et notamment la théorie « source-puits » (Figueira et Crowder 2006 ; Hanski 1999). Ces notions ont été largement abordées dans le contexte de l'étude de l'efficacité d'aires marines protégées (Botsford et al. 2009; Gerber et al. 2005 ; Grüss, Kaplan, et Hart 2011). Les intégrer pour étudier l'impact de la dégradation/restauration locale des habitats à l'échelle de la population offre des pistes de recherche intéressantes. À ce titre le degré de connectivité d'une métapopulation pourrait être envisagé comme un trait d'histoire de vie (gradient entre populations résidentes et dispersives) et intégré dans notre approche pour explorer son influence sur la réponse d'une population. La représentation spatiale des ZFHI pourrait être complexifiée graduellement, par exemple pour tendre vers des scénarios de gestion spatialisés plus réalistes, mais aussi moins génériques.

### 5.3.3 Paramétrisation de l'impact de la dégradation de la qualité des habitats

Dans les travaux développés au cours de cette thèse le terme « qualité » fait notamment référence à la présence de contaminants (chapitre 2 et 3) ou à la baisse de la teneur en oxygène (hypoxie, chapitre 4) au sein des habitats. Pour ces perturbations anthropiques, le lien pression-impact à l'échelle d'une population est rarement quantifié. En effet, de nombreuses études ont mis en évidence les effets négatifs de l'exposition aux polluants des juvéniles, avec des conséquences sur leur croissance, leur survie et leur capacité reproductive à venir (niveau de fécondité mais aussi viabilité des œufs, Daouk et al. 2011 ; Fonds et al. 1995 ; Horri et al. 2018). Il en va de même pour l'exposition à de faibles teneurs en oxygène (Chabot et Dutil 1999 ; Eby et al. 2005 ; McNatt et Rice 2004 ; Meng, Powell, et Taplin 2001 ; Pichavant et al. 2001). Cependant des estimations quantitatives de l'effet de ces pressions sur la survie ou la fécondité future des juvéniles en milieu naturel restent rares, voire inexistantes. Ce manque de connaissance du transfert d'effets individuels à la population a été largement souligné, que ce soit de façon générale (Brown et al. 2018 ; Rabalais 2015 ; Vasconcelos et al. 2014), ou plus spécifiquement pour les polluants (Champagnat et al. 2021 ; Ono et al. 2019 ; Schneeweiss et al. 2023) ou l'anoxie (Rose et al. 2018 ; Thomas et al. 2019). La difficulté du changement d'échelle se niche dans la complexité des histoires de vie des poissons et la multiplicité des processus d'impact et des autres sources de variabilité (Hamilton et al. 2016 ; Rose et al. 2003), ce qui rend l'isolement et la quantification de l'influence d'une pression sur la dynamique d'une population très complexe (Rose et al., 2009).

Une des approches de cette thèse a consisté à tester théoriquement les effets de ces pressions à l'aide de multiplicateurs appliqués aux taux de mortalité instantanée densité-indépendants ou densité-dépendants des juvéniles (chapitre 3.1) ou sur la survie des œufs, juvéniles et adultes reproducteurs (chapitre 4).

En l'absence d'informations, nous avons fait l'hypothèse que le multiplicateur de qualité impactait de façon similaire les taux de mortalité densité-dépendants et -indépendants (chapitre 3.1). Durant la phase juvénile, les individus subissent deux mortalités. L'une est densité-dépendante, c'est-à-dire associée à des interactions avec des congénères (principalement la compétition pour l'alimentation et l'espace, Maunder 2022) qui impactent la croissance, la reproduction ou les mouvements et *in fine* la survie (Craig et al. 2007 ; Le Pape et Bonhommeau 2015 ; Stige et al. 2019). La seconde est densité-indépendante et implique d'autres processus liés à un large panel de pressions environnementales (Ono et al., 2019 ; Rose et al., 2003). Conceptuellement les polluants ou le manque d'oxygène peuvent affecter les deux

types de mortalité. En effet, une altération de la physiologie individuelle peut modifier la mortalité densité-indépendante, mais aussi affecter la communauté, par exemple la disponibilité des proies ou l'abondance de prédateurs, et impacter la mortalité densité-dépendante. Néanmoins, aucune donnée ne permettait de paramétrer différenciellement l'impact des pressions sur ces deux mortalités (Johnson, 2007); l'hypothèse a donc été faite d'un multiplicateur unique agissant identiquement sur les deux composantes de la mortalité. Cet effet conjugué conduit mécaniquement à accroître l'impact estimé par le modèle des scénarios portant sur la qualité par rapport à ceux n'agissant que sur la surface par exemple.

Par ailleurs, l'utilisation de multiplicateurs exprimés dans l'échelle des taux de mortalité instantanée en parallèle avec des multiplicateurs de la surface d'habitat, tels que paramétrés au chapitre 3.1, pose des problèmes d'échelle pour l'interprétation des résultats. En effet, des variations relatives identiques sur ces deux multiplicateurs (par exemple -25/+25%) ont des conséquences contrastées en termes d'intensité des réponses. Ce problème d'échelle nous incite à comparer les réponses aux scénarios de surface et de qualité uniquement de façon qualitative et non quantitative. Il nous a aussi suggéré une évolution de la paramétrisation des multiplicateurs entre les chapitres 3 et 4. Dans le chapitre 4, pour comparer l'impact de pressions agissant à différents stades de vie, nous avons utilisé des multiplicateurs dans l'échelle de la survie déjà intégrée sur le pas de temps de la transition. Cette formulation a permis de limiter les effets d'échelle de sensibilité aux scénarios liés aux fortes disparités de mortalité entre stades de vie (Levin and Stunz, 2005).

Pour le chapitre 4, nos connaissances sur les processus d'impact et les réponses des adultes reproducteurs à l'hypoxie étaient encore plus lacunaires. Nous avons testé deux hypothèses correspondant à deux comportements plausibles : l'évitement ou la persistance (McKenzie, 2011). Ces comportements dépendent de la tolérance de l'espèce, de l'intensité de l'hypoxie et l'exposition passée de l'individu (Cook et Herbert 2012 ; Ferrari et al. 2016). La réponse est donc susceptible de varier pour les individus d'une même population, mais aussi entre populations et entre espèces. En l'absence d'information pour préciser les scénarios, nous avons évalué l'impact relatif des deux hypothèses, et comment les réponses variaient en fonction des THV des espèces.

Lors de l'application à des cas d'étude (chapitre 2 et 3.2), la paramétrisation des scénarios de qualité s'est basée sur des comparaisons de densité de juvéniles entre zones plus ou moins polluées. Dans le chapitre 2, dans les scénarios de restauration, les paramètres SR (taux de survie à faible densité et capacité d'accueil par unité de surface) de la nurserie de Seine

(fortement polluée) ont été remplacés par ceux d'une nourricerie voisine, moins contaminée. Dans l'étude multi-stocks du chapitre 3.2, une perte globale de capacité d'accueil par unité de surface a été estimée pour un estuaire pollué à partir des données de Courrat et al. (2009). Il s'agit d'une estimation portant sur un large panel de données, utilisées pour estimer la qualité des estuaires sur la base des peuplements de poissons, dans le cadre de la Directive Cadre européenne sur l'Eau (DCE, Delpech et al. 2010). Cette perte de densité a été utilisée pour calculer un multiplicateur qui a été appliqué aux mortalités juvéniles.

Enfin, quelle que soit la façon de paramétrer l'impact de la dégradation de la qualité dans les ZFHI, certains effets des polluants (e.g., effets synergiques) et de l'hypoxie (e.g., captivité accrue des espèces benthiques ; Rose et al. 2018) n'ont pas été pris en compte. Le manque d'information sur les impacts de la dégradation de la qualité des habitats sur la démographie des poissons marins représente un verrou majeur à la quantification de ces impacts à l'échelle des populations (Brown et al., 2018) et mérite de plus amples recherches.

## 5.4 Perspectives et appui à la gestion

### 5.4.1 Périmètre d'application du modèle

#### 5.4.1.1 *Transférabilité du modèle*

La démarche générique développée au cours de la thèse présente de larges perspectives d'application. La paramétrisation du modèle générique développé au chapitre 3.1 et complété au chapitre 4 nécessite des données biologiques aux âges (maturité, poids, fécondité, mortalité naturelle) et des paramètres stock-recrutement (steepness et capacité d'accueil). Les données nécessaires pour appliquer le modèle générique sont largement disponibles et son potentiel d'application paraît important. En effet, ces données sont accessibles dans la littérature (par exemple dans des bases de données comme FishBase, Froese et Pauly 2022 ; des méta-analyses comme FishLife, Thorson 2020 ; Thorson et al. 2017), ou à partir des données d'entrée de modèles d'évaluation de stock. Afin de calibrer le modèle pour une population spécifique (chapitre 3.2), les sorties des modèles d'évaluation de stock sont nécessaires pour estimer la capacité d'accueil du stock (i.e., dimensionner la population, cf. chapitre 3.2). Les stocks faisant l'objet d'une évaluation par modèle analytique représentent 43% des 256 stocks évalués en Atlantique Nord-Est (Scientific, Technical and Economic Committee for Fisheries; STECF 2022). Au niveau mondial, la base RAM (Myers et al., 1995) compile des sorties de modèles analytiques pour 1359 stocks (extraction en février 2023). Cependant l'application de la

méthode reste inaccessible pour toute une frange de stocks exploités (catégories CIEM 3 à 6) pour lesquels on ne dispose pas des données suffisantes pour utiliser les modèles analytiques (Costello 1992 ; STECF 2022).

#### 5.4.1.2 Paramétrisation de scénarios

L'application à des cas d'étude spécifiques exige aussi des données pour paramétrer des scénarios d'habitat réalistes. Même si l'accès à ces informations est plus réduit que la disponibilité des paramètres démographiques, des informations et données existantes peuvent être mobilisées dans un certain nombre de cas.

Pour les scénarios de surface, une quantification de l'évolution des surfaces d'habitats juvéniles est nécessaire. Ces informations peuvent être issues :

- (i) de comparaison de cartes entre plusieurs années : bathymétrie provenant d'EMODnet (utilisée au chapitre 3.1) ou d'autres sources (Stamp et al., 2022, utilisée pour une application de la démarche du chapitre 3.2 à la sole de mer Celtique dans le cadre du projet européen Seawise, Dubost et al., 2023). Le développement de techniques de télédétection a permis de généraliser l'évaluation des pertes d'habitats sur des périodes récentes (Klemas, 2010; Li and Damen, 2010; Teferi et al., 2010).
- (ii) de modélisation hydrosédimentaire (Grasso et Le Hir 2019, utilisée au chapitre 2).

Conjointement aux estimations de perte de surface, la construction de scénarios concernant la réduction de la taille des habitats requiert des informations sur la concentration des juvéniles sur les habitats de nourricerie. Il faut connaître la proportion de juvéniles présents dans l'habitat concerné (par exemple la bande des 0-5m dans le chapitre 3.2). Pour cela des estimations quantitatives sont nécessaires, généralement issues de modèles d'habitat, de plus en plus répandus (Le Pape et al. 2014).

Comme mentionné en 5.3.3, l'estimation des effets populationnels de la baisse de qualité des habitats requiert des informations rarement accessibles (Brown et al., 2018). L'idéal serait de disposer de longues séries temporelles (plusieurs décennies) de suivi des juvéniles, et de réussir à quantifier l'influence des variations de la qualité de l'habitat sur les abondances. Pour les estuaires français, malgré les campagnes annuelles de suivi des juvéniles, les séries temporelles sont trop courtes pour observer ces variations. Nous avons donc utilisé une approche de substitution du temps par l'espace en comparant la densité de juvéniles entre plusieurs sites (chapitre 3.2, Courrat et al. 2009). Cela requiert que les protocoles d'échantillonnage soient

standardisés. Bien que ce type d'échantillonnage ne soit pas systématique, il est appliqué dans le cadre de suivis environnementaux institutionnels (e.g. DCE) qui sont de plus en plus répandus.

#### 5.4.1.3 *Potentiel pour l'appui à la gestion*

Malgré son potentiel d'application, les possibilités d'inclusion directe de notre approche dans une perspective d'évaluation de stock nous paraissent limitées. En effet, notre cadre méthodologique vise à comparer des états d'équilibre plutôt que des variations interannuelles (en relation avec le déterminisme du modèle, cf. 5.3.1). Or, les objectifs de gestion des pêches se structurent majoritairement à des horizons temporels à court terme, même si le développement de plans pluriannuels de gestion tend à faire évoluer cette temporalité. Par contraste, la restauration des habitats s'étend sur des échelles de temps bien plus longues : de plusieurs années à des décennies (Duarte et al. 2020; Jokinen et al. 2016 ; Moreno-Mateos et al. 2012; Orth et al. 2020). À titre d'exemple, 15 ans ont été nécessaires pour réduire le niveau d'eutrophisation en baie de Chesapeake de 40% (Leslie, 2018) ; en estuaire de Seine entre 1990 et 2010 des réductions de 68, 81 et 40% ont été observées pour le PCB-153, le DDT et le plomb respectivement (Champagnat et al., 2021). Dans sa méta-analyse sur la restauration des zones humides, Schmitz (2012) précise que les échelles de temps de rétablissement (retour à ou proche d'un état de référence) varient selon le compartiment : environ 5 ans pour la composition et l'abondance des vertébrés, de 50 à 100 ans pour un retour à la normale du cycle des nutriments. En cela notre cadre méthodologique se rapproche plutôt des études qui simulent l'impact du changement climatique sur les différentes composantes des écosystèmes (Cheung et al. 2010 ; Free et al. 2019; Rijnsdorp et al. 2010 ; Yeung et Yang 2018). Plutôt que d'ambitionner une visée opérationnelle directe à des fins d'évaluation de stock, l'approche développée au chapitre 3 vise à produire des estimations de l'impact à long terme de la dégradation des habitats sur les populations en vue de les transmettre aux instances de gestion, par exemple l'OFB (financier de ce projet). Des applications à des cas d'étude précis peuvent alimenter la réflexion sur des zones particulièrement importantes à conserver ou à restaurer. Dans cette optique, l'utilisation du modèle en parallèle pour plusieurs espèces dépendantes de ZFH communes dans une unité de gestion (comme dans le chapitre 3.2) permet de déterminer les enjeux de conservation/restauration des ZFHI en dépassant le cadre monospécifique.

L'exploration de scénarios d'habitat sur des populations théoriques a également permis de faire ressortir les traits d'histoire de vie qui déterminent les réponses des populations (chapitre 3.1 et



4). Informer la gestion sur la base de traits d'histoire de vie des espèces est une idée soulevée par de nombreux auteurs. Kindsvater et al. (2016) suggèrent d'utiliser le cadre conceptuel qu'ils ont développé pour déterminer la vulnérabilité d'un stock à l'exploitation par la pêche si l'espèce est « data-poor ». Ils soulignent aussi l'importance d'adapter les efforts de conservation aux caractéristiques des espèces cibles, ce qui, comme le démontre ce travail, est tout aussi pertinent en ce qui concerne la protection/restauration des ZFHI.

#### 5.4.1.4 *Extension du cadre méthodologique à d'autres pressions anthropiques*

Les scénarios élaborés se sont focalisés sur (i) les pertes de surfaces des nourriceries ou (ii) des altérations de qualité des nourriceries ou des frayères en réponse à la présence de contaminants ou à une baisse d'oxygène. L'impact d'autres pressions pourrait être quantifié en utilisant des formulations de scénarios identiques ou proches. Par exemple les conséquences de la perte de surface de frayères pourraient être évaluées dans divers contextes (e.g. extraction de granulats ; perte de substrat spécifique à la ponte du hareng en Baltique Sud-Ouest, Kanstinger et al. 2018). Pour les nourriceries, l'impact de la réduction d'habitats favorables en lien avec les marées vertes (Le Luherne et al., 2016) ou la prolifération d'espèces invasives comme les crépidules (Kostecki et al., 2011) pourrait être estimé. La baisse de débit des fleuves (en lien avec le changement climatique) pourrait aussi affecter la quantité et la qualité des habitats de juvéniles dans les estuaires (e.g. sole du Golfe de Gascogne, Le Pape et al., 2003).

#### 5.4.2 La restauration des habitats - le parent pauvre de la gestion des ressources halieutiques ?

De nombreuses études de modélisation ont souligné le fort potentiel de la restauration des habitats juvéniles pour augmenter la taille des populations (Hughes et al. 2015 ; Levin et Stunz 2005 ; van de Wolfshaar et al. 2015). Les résultats de nos scénarios de restauration des ZFHI concordent et indiquent des gains substantiels de biomasse, ainsi que de captures potentielles au rendement maximal durable. Si ces résultats sont encourageants, ils ne peuvent malheureusement pas être confrontés à des données de terrain pour une validation *ad hoc*. Mais des exemples de restauration concrète des habitats existent et confortent l'efficacité, estimée par modélisation, de ces actions :

- (i) En milieu aquatique continental, les actions de restauration des habitats ont une plus longue histoire et les études sur leurs acquis bénéficient de plus de recul. L'arasement des barrages pour restaurer la continuité des cours d'eau est un exemple typique d'action qui a un effet positif sur les populations de poissons diadromes (Pess et al., 2014). Dans une étude à large échelle portant sur vingt lacs suivis pendant six ans, la création de

zones littorales peu profondes par excavation augmente l'abondance des populations de poissons (Radinger et al., 2023).

- (ii) En milieu côtier et estuarien, les efforts de restauration sont en plein essor depuis le début du 21<sup>ème</sup> siècle, avec plusieurs milliers de projets reportés et probablement de nombreux autres non recensés (Duarte et al., 2020). Des métaanalyses ont permis de tirer de grands résultats par type de milieu (e.g. zones humides, Schmitz 2012 ; champs d'algues, Earp et al. 2022) ou par région (e.g. Golfe du Mexique, Greening et al. 2023). Certaines études soulignent de forts gains d'abondance, de biodiversité ou de services écosystémiques entre état dégradé et restauré (Benayas et al. 2009; Duarte et al. 2020; Orth et al. 2020 ; Schmitz 2012). D'autres insistent sur le fait que les écosystèmes ne reviennent pas à leurs états de référence et ne retrouvent donc pas pleinement leur fonctionnement (Moreno-Mateos et al., 2012). Ces «défauts» de fonctionnement peuvent être multiples en fonction du compartiment physique ou biotique et/ou de la fonction étudiés.

L'efficacité de mesures de restauration surfacique est difficilement prévisible. Si l'on se concentre sur la capacité de l'écosystème à supporter le rôle de nourricerie, il s'agit de savoir s'il assure des fonctions de refuge et d'alimentation. Par exemple, Stamp et al. (2023) comparent les taux d'alimentation de plusieurs juvéniles dans des marais salants « naturels » vs « restaurés » et montrent qu'ils sont plus faibles dans ces derniers pour le mulot et le bar, mais pas pour le gobie. Au-delà de la surface, la restauration de la fonction de certains habitats peut aussi être complexe. Dans le cas de la sole par exemple, la favorabilité de l'habitat pour les juvéniles dépend de combinaisons de bathymétrie et de sédiments qui sont gouvernés par des mécanismes hydrosédimentaires difficiles à contrôler et à prévoir (Grasso et al. 2018 ; Schulz et al. 2018). D'autres difficultés contraignent la restauration des habitats en pratique. Pour ce qui est des augmentations de surface en milieu côtier et estuarien, le problème fondamental est « la demande » ou « course pour l'espace ». En effet ces espaces sont au cœur de multiples usages et donc fortement soumis à la pression des divers usagers. Le potentiel de surface à restaurer reste donc assez limité. La montée du niveau des eaux risque d'aggraver encore ce contexte de fortes pressions, en provoquant la disparition de zones humides côtières (Greening et al., 2023; Nicholls et al., 1999) sans laisser en amont d'espaces naturels où ces écosystèmes pourraient se redéployer.

L'amélioration de la qualité des milieux estuariens et côtiers est aussi à mettre en lien avec la qualité des masses d'eaux sur les bassins versants, pour lesquelles des mesures de restauration

paraissent plus simples au premier abord. De nombreuses réglementations (e.g. DCE) ont été mises en place et contraignent à restaurer un bon état écologique. Quand de telles réglementations sont implémentées, la qualité des masses d'eaux peut être régulée et tend à s'améliorer, ce qui limite la présence de polluants, ainsi que les excès de nutriments responsables de l'eutrophisation. Cependant la contamination persiste notamment dans les sédiments, où vivent les juvéniles de nombreuses espèces dépendantes des nourriceries, et une large partie de leurs proies. Les temps de décontamination de ces sédiments restent difficilement évaluables et la présence de polluants persistants (POP) questionne notre capacité à décontaminer les estuaires.

La complexité de la restauration des habitats invite à un constat : la conservation des milieux naturels ne doit pas tout miser sur cette solution mais rester vigilante sur leur protection. Dans ce contexte, la séquence ERC (Eviter, Réduire, Compenser) et l'objectif de Zéro artificialisation nette prennent tout leur sens, dans les milieux côtiers comme au sein des systèmes continentaux. Il est nécessaire d'insister sur l'importance conjointe de ces actions de protection, d'atténuation des impacts et de restauration (Buelow et al. 2022; Moreno-Mateos et al. 2012; Possingham, Bode, et Klein 2015 ; Saunders et al. 2017). Les Nations Unies ont appelé à ce que cette décennie soit celle de la restauration des écosystèmes (<https://www.decadeonrestoration.org>), il est urgent de considérer la protection et restauration (Duarte et al., 2020; Radinger et al., 2023) des ZFC dans les plans de conservation (Horwood et al., 1998) et dans l'approche écosystémique des pêches (Kraufvelin et al., 2018).

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## **7. Annexes**

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## 7.1 Annexes du chapitre 2

### 7.1.1 Supp. Mat. 2.1: Simulation model details

#### 7.1.1.1 *Life-cycle Model used for simulations*

Subscript  $y$  denotes the years in the time series,  $i$  denotes the nursery sector ( $i=1,\dots,5$ , with 1=UK West, 2=Rye, 3=Somme, 4=Seine, 5=Veys), and  $r$  denotes the component of the metapopulation ( $r=1,2,3$  with 1=West FR, associated with nursery grounds Seine and Veys; 2=UK, associated with nursery grounds UK West and Rye; 3=East FR, associated with nursery ground Somme).

All parameter values are defined in Table S2.1.2.

#### Eggs and larval drift

The number of settling larvae (i.e., post-larvae) in nursery sector  $i$  at year  $y$ ,  $L_{y,i}$  result from the survival and drift of eggs spawned by adult females:

$$(S1.1) \quad L_{y,i} = \sum_{r=1}^{r=3} \omega_{y,r} \cdot D_{r,i}^{larvae}$$

where  $\omega_{y,r}$  is the egg pool for the subpopulation  $r$  at year  $y$  and  $D_{y,r,i}^{larvae}$  is the probability of success for an egg from the egg pool  $r$  to reach the nursery sector  $i$  at year  $y$ . The egg pool for each year and each subpopulation is calculated from the spawning stock biomass (all fish between age 3 and 15 take part in reproduction, ICES, 2010):

$$(S1.2) \quad \omega_{y,r} = \sum_{a \geq 3} N_{a,y,r} \cdot pf_a \cdot fec_a$$

where  $pf_a$  is the proportion of females for age class  $a$  (known, considered constant over the time series and homogeneous across areas, Rochette et al., 2012), and  $fec_{a,y}$  is the number of eggs per female of age  $a$ , calculated from the weight at age  $w_{a,y}$  as (ICES 2010; Rochette et al. 2012):

$$(S1.3) \quad fec_{a,y} = e^{5.6 + 1.17 * \log(w_{a,y})}$$

#### Post-larvae to juvenile on nursery grounds, from settlement to summer's end

The number of age-0 fish at year  $y$  in nursery  $i$ ,  $N_{0,y,i}$  is defined from a density dependent Beverton-Holt equation parameterized with  $\alpha_i$ , the nursery-specific maximum survival rate;  $K_i$ , the nursery-specific carrying capacity per unit of surface (1000 fish  $\cdot km^{-2}$ ); and  $S_i$ , the surface of nursery sector  $i$  ( $km^2$ ):

Unexplained random variations (environmental stochasticity) are captured by independent lognormal random noise with the same variance  $\sigma_{BH}^2$  for all nursery sectors:

$$(S1.4) \quad N_{0,y,i} = \frac{\alpha_i L_{y,i}}{1 + \frac{\alpha_i}{K_i S_i} L_{y,i}} \cdot e^{\varepsilon_{L,y,i} - 0.5 \cdot \sigma_{BH}^2}$$

Natural mortality of age 0 from summer's end to December

The number of age-1 fish in nursery  $i$ ,  $N_{1,y+1,i}$ , is defined as

$$(S1.5) \quad N_{1,y+1,i} = N_{0,y,i} \cdot e^{-1/3 \cdot M_0} \cdot e^{\varepsilon_{0,y,i} - 0.5 \cdot \sigma_0^2}$$

where  $N_{0,y,i}$  is the number of age-0 fish in the nursery  $i$ ,  $M_0$  is the annual natural mortality rate at age 0 and  $\varepsilon_{0,y,i}$  is normal environmental noise with variance  $\sigma_0^2$ .

Natural and fishing mortality at age 1 and emigration from nursery to adult population

The number of age-2 fish in nursery  $i$  at the very beginning of year  $y + 1$ ,  $N_{2,y+1,i}$ , is defined as

$$(S1.6) \quad N_{2,y+1,i} = N_{1,y,i} \cdot e^{-Z_{1,i}} \cdot e^{\varepsilon_{1,y,i} - 0.5 \cdot \sigma_p^2}$$

where  $Z_{1,i} = M_1 + F_{1,r}$  is the total mortality,  $M_1$  is the annual natural mortality rate at age 1,  $F_{1,r}$  is the fishing mortality in subpopulation  $r$  associated with nursery  $i$ , and  $\varepsilon_{1,y,i}$  is normal environmental noise with variance  $\sigma_p^2$ .

Age-2 fish leave nurseries at the very beginning of the year and are supposed to contribute directly to the subpopulation  $r$  adjacent to the nursery. Fish from the Seine and Veys nurseries contribute to subpopulation  $r=1$ =West FR; UK West and Rye nurseries contribute to subpopulation  $r=2$ =UK; and the Somme nursery contributes to subpopulation  $r=3$ =East FR. Starting from  $N_{2,y+1,i}$  as defined in eq. (A.7), the number of age-2 fish in each subpopulation  $r$ ,  $N_{2,y+1,r}$  (note the subscript  $r$  and not  $i$ ), is defined as follows:

$$(S1.7) \quad \begin{cases} N_{2,y+1,r=1} = \sum_{i=4}^{i=5} N_{2,y+1,i} \\ N_{2,y+1,r=2} = \sum_{i=1}^{i=2} N_{2,y+1,i} \\ N_{2,y+1,r=3} = N_{2,y+1,i=3} \end{cases}$$

Natural and fishing mortality at the adult stage

Prior to any mortality fishes are assumed to move from a region to another according to a connectivity matrix estimated from capture-mark-recapture data (Lecomte et al. 2020), then the number of fish from age 2 to 15 then follows the classical dynamics:

$$(S1.8) \quad N_{a+1,y+1,r} = \left( \sum_{j=1}^{j=3} N_{a,y,r} \cdot D_{r,j}^{adult} \right) \cdot e^{-Z_{a,r}} \cdot e^{\varepsilon_{a,y,r} - 0.5 \cdot \sigma_p^2}$$

where  $N_{a,y,r}$  is the number of fish of age  $a$  in component  $r$  at year  $y$ ,  $Z_{a,y,r}$  is the total mortality rate ( $Z_{a,r} = F_{a,r} + M_a$ ) and  $\varepsilon_{a,y,r}$  is a normal environmental noise with variance  $\sigma_p^2$ .  $D_{r,r}^{adult}$  is the connectivity matrix of size 3\*3 (region\*region).

All remaining fish are assumed to die at age 15.

### 7.1.1.2 Bayesian fitting of the population dynamic model

A Bayesian hierarchical framework using Monte Carlo Markov Chain methods is used to estimate all model parameters by assimilating an extensive data set. The details of the Bayesian methods used to fit the model are given in Archambault et al. (2016). The data assimilated in the model are summarised in the Table S2.1.1. This includes:

- (i) the outputs of a biophysical model which provide larval survival and dispersal from spawning areas to the five nursery sectors (Savina et al. 2016);
- (ii) annual juvenile (ages 0 and 1) abundance indices over the five nursery sectors. Those data were updated from Archambault et al. (2016) by adding 7 years of data in the Somme and Seine sectors, and two years in the Veys sector;
- (iii) annual catch-at age and abundance indices (ages 2 to 15) directly derived from the stock assessment working groups (ICES, 2020), available at the scale of the EEC and also spatially desegregated for the three subpopulations of adults fish. Those data were updated from Archambault et al., (2016) with 8 and 7 years of recent data, respectively;
- (iv) a connectivity matrix to disperse age 2 to 15 individuals between the three subpopulations but parameterised so that only low connectivity between the three sub-populations occurs in the model. Extreme a priori hypotheses on meta-population structure on adult-mediated connectivity (i.e., no inter-regional connectivity after larval drift / full mixture) previously made by Archambault et al., (2016) were replaced by a connectivity matrix estimated from mark-recapture data (Lecomte et al. 2020) to disperse age 2 to 15 individuals between the three subpopulations with a low, but non-null, mixing rate.

Bayesian posterior distributions were approximated via Monte Carlo Markov Chain (MCMC) methods using the Nimble package (<https://r-nimble.org>; release 0.9.0). The same procedure than the one detailed in Archambault et al. (2016) was used for model fitting. Convergence of the MCMC chains was assessed using the Gelman-Rubin (Brooks and Gelman, 1998) and the

Heidelberg and Welch tests as implemented in the R Coda package (`gelman.diag()` and `heidel.diag()` function, respectively).

Bayesian uncertainties around estimated parameters were not considered in simulations. Values of all parameters were fixed to the mode of their posterior distributions (see Table S1.2).

*Table S2.1.1. Synthesis of data and results of previous models used as inputs for the Bayesian integrated life cycle model (updated from Archambault et al., 2016).*

Stage	Details	Nature of the information	Source	Time series
<b>Eggs &amp; larvae</b>	Survival and allocation from spawning areas to the five nursery sectors	Outputs of biophysical IBM model	Updated run of Rochette et al. (2012); Savina et al. (2016)	1982-2007
<b>Juveniles</b>	Abundance indices available for each nursery sector			
	West UK			1982-1999
	Rye			1982-2006
	Somme			1982-1983; 1987-2018
	Seine	Outputs of a habitat suitability model	Updated from Rochette et al. (2010)	1995-2002; 2006; 2008-2018
	Veys			2006. 2010-2011. 2016-2017
<b>Adults</b>	<i>Available at EEC scale</i>			
	Catches at age			1982-2019
	UK commercial CPUE (UKCBT)			1986-2017
	Belgium commercial CPUE (BECBT)	Data	ICES	2004-2017
	French commercial CPUE (FRCOT)			2002-2017
	<i>Available for the three subpopulations</i>			
	Spatial repartition of catches (total weights, no age structure) among the three areas (East FR, UK, West FR)	Data	ICES (2003–2019) Vermard, Pers. comm. (1982–2002)	1982-2019
Spatial Scientific Abundance Index (UKSBT)	Data	Vermard, Pers. comm.	1990-2018	
Movement of adult between the three populations	Output of a mark-recapture model	Lecomte et al. (2020)	X	

Table S2.1.2. Fixed values for the parameters of the spatially and age-structured life-cycle simulation model.

Parameters	Value	Description
$M_a$	Age 0: 1.5; Age 1: 2.6; Age 3-11: 0.1; Age 12: 0.2; Age 13: 0.3; Age 14: 0.4; Age 15: 0.5	Natural mortality at age $a$ ( $y^{-1}$ )
$\sigma_p^2$	0.001	Variance of process errors on the dynamics of adult stages
$W_a$	Age 1: 0.094; Age 2: 0.122; Age 3: 0.169; Age 4: 0.208; Age 5: 0.236; Age 6: 0.287; Age 7: 0.288; Age 8: 0.335; Age 9: 0.381; Age 10: 0.416; Age 11-15: 0.566.	Weight at age $a$ (kg)
$F_{a,r}$	<b>In region 1 (West FR)</b> Age 1: 0.00248; Age 2: 0.107; Age 3: 0.181; Age 4-10: 0.183; Age 11-15: 0.182. <b>In region 2 (UK)</b> Age 1: 0.00357; Age 2: 0.154; Age 3: 0.261; Age 4-15: 0.262 <b>In region 3 (East FR)</b> Age 1: 0.00431; Age 2: 0.186; Age 3: 0.315; Age 4-10: 0.317; Age 11-15: 0.316	Fishing mortality at age $a$ ( $y^{-1}$ )
$\alpha_i$	West UK: 0.885; Rye: 0.961; Somme: 0.861; Seine: 0.882; Veys : 0.893.	Nursery-specific maximum survival rates.
$K_i$	West UK: 61.2; Rye: 229.4; Somme: 127.7; Seine: 78.9; Veys :122	Nursery-specific carrying capacity per unit of surface (1000 fish·km <sup>-2</sup> ).
$S_i$	West UK: 2407.8; Rye: 661.6; Somme: 2185.8; Seine: 1424.1; Veys :312.7.	Nursery-specific surface (km <sup>2</sup> ).
$\sigma_{BH}^2$	0.323	Variance of process errors on the post-larvae to juvenile BH relationship
$\sigma_0^2$	0.137	Variance of process errors from age-0 to age-1 fish
$fec_a$	Age 0-2: 0; Age 3: $1.1 \cdot 10^5$ ; Age 4: $1.4 \cdot 10^5$ ; Age 5: $1.6 \cdot 10^5$ ; Age 6-7: $2.1 \cdot 10^5$ ; Age 8: $2.5 \cdot 10^5$ ; Age 9: $2.9 \cdot 10^5$ ; Age 10: $3.1 \cdot 10^5$ ; Age 11-15: $4.5 \cdot 10^5$	The number of eggs per female of age $a$
$D_{r,i}^{larvae}$	<b>From region West FR to</b> West UK : $6.295 \cdot 10^{-8}$ ; Rye: $1.519 \cdot 10^{-8}$ ; Somme: $3.113 \cdot 10^{-6}$ ; Seine: $2.621 \cdot 10^{-3}$ ; Veys: $2.788 \cdot 10^{-3}$ . <b>From region UK to</b> West UK: $9.299 \cdot 10^{-4}$ ; Rye: $2.511 \cdot 10^{-4}$ ; Somme: $2.062 \cdot 10^{-5}$ ; Seine: $1.510 \cdot 10^{-6}$ ; Veys: $8.942 \cdot 10^{-9}$ . <b>From region East FR to</b> West UK: $2.921 \cdot 10^{-5}$ ; Rye: $2.236 \cdot 10^{-5}$ ; Somme: $5.577 \cdot 10^{-3}$ ; Seine: $2.115 \cdot 10^{-5}$ ; Veys: $7.199 \cdot 10^{-9}$ .	Larval drift matrix
$D_{r,r}^{adult}$	<b>From region West FR to</b> West FR: 0.96; UK: 0.01; East FR: 0.03 <b>From region UK to</b> West FR: 0.02; UK: 0.97; East FR: 0.01 <b>From region East FR to</b>	Adult movement matrix

	<b>West FR: 0.01; UK: 0.01; East FR: 0.98</b>	
<b><math>pf_a</math></b>	<b>Age 1: 0.436715, Age 2: 0.473897, Age 3: 0.509978, Age 4: 0.544574, Age 5: 0.577386, Age 6: 0.608202, Age 7: 0.636891, Age 8: 0.663395, Age 9: 0.687714, Age 10: 0.709895, Age 11: 0.73002, Age 12: 0.748194, Age 13: 0.764535, Age 14: 0.779171, Age 15: 0.792227</b>	Proportion of female in the class of age a.

## 7.1.2 Supp. Mat 2.2: Systematic literature review

### 7.1.2.1 *Methods*

We searched the available literature to assess the effect of pollutant exposure on vital rates of marine juvenile fish in nearshore nursery ground. The analysis of retained papers aimed at pooling these data to estimate a range of values of the effects of pollutants on juvenile on two demographic traits (survival and future fecundity). We also tried to assess the potential drivers of the range of these effects (experiment/observation, species, pollutant level, and time of exposure).

First, a request to the Web of Science database was conducted in November 2018, using a search string designed to link four items: the target of study (fish species), one or several pollutants, the vital rates, and the life stage (juvenile):

*Request: fish AND (pollu\* OR OHC OR PBDE OR PCB OR DDT OR PFAS OR PAH OR hydrocarbon OR metal\* OR xenob\* OR organic\*) AND (mortality OR growth OR fecundity OR recruitment OR metabol\* OR survival OR vulnerability OR reproduction) AND (nursery OR recruitment OR juvenile OR youn\*)*

The references returned by this search were evaluated for inclusion in our study. To be retained, a publication had to include at least one study (i.e., experimental or *in situ*) that met 4 criteria: (i) focus on marine fish, (ii) reports on pollutant(s) effects, (iii) links between the pollutant(s) and demographic traits, (iv) focus on juveniles. We assessed the publications in a three-stage screening process, according to the set of predefined inclusion criteria: the titles to remove any publications dealing with unrelated topics, then abstracts of the remaining publications, and finally, the full text of the articles.

Second, this collection was increased from searches of the same format using Google Scholar (November 2018) with the same selection procedure, references cited in selected papers, and authors' own literature databases.

### 7.1.2.2 *Results summary*

From the 1638 studies returned by the search on Web of Science, 106 relevant references that provided a range of values on the effects of pollutants on demographic traits of juvenile fish were finally retained. Among these references, a large part focused on growth, metabolism, or behavior. A total of 32 references provided information on survival rate and mortality, while only one addressed the future fecundity of juvenile marine fish.

Regarding survival and mortality, 6 references were added based on the complementary search

performed with Google Scholar. After screening references cited in the 38 selected papers and authors' own literature databases, 12 more references were added. As some of these 50 references account for several experiments and/or species, they provide data on 195 individual case study (1 experiment  $\times$  1 species; Supp. Mat 1).

These references contained various data types: survival or mortality rates, or lethal concentration LC50 or LC20. They used a large diversity of approaches (i.e., field studies or laboratory-controlled experiments), species (30), pollutants (i.e., metals, organic pollutants or mixtures, cocktail in sediment, microplastics), levels of exposure (from realistic levels of contamination to several orders of magnitude higher to estimate LC50) and durations of exposure (two days to one year). Both the low sample size and its huge heterogeneity did not allow for reliable aggregation nor statistical treatment of these data to estimate a range of change in survival or mortality related to realistic *in situ* exposure to pollutants.



### 7.1.2.3 Retained references

*Table. S2.2.1. Literature review results: experiments details from selected studies. 1 line = 1 experiment × 1 specie. Realism column characterises the study protocol compared to environmentally relevant condition: from low (0) to high (1) realism*

Specie	Concentration/Control	Mortality Δ%	Control	Contaminant	Realism	Duration	Study reference
Meagre ( <i>Argyrosomus regius</i> )	20μg/L, 160μg/kg	No mortality	Control non-contaminated feed	Venlafaxine	0	28d	Annexes Chapitre 2 Maulvault et al. - 2018 -
Cobia ( <i>Rachycentron canadum</i> L.)	0.31mg Cd/kg	Not significant	No Cadmium added (0.31mg Cd/kg)	Cadmium	1	112d	Liu et al. -2015 -
Cobia ( <i>Rachycentron canadum</i> L.)	3.14mg Cd/kg	Not significant	No Cadmium added (0.31mg Cd/kg)	Cadmium	1	112d	Liu et al. -2015 -
Cobia ( <i>Rachycentron canadum</i> L.)	3.32mg Cd/kg	Not significant	No Cadmium added (0.31mg Cd/kg)	Cadmium	1	112d	Liu et al. -2015 -
Cobia ( <i>Rachycentron canadum</i> L.)	5.576mg Cd/kg	Not significant	No Cadmium added (0.31mg Cd/kg)	Cadmium	1	112d	Liu et al. -2015 -
Cobia ( <i>Rachycentron canadum</i> L.)	5.425mg Cd/kg	Not significant	No Cadmium added (0.31mg Cd/kg)	Cadmium	1	112d	Liu et al. -2015 -
Cobia ( <i>Rachycentron canadum</i> L.)	10.90 mg Cd/kg	0-25	No Cadmium	Cadmium	1	112d	Liu et al. -2015 -
Target fish ( <i>Terapon jarbua</i> )	up to 64,8μg/g dw	Not significant	Control fish diet	Cadmium	1	28d	Dang and Wang - 2009 -
Parrotfish ( <i>Oplegnathus fasciatus</i> )	0.30mg Cd/kg	Not significant	0.30mg Cd/kg	Cadmium	1	112d	Okorie et al. - 2014 -
Parrotfish ( <i>Oplegnathus fasciatus</i> )	21.0mg Cd/kg	Not significant	0.30mg Cd/kg	Cadmium	1	112d	Okorie et al. - 2014 -
Parrotfish ( <i>Oplegnathus fasciatus</i> )	40.7mg Cd/kg	Not significant	0.30mg Cd/kg	Cadmium	0	112d	Okorie et al. - 2014 -
Parrotfish ( <i>Oplegnathus fasciatus</i> )	83.5mg Cd/kg	Not significant	0.30mg Cd/kg	Cadmium	0	112d	Okorie et al. - 2014 -

Parrotfish ( <i>Oplegnathus fasciatus</i> )	162mg Cd/kg	Not significant	0.30mg Cd/kg	Cadmium	0	112d	Okorie et al. - 2014 -
Parrotfish ( <i>Oplegnathus fasciatus</i> )	1387mg Cd/kg	Not significant	0.30mg Cd/kg	Cadmium	0	112d	Okorie et al. - 2014 -
Parrotfish ( <i>Oplegnathus fasciatus</i> )	2743mg Cd/kg	25-50	0.30mg Cd/kg	Cadmium	0	112d	Okorie et al. - 2014 -
Large yellow croaker ( <i>Pseudoscianea crocea</i> )	0.21mg Cd/kg diet	Not significant	Control 0.21mg/Cd/kg (No SVM)	Cadmium	1	56d	Li et al. - 2009 -
Large yellow croaker ( <i>Pseudoscianea crocea</i> )	7.26mg Cd/kg diet	Not significant	Control 0.21mg/Cd/kg (No SVM)	Cadmium	1	56d	Li et al. - 2009 -
Large yellow croaker ( <i>Pseudoscianea crocea</i> )	12.08 mg Cd/kg diet	Not significant	Control 0.21mg/Cd/kg (No SVM)	Cadmium	1	56d	Li et al. - 2009 -
Tiger Perch ( <i>Terapon jarbua</i> )	Control	Not significant	No Pb	Pb	1	30d	Hariharan et al. - 2016 -
Tiger Perch ( <i>Terapon jarbua</i> )	0,008mg/L	Not significant	No Pb	Pb	1	30d	Hariharan et al. - 2016 -
Tiger Perch ( <i>Terapon jarbua</i> )	0,017mg/L	0-25	No Pb	Pb	1	30d	Hariharan et al. - 2016 -
Tiger Perch ( <i>Terapon jarbua</i> )	0,035mg/L	25-50	No Pb	Pb	1	30d	Hariharan et al. - 2016 -

Tiger Perch ( <i>Terapon jarbua</i> )	0,070mg/L	50-75	No Pb	Pb	0	30d	Hariharan et al. - 2016 -
Tiger Perch ( <i>Terapon jarbua</i> )	0,140mg/L	50-75	No Pb	Pb	0	30d	Hariharan et al. - 2016 -
Flathead grey mullet ( <i>Mugil cephalus</i> )	Control	No mortality	No Pb	Pb	1	30d	Hariharan et al. - 2016 -
Flathead grey mullet ( <i>Mugil cephalus</i> )	0.007mg/L	No mortality	No Pb	Pb	1	30d	Hariharan et al. - 2016 -
Flathead grey mullet ( <i>Mugil cephalus</i> )	0.017mg/L	No mortality	No Pb	Pb	1	30d	Hariharan et al. - 2016 -
Flathead grey mullet ( <i>Mugil cephalus</i> )	0.030mg/L	0-25	No Pb	Pb	1	30d	Hariharan et al. - 2016 -
Flathead grey mullet ( <i>Mugil cephalus</i> )	0.070mg/L	25-50	No Pb	Pb	0	30d	Hariharan et al. - 2016 -
Flathead grey mullet ( <i>Mugil cephalus</i> )	0.118mg/L	50-75	No Pb	Pb	0	30d	Hariharan et al. - 2016 -
Rockfish ( <i>Sebastes schlegelii</i> )	0mg/L	No mortality	No Pb	Pb	1	28d	Kim et Kang - 2017 -
Rockfish ( <i>Sebastes schlegelii</i> )	120mg/L	No mortality	No Pb	Pb	1	28d	Kim et Kang - 2017 -

Rockfish ( <i>Sebastes schlegelii</i> )	240mg/L	No mortality	No Pb	Pb	1	28d	Kim et Kang - 2017 -
Gilt-head bream ( <i>Sparus aurata</i> )	Spill oil sediment: up to 5,10 mg/kg dry weight, 2mg/kg dw Cr, 6,45mg/kg dw Zn, 1,26 Pb mg/kg dw, 1,19 mg/kg dw Cu, 0,92 mg/kg dw Cd, 1,71 mg/kg dw Ni	No mortality	Clean sediment	Contaminated Sediments	1	60d	Morales-Caselles et al. - 2006 -
Longjaw mudsucker ( <i>Gillichthys mirabilis</i> )	80-240ppb PCBs, 10-34ppb DDTs, 5.89-20.9 Chlordanes	0-25	Reference marsh (TB)	Contaminated Sediments	1	NA	McGourty et al. -2009 -
European bar( <i>Dicentrarchus labrax</i> )	Contaminated sediments (Chrome 50.60±4.56, Nickel 21.65±3.62, Copper 14.99±2.35, Zinc 57.05±4.38, Arsenic 5.75±0.88,	No mortality	Control (7.73µg/g ww or µg/L)	Contaminated sediments, especially Mercury	1	30d	De Domenico et al. - 2013 -

	Cadmium 0.12±0.02, Lead 11.21±0.5, Mercury 17.63±1.7µg/g)						
Sheepshead minnow ( <i>Cyprinodon variegatus</i> )	26.42ppm Ba, 0.105Cd,0.050U, 7.92V	Not significant	Uncontaminated sediment	Solid coal combustion residue (CCR), As, Cd, Cr, Cu, Hg, Se, V, ...	1	365d	Rowe - 2003 -
Pacific herring ( <i>Clupea pallasi</i> )	9.6±2.5µg/L	Not significant	No PAH (0.2 ±0.1µg/L)	PAH	1	56d	Kennedy et al. - 2006
Pacific herring ( <i>Clupea pallasi</i> )	96h/1344h 40.7±6.9g/L	0-25	No PAH (0.2 ±0.1µg/L)	PAH	1	56d	Kennedy et al. - 2006
Pacific herring ( <i>Clupea pallasi</i> )	1344h 120.2 ±11.4g/L	25-50	No PAH (0.2 ±0.1µg/L)	PAH	1	56d	Kennedy et al. - 2006
Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	<1 (sediment control), 52,109, 199, 358, and 751 mg tPAH/kg sediment	No mortality	Control sediment	PAH	1	133d	Raimondo et al. - 2016 -

Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	52mg tPAH/kg sediment	No mortality	Control sediment	PAH	1	133d	Raimondo et al. - 2016 -
Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	109mg tPAH/kg sediment	No mortality	Control sediment	PAH	1	133d	Raimondo et al. - 2016 -
Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	199mg tPAH/kg sediment	No mortality	Control sediment	PAH	1	133d	Raimondo et al. - 2016 -
Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	358mg tPAH/kg sediment	No mortality	Control sediment	PAH	1	133d	Raimondo et al. - 2016 -
Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	751mg tPAH/kg sediment	No mortality	Control sediment	PAH	1	133d	Raimondo et al. - 2016 -
Senegalese sole ( <i>Solea senegalensis</i> )	Polluted site 882.37 +/- 150.0 ng/g sediment dw	0-25	Sediment reference	PAH	1	28d	Costa et al. - 2009 -
Senegalese sole ( <i>Solea senegalensis</i> )	High polluted site 1100.48 +/- 187.08 ng/g sediment dw	25-50	Sediment reference	PAH	1	28d	Costa et al. - 2009 -
Common sole ( <i>Solea solea</i> )	fuel-exposed 39ng/L PAH	25-50	4ng/L PAH	PAH	1	90d	Claireaux et al. - 2004 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	0.247mg/kg	0-25	No PAH	PAH	1	28d	Brown-Peterson et al. -2017 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	0.431mg/kg	0-25	No PAH	PAH	1	28d	Brown-Peterson et al. -2017 -

Southern flounder ( <i>Paralichthys lethostigma</i> )	33.33mg/kg	0-25	No PAH	PAH	1	28d	Brown-Peterson et al. -2017 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	691.85mg/kg	25-50	No PAH	PAH	1	28d	Brown-Peterson et al. -2017 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	3,940.36mg/kg	75-100	No PAH	PAH	0	28d	Brown-Peterson et al. -2017 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	0.8mg/kg	No mortality	No PAH	PAH	1	28d	Brown-Peterson et al. -2015 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	9.7mg/kg	No mortality	No PAH	PAH	1	28d	Brown-Peterson et al. -2015 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	80mg/kg	25-50	No PAH	PAH	1	28d	Brown-Peterson et al. -2015 -
Southern flounder ( <i>Paralichthys lethostigma</i> )	395mg/kg	75-100	No PAH	PAH	1	28d	Brown-Peterson et al. -2015 -
Spot ( <i>Leiostomus xanthurus</i> )	Control	No mortality	Control sediment (no PAH)	PAH	1	28d	Hargis et al. - 1984 -
Spot ( <i>Leiostomus xanthurus</i> )	2500ppm	25-50	Control sediment (no PAH)	PAH	1	18d	Hargis et al. - 1984 -
Spot ( <i>Leiostomus xanthurus</i> )	2500ppm	50-75	Control sediment (no PAH)	PAH	1	28d	Hargis et al. - 1984 -



European sea bass ( <i>Dicentrarchus labrax</i> )	47+/-4 ppb Zinc, 68+/- 7ppb benzene	No mortality	Control undosed sea water	PAH	1	42d	Sakanari et al. - 1984 -
Areolated grouper ( <i>Epinephelus areolatus</i> )	0.25 µg Benzo[a]Pyrene/g body wt/d	No mortality	NA	PAH	1	28d	Wu et al. - 2003 -
Areolated grouper ( <i>Epinephelus areolatus</i> )	12.5 µg Benzo[a]Pyrene/g body wt/d	No mortality	NA	PAH	1	28d	Wu et al. - 2003 -
Common sole ( <i>Solea solea</i> )	50 ng/L	0-25	Control no fuel added	PAH	1	90d	Gilliers et al. - 2012 -
Pacific herring ( <i>Clupea pallasi</i> )	9.7 ± 6.5µg/L	No mortality	Beads not soaked in oil	PAH	1	58d	Kennedy and Farrell - 2005 -
Pacific herring ( <i>Clupea pallasi</i> )	37.9 ± 8.6µg/L	No mortality	Beads not soaked in oil	PAH	1	58d	Kennedy and Farrell - 2005 -
Pacific herring ( <i>Clupea pallasi</i> )	99.3 ± 5.6 µg/L	No mortality	Beads not soaked in oil	PAH	1	58d	Kennedy and Farrell - 2005 -
Turbot ( <i>Scophthalmus maximus</i> )	0.001±1% produced water (PW)	Not significant	0% produced water	PAH	1	42d	Stephens et al. - 2000 -
Altantic cod ( <i>Gadus morhua L.</i> )	produced water till 200ppm	Not significant	Control (0ppm)	PAH	1	154d	Pérez-Casanova et al. - 2010 -
Turbot ( <i>Scophthalmus maximus</i> )	0.5µg/g	Not significant	Uncontaminated feed, no fuel added	PAH	1	42d	Saborido-Rey et al. - 2007 -

Turbot ( <i>Scophthalmus maximus</i> )	2.5µg/g	Not significant	Uncontaminated feed, no fuel added	PAH	1	42d	Saborido-Rey et al. - 2007 -
Turbot ( <i>Scophthalmus maximus</i> )	49µg/g	Not significant	Uncontaminated feed, no fuel added	PAH	1	42d	Saborido-Rey et al. - 2007 -
Turbot ( <i>Scophthalmus maximus</i> )	114µg/g	Not significant	Uncontaminated feed, no fuel added	PAH	0	42d	Saborido-Rey et al. - 2007 -
Turbot ( <i>Scophthalmus maximus</i> )	162µg/g	Not significant	Uncontaminated feed, no fuel added	PAH	0	42d	Saborido-Rey et al. - 2007 -
Turbot ( <i>Scophthalmus maximus</i> )	260µg/g	Not significant	Uncontaminated feed, no fuel added	PAH	0	42d	Saborido-Rey et al. - 2007 -
Wolfish ( <i>Anahrichas denticulatus</i> )	14µg/L	0-25	Seawater	TPH	0	35d	Sandrini-Neto et al. - 2016 -
Wolfish ( <i>Anahrichas denticulatus</i> )	23µg/L	0-25	Seawater with dispersant	TPH	0	35d	Sandrini-Neto et al. - 2016 -
Pacific halibut ( <i>Hippoglossus stenolepis</i> )	1636µg/g	Not significant	0µg/g	TPH	0	90d	Moles and Norcross -1998 -
Pacific halibut ( <i>Hippoglossus stenolepis</i> )	4700µg/g	75-100	0µg/g	TPH	0	90d	Moles and Norcross -1998 -
Rock sole ( <i>Lepidopsetta bilineata</i> )	1840µg/g	Not significant	0µg/g	TPH	0	90d	Moles and Norcross -1998 -

Rock sole ( <i>Lepidopsetta bilineata</i> )	4711µg/g	Not significant	0µg/g	TPH	0	90d	Moles and Norcross -1998 -
Yellowfin sole ( <i>Limanda aspera</i> )	1840µg/g	Not significant	0µg/g	TPH	0	90d	Moles and Norcross -1998 -
Yellowfin sole ( <i>Limanda aspera</i> )	4711µg/g	Not significant	0µg/g	TPH	0	90d	Moles and Norcross -1998 -
Psetta maxima ( <i>Scophthalmus maximus</i> )	Recirculating aquaculture systems, 12mg/L de Zn, 15 Fe, 9 Cu, 10 NO2-N, 9 NO3-N, 9 PO4-P, 9 µg/L de CO et de Mn,	No mortality	Disinfected sea water	Fe, Zn, Cu, Co, Mn	1	63d	Van Bussel -2014 -
Blackhead seabream ( <i>Acanthopagrus schlegelii schlegelii</i> )	50µg/g	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	14d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii schlegelii</i> )	50µg/g	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	28d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii schlegelii</i> )	250µg/g	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	14d	Dang and Wang - 2012 -

Blackhead seabream ( <i>Acanthopagrus schlegelii</i> <i>schlegelii</i> )	250µg/g	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	28d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii</i> <i>schlegelii</i> )	1000µg/g	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	14d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii</i> <i>schlegelii</i> )	1000µg/g	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	28d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii</i> <i>schlegelii</i> )	100µg/L	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	14d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii</i> <i>schlegelii</i> )	100µg/L	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	28d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii</i> <i>schlegelii</i> )	500µg/L	0-25	0.6±0.2±gCd/g and nanopure water	Copper	1	14d	Dang and Wang - 2012 -
Blackhead seabream ( <i>Acanthopagrus schlegelii</i> <i>schlegelii</i> )	500µg/L	25-50	0.6±0.2±gCd/g and nanopure water	Copper	1	28d	Dang and Wang - 2012 -

Common sole ( <i>Solea solea</i> )	BDE-209 184.2 ng/g ww, BDE-153 181.1, BDE-100 93.1, BDE-99 85.7, BDE-47 82.2, BDE-28 84.8ng/g ww	Not significant	Solvent-control fish,Control fish	PBDE congeners (BDE-28, -47, -99, -100, -153, -209)	1	84d	Munschy et al. - 2010 -
Gilt-head bream ( <i>Sparus aurata</i> )	23ng	Not significant	No PCDD/FS (fed with dry feed coated with an olive oil)	PCDD/FS	1	390d	Abalos et al. - 2008 -
Atlantic cod ( <i>Gadus morhua</i> )	0.5µmol/L	Not significant	No 4 n-heptyphenol	4 n-heptylphenol	1	8d	Tollefsen et al. - 1998 -
Atlantic cod ( <i>Gadus morhua</i> )	1µmol/L	No mortality	No 4 n-heptyphenol	4 n-heptylphenol	1	3d	Tollefsen et al. - 1998 -
Atlantic cod ( <i>Gadus morhua</i> )	2.1µmol/L	No mortality	No 4 n-heptyphenol	4 n-heptylphenol	1	2d	Tollefsen et al. - 1998 -
Atlantic cod ( <i>Gadus morhua</i> )	4.2µmol/L	No mortality	No 4 n-heptyphenol	4 n-heptylphenol	1	3d	Tollefsen et al. - 1998 -
Atlantic cod ( <i>Gadus morhua</i> )	2.1µmol/L	0-25	No 4 n-heptyphenol	4 n-heptylphenol	1	6d	Tollefsen et al. - 1998 -

Atlantic cod ( <i>Gadus morhua</i> )	2.1µmol/L	0-25	No 4 n-heptyphenol	4 n-heptylphenol	1	7d	Tollefsen et al. - 1998 -
Atlantic cod ( <i>Gadus morhua</i> )	4.2µmol/L	50-75	No 4 n-heptyphenol	4 n-heptylphenol	1	3d	Tollefsen et al. - 1998 -
Atlantic cod ( <i>Gadus morhua</i> )	4.2µmol/L	75-100	No 4 n-heptyphenol	4 n-heptylphenol	1	4d	Tollefsen et al. - 1998 -
Target fish ( <i>Terapon jarbua</i> )	As(III) 50µg/L	Not significant	Control 1.4±0.04µg/L	Arsenic	1	10d	Zhang et al. -2012 -
Target fish ( <i>Terapon jarbua</i> )	As(III) 150µg/L	Not significant	Control 1.4±0.04µg/L	Arsenic	1	10d	Zhang et al. -2012 -
Target fish ( <i>Terapon jarbua</i> )	As(III) 500µg/L	Not significant	Control 1.4±0.04µg/L	Arsenic	1	10d	Zhang et al. -2012 -
Target fish ( <i>Terapon jarbua</i> )	As(V) 50µg/L	Not significant	Control 1.4±0.04µg/L	Arsenic	1	10d	Zhang et al. -2012 -
Target fish ( <i>Terapon jarbua</i> )	As(V) 150µg/L	Not significant	Control 1.4±0.04µg/L	Arsenic	1	10d	Zhang et al. -2012 -
Target fish ( <i>Terapon jarbua</i> )	As(V) 500µg/L	Not significant	Control 1.4±0.04µg/L	Arsenic	1	10d	Zhang et al. -2012 -
Target fish ( <i>Terapon jarbua</i> )	Waterborne As(III) 100µg/L	Not significant	Control 1.4±0.04µg/L	Arsenic	1	10d	Zhang et al. -2012 -
Thin-lipped grey mullets ( <i>Liza ramada</i> )	0.17mg/L	0-25	No Atrazine	Atrazine	0	20d	Biagiанти-Risbourg et Bastide - 1995 -
Thin-lipped grey mullets ( <i>Liza ramada</i> )	0.17mg/L	25-50	No Atrazine	Atrazine	0	29d	Biagiанти-Risbourg et Bastide - 1995 -
Spot ( <i>Leiostomus xanthurus</i> )	0.0044	Not significant	Control unhalogenated clarifier effluent	Cl2 Effluent + Cl2	1	9d	Roberts - 1980 -

Spot ( <i>Leiostomus xanthurus</i> )	0.005mg/L	Not significant	Control unhalogenated clarifier effluent	Cl <sub>2</sub> Effluent + Cl <sub>2</sub>	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.0011mg/L	Not significant	Control unhalogenated clarifier effluent	BrCl Effluent + BrCl	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.023mg/L	Not significant	Control unhalogenated clarifier effluent	BrCl Effluent + BrCl	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.06	Not significant	Control unhalogenated clarifier effluent	Cl <sub>2</sub> Effluent + Cl <sub>2</sub>	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.18	Not significant	Control unhalogenated clarifier effluent	Cl <sub>2</sub> Effluent + Cl <sub>2</sub>	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.05	Not significant	Control unhalogenated clarifier effluent	BrCl Effluent + BrCl	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.13mg/L	Not significant	Control unhalogenated clarifier effluent	BrCl Effluent + BrCl	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.208mg/L	Not significant	Control unhalogenated clarifier effluent	Cl <sub>2</sub> Effluent + Cl <sub>2</sub>	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.183mg/L	Not significant	Control unhalogenated clarifier effluent	Cl <sub>2</sub> Effluent + Cl <sub>2</sub>	1	9d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.21mg/L	0-25	Control unhalogenated clarifier effluent	BrCl Effluent + BrCl	1	6d	Roberts - 1980 -

Spot ( <i>Leiostomus xanthurus</i> )	0.32mg/L	75-100	Control unhalogenated clarifier effluent	Cl2 Effluent + Cl2	0	6d	Roberts - 1980 -
Spot ( <i>Leiostomus xanthurus</i> )	0.41mg/L	75-100	Control unhalogenated clarifier effluent	BrCl Effluent + BrCl	0	6d	Roberts - 1980 -
Marine jacoever ( <i>Sebastes schlegelii</i> )	10 <sup>6</sup> microplatic	No mortality	No Microplastic	Microplastic	1	21d	Yin et al. - 2018 -
Turbot ( <i>Scophthalmus maximus</i> )	2.24mg/kg	0-25	Reference sediment	Contaminated sediment PAH	1	26d	Kerambrun et al. - 2014 - (previous study Kerambrun et al. - 2012 -)
Turbot ( <i>Scophthalmus maximus</i> )	10.2mg/kg	50-75	Reference sediment	Contaminated sediment PAH	1	26d	Kerambrun et al. - 2014 - (previous study Kerambrun et al. - 2012 -)
Turbot ( <i>Scophthalmus maximus</i> )	1.27mg/kg	No mortality	No PAH	Contaminated sediment PAH	1	21d	Kerambrun et al. -2012 -
Turbot ( <i>Scophthalmus maximus</i> )	2.44+/-0.95 mg/kg	No mortality	No PAH	Contaminated sediment PAH	1	21d	Kerambrun et al. -2012 -
Spot ( <i>Leiostomus xanthurus</i> )	16µg/L	No mortality	No PAH	PAH	1	14d	Sved et al. - 1992 -
Spot ( <i>Leiostomus xanthurus</i> )	35µg/L	No mortality	No PAH	PAH	1	14d	Sved et al. - 1992 -
Spot ( <i>Leiostomus xanthurus</i> )	76µg/L	Mortality	No PAH	PAH	1	14d	Sved et al. - 1992 -



Spot ( <i>Leiostomus xanthurus</i> )	150µg/L	Mortality	No PAH	PAH	1	14d	Sved et al. - 1992 -
Spot ( <i>Leiostomus xanthurus</i> )	320µg/L	Mortality	No PAH	PAH	1	14d	Sved et al. - 1992 -
Gilt-head bream ( <i>Sparus aurata</i> )	0.02mg/L	No mortality	Control no PAH	PAH	1	4d	Correia et al. - 2007 -
Gilt-head bream ( <i>Sparus aurata</i> )	0.1mg/L	No mortality	Control no PAH	PAH	1	4d	Correia et al. - 2007 -
Florida pompano ( <i>Trachinotus carolinus</i> )	2.83ppm	0-25	Control no Naphtalene	PAH	0	12d	Dos Santos et al. - 2006 -
Freckled blennies ( <i>Hypsoblennius ionthas</i> )	30mg/kg	Not significant	Control no TNT	TNT	0	7d	Lotufo et al. - 2010 -
Freckled blennies ( <i>Hypsoblennius ionthas</i> )	100mg/kg	Not significant	Control no TNT	TNT	0	7d	Lotufo et al. - 2010 -
Freckled blennies ( <i>Hypsoblennius ionthas</i> )	300mg/kg	Not significant	Control no TNT	TNT	0	7d	Lotufo et al. - 2010 -
Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	7mg/kg	0-25	Control no TNT	TNT	0	4d	Lotufo et al. - 2010 -
Sheepshead Minnow ( <i>Cyprinodon variegatus</i> )	340mg/kg	75-100	Control no TNT	TNT	0	4d	Lotufo et al. - 2010 -
Common goby ( <i>Pomatoschistus microps</i> )	20µg/L	No mortality	20µg/L pyrene	Pyrene	1	4d	Oliveira et al. - 2013 -

Commong goby ( <i>Pomatoschistus microps</i> )	20µg/L + 18.4µg/L	No mortality	20µg/L pyrene	Pyrene + Micro particule	1	4d	Oliveira et al. - 2013 -
Commong goby ( <i>Pomatoschistus microps</i> )	20µg/L + 184µg/L	No mortality	20µg/L pyrene	Pyrene + Micro particule	1	4d	Oliveira et al. - 2013 -
Commong goby ( <i>Pomatoschistus microps</i> )	18,4µg/L	No mortality	20µg/L pyrene	Micro particule	1	4d	Oliveira et al. - 2013 -
Commong goby ( <i>Pomatoschistus microps</i> )	184µg/L	No mortality	20µg/L pyrene	Micro particule	1	4d	Oliveira et al. - 2013 -
Commong goby ( <i>Pomatoschistus microps</i> )	200µg/L	75-100	20µg/L pyrene	Pyrene	1	2d	Oliveira et al. - 2013 -
Commong goby ( <i>Pomatoschistus microps</i> )	200µg/L + 18,4 µg/L	75-100	20µg/L pyrene	Pyrene + Micro particule	1	3d	Oliveira et al. - 2013 -
Commong goby ( <i>Pomatoschistus microps</i> )	200µg/L + 184µg/L	75-100	20µg/L pyrene	Pyrene + Micro particule	1	3d	Oliveira et al. - 2013 -
Commong goby ( <i>Pomatoschistus microps</i> )	12.6mg/L	No mortality	No Cr(VI), No Microplastic	Cr(VI) sediment M- est	1	4d	De Sà et al. - 2015 -

Commong goby ( <i>Pomatoschistus microps</i> )	18.9mg/L	25-50	No Cr(VI), No Microplastic	Cr(VI) sediment M- est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	28.4mg/L	25-20	No Cr(VI), No Microplastic	Cr(VI) sediment M- est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	12.6mg/L	25-50	No Cr(VI), No Microplastic	Cr(VI) sediment L- est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	18.9mg/L	25-50	No Cr(VI), No Microplastic	Cr(VI) sediment L- est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	28.4mg/L	75-100	No Cr(VI), No Microplastic	Cr(VI) sediment L- est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	1.8mg/L + 0.216mg/L	No mortality	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment M- est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	3.9mg/L + 0.216mg/L	No mortality	No Cr(VI), No Microplastic	Cr(VI) + Microplastic	1	4d	De Sà et al. - 2015

				sediment M-est			
Commong goby ( <i>Pomatoschistus microps</i> )	8.0mg/L + 0.216mg/L	0-25	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment M-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	18.9mg/L + 0.216mg/L	0-25	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment M-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	28.4mg/L + 0.216mg/L	50-75	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment M-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	1.8mg/L + 0.216mg/L	No mortality	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment L-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	3.9mg/L + 0.216mg/L	0-25	No Cr(VI), No Microplastic	Cr(VI) + Microplastic	1	4d	De Sà et al. - 2015

				sediment L-est			
Commong goby ( <i>Pomatoschistus microps</i> )	8.0mg/L + 0.216mg/L	0-25	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment L-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	18.9mg/L + 0.216mg/L	0-25	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment L-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	28.4mg/L + 0.216mg/L	75-100	No Cr(VI), No Microplastic	Cr(VI) + Microplastic sediment L-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	0.216mg/L	25-50	No Cr(VI), No Microplastic	Microplastic sediment M-est	1	4d	De Sà et al. - 2015
Commong goby ( <i>Pomatoschistus microps</i> )	0.216mg/L	25-50	No Cr(VI), No Microplastic	Microplastic sediment L-est	1	4d	De Sà et al. - 2015

Senegalese sole ( <i>Solea senegalensis</i> )	0.01mg/L	No mortality	Control no Copper	Copper	1	4d	Oliva et al. - 2009 -
Senegalese sole ( <i>Solea senegalensis</i> )	0.1mg/L	No mortality	Control no Copper	Copper	1	4d	Oliva et al. - 2009 -
Senegalese sole ( <i>Solea senegalensis</i> )	1mg/L	25-50	Control no Copper	Copper	0	1d	Oliva et al. - 2009 -
Senegalese sole ( <i>Solea senegalensis</i> )	1mg/L	75-100	Control no Copper	Copper	0	2d	Oliva et al. - 2009 -
Senegalese sole ( <i>Solea senegalensis</i> )	1mg/L	75-100	Control no Copper	Copper	0	3d	Oliva et al. - 2009 -
Senegalese sole ( <i>Solea senegalensis</i> )	1mg/L	75-100	Control no Copper	Copper	0	4d	Oliva et al. - 2009 -
Common goby ( <i>Pomatoschistus microps</i> )	1.3mg/L	No mortality	No Cefalexin	Cefalexin (25°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	2.5mg/L	No mortality	No Cefalexin	Cefalexin (25°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	5mg/L	0-25	No Cefalexin	Cefalexin (25°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	10mg/L	0-25	No Cefalexin	Cefalexin (25°C)	0	4d	Fonte et al. - 2016 -

Common goby ( <i>Pomatoschistus microps</i> )	1.3mg/L	No mortality	No Cefalexin	Cefalexin (20°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	2.5mg/L	No mortality	No Cefalexin	Cefalexin (20°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	5mg/L	0-25	No Cefalexin	Cefalexin (20°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	10mg/L	0-25	No Cefalexin	Cefalexin (20°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	0.184mg/L	0-25	No Microplastic	Microplastic (25°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	0.184mg/L	0-25	No Microplastic	Microplastic (20°C)	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	8mg/L + 0.184mg/L	0-25	No Cefalexin no Microplastic	Cefalexin + MP	0	4d	Fonte et al. - 2016 -
Common goby ( <i>Pomatoschistus microps</i> )	10mg/L + 0.184mg/L	0-25	No Cefalexin no Microplastic	Cefalexin + MP	0	4d	Fonte et al. - 2016 -
Starry flounder ( <i>Platichthys stellatus</i> )	6.91mg/L	Mortality	No Control	PAH	0	4d	Rice and al. - 1979 -
Starry flounder ( <i>Platichthys stellatus</i> )	1.42mg/L	Mortality	No Control	PAH	0	4d	Rice and al. - 1979 -

European sea bass ( <i>Dicentrarchus labrax</i> )	75.6mg/L	Mortality	Not Contaminated	PAH	0	4d	Dussauze et al. - 2015 -
European sea bass ( <i>Dicentrarchus labrax</i> )	9.60 ± 2.86 mg/L	Not significant	No PAH	PAH	1	4d	Kerambrun et al. -2012 -
European sea bass ( <i>Dicentrarchus labrax</i> )	18.6 ± 3.6 mg/L	Not significant	No PAH	PAH	1	4d	Kerambrun et al. -2012 -
Killifish ( <i>Fundulus heteroclitus</i> )	1mg/L	Mortality	Control Pristine estuary	Mercury	1	4d	Khan and Weis - 1986 -



## 7.1.2.4 Literature cited

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## 7.2 Annexes du chapitre 3.1

### 7.2.1 Supp. Mat. 3.1.1: Age structured model based on life history data

Population dynamics is simulated by a deterministic life cycle model structured by age ( $a$  subscript) and stage with a year time step ( $y$  subscript).

Fish are supposed to recruit at age  $a_{rec}$ . For all ages classes  $a_{rec} < a \leq a_{max}$ , population abundance ( $N$ ) is described by:

$$N_{a+1,y+1} = N_{a,y} \times e^{-(M+F_{a,y})} \quad (\text{eq. S1.1})$$

with  $M$  and  $F$  the natural and fishing mortality rates, respectively.

Fishing mortality at age is defined as the product of selectivity at age and a maximum fishing mortality value:  $F_{a,y} = sel_a \times F_y$ .

For simplicity we assumed a knife edge formulation for maturity and selectivity:

$$sel_a = mat_a = \begin{cases} 0 & \text{if } a < a_{mat} \\ 1 & \text{if } a \geq a_{mat} \end{cases} \quad (\text{eq.n S1.2})$$

thus supposing that the age fish start to be caught by the fishery is also the age at maturity.

Catches in weight are computed based on Baranov equation:

$$C_y = \sum_{a_{mat}}^{a_{max}} N_{a,y} \times \frac{F_{a,y}}{F_{a,y}+M} \times (1 - e^{-(F_{a,y}+M)}) \times W_a \quad (\text{eq. S1.3})$$

Weight at age ( $W_a$ ) is then computed as a simple power function of length at a given age:

$$W_a = b \times L_a^c \quad (\text{eq. S1.4})$$

with  $b$  and  $c$  being the proportion and shape parameters estimated with a hierarchical Bayesian model (Froese et al, 2014).

Length at age is computed based on Von Bertalanffy equation:

$$L_a = L_{inf} \times (1 - e^{-k \times (a - a_0)}) \quad (\text{eq. S1.5})$$

with  $L_{inf}$  the asymptotic length and  $k$  the growth coefficient both extracted from FishLife.  $a_0$  is the theoretical age at size 0 which was assumed to be equals to -0.1 (Thorson, 2020).

The number of eggs spawned any year  $y$  is computed based on adult abundance:

$$\omega_y = \sum_a N_{a,y} \times e^{-ts(M_{a,y}+F_{a,y})} \times pf_a \times mat_a \times fec_a \quad (\text{eq. S1.6})$$

with  $mat_a$  the probability of being mature as defined in equation S1.2,  $fec_a$  the fecundity (number of eggs per female),  $pf_a$  is the female proportion set at 0.5 for all age (time invariant variables).  $ts$  is a time scaling factor considering the mortality happening before spawning, it was set similarly for all species at 0.27.

Eggs are supposed to first survive to the larval drift with density-independent survival  $e^{-M_{larvae}}$  before settling in the nurseries area where they suffer density dependent mortality before recruiting. The larval mortality during larval drift was set at  $10^3$  for Teleosts fish (Le Pape & Bonhommeau, 2015) and 1 for elasmobranch.

The age at recruitment,  $a_{rec}$ , was set a 1 for all species, which implies a hypothesis of density dependent processes impacting only the survival from larval to age 1. The number of recruits for year  $y$  is computed with a Beverton-Holt relationship based on eggs numbers of the previous year:

$$N_{a_{rec},y} = \frac{4h\omega_{y-a_{rec}}}{\bar{W}(1-h) + \frac{4h\omega_{y-a_{rec}}}{K}} \quad (\text{eq. S1.7})$$

with  $h$  the steepness,  $\bar{W}$  the number of eggs produced on average by a recruit during its lifetime in the absence of any fishing and  $K$  the carrying capacity of the nursery (see SupMat 2).

The number of eggs produced on average by a recruit during its lifetime in the absence of any fishing,  $\bar{W}$ , is defined as:

$$\bar{W} = \sum_{a=a_{rec}+1}^{a_{max}} S_a \times pf_a \times p_{mat,a} \times fec_a \quad (\text{eq. S1.8})$$

with  $S_a$  the cumulative survival to age  $a$  as:

$$S_a = \prod_{i=a_{rec}}^{a-1} e^{-M_i} \quad (\text{eq. S1.9})$$

### 7.2.2 Supp. Mat. 3.1.2: Parameterization of the stock-recruitment relationships in terms of steepness

Let's define  $\bar{W}$  the number of eggs produced on average by a recruit during its lifetime in the absence of any fishing (e.g., Lifetime egg production (Mangel et al., 2010) or Egg per recruit (Goodyear, 1993)).

$$\bar{W} = \sum_{a=a_{rec}+1}^{a_{max}} S_a \times p_{f_a} \times p_{mat,a} \times fec_a \quad (\text{eq. S2.1})$$

$$S_a = \prod_{i=a_{rec}}^{a-1} e^{-M_i} \quad (\text{eq. S2.2})$$

with  $S_a$  the cumulative survival to age  $a$  as defined in equation S2.2,  $p_{f_a}$  the female proportion at age  $a$ ,  $p_{mat,a}$  the probability of being mature at age  $a$ , and  $fec_a$  the fecundity at age  $a$ .

From  $\bar{W}$  and the recruitment  $R$  (as expressed in number of fish) we can deduce the recruitment in terms of eggs potentially spawned on average by recruits,  $R_{eggs}$ :

$$R_{eggs} = R \times \bar{W} \quad (\text{eq. S2.3})$$

$$\text{At an unfished equilibrium state, we can write: } R_{eggs} = \omega_0 \quad (\text{eq. S2.4})$$

with  $\omega_0$  the number of eggs produced at this unfished equilibrium state.

Combining the Beverton-Holt expression of the recruitment  $R$  in equation S1.7 with the equilibrium equation S2.4 we get:

$$\frac{e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \omega_0}{1 + \frac{M_{DD}}{M_{DI} S} \times (e^{M_{DI} \times a_{rec}} - 1) \times e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \omega_0} \times \bar{W} = \omega_0 \quad (\text{eq. S2.5})$$

which gives

$$\omega_0 = \frac{e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W} - 1}{\frac{M_{DD}}{M_{DI} S} \times (e^{M_{DI} \times a_{rec}} - 1) \times e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}}} \quad (\text{eq. S2.6})$$

Steepness (Mace and Doonan, 1988) is defined as the fraction of recruitment from an unfished population at equilibrium obtained when the spawning stock biomass is 20% of its unfished level (thus produce  $\omega_0$ ), so:

$$h = \frac{R(0.2 \times \omega_0)}{R(\omega_0)} = \frac{R(0.2 \times \omega_0)}{\omega_0 / \bar{W}} \quad (\text{eq. S2.7})$$

Combining equation S2.7 with the expression of  $\omega_0$  in equation S2.6, we obtain

$$h = \frac{e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}}{4 + e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \bar{W}} \quad (\text{eq. S2.8})$$

### 7.2.3 Supp. Mat. 3.1.3: Selection of contrasted LHT

The Fishlife package (Thorson et al., 2017) uses size, growth, mortality and maturity data for thousands of fish worldwide as compiled by FishBase (Froese and Pauly, 2022) and stock-recruitment data from the RAM database (Myers et al., 1995) to predict key life histories and stock-recruitment parameters. Predictions exist for any species having measurement records in FishBase, however, not all of these species are exploited marine species. To restrict our study to commercial species, we select the species for which the European Scientific, Technical and Economic Committee for Fisheries (STECF) has stock status (Scientific, Technical and Economic Committee for Fisheries (STECF), 2019).

Then we conducted a Principal Component Analysis (PCA) to synthesize the variations of LHT among species and select species with highly contrasted life histories. PCA was based on the LHT required to calibrate the population model: maximum age ( $age_{max}$ ), age at maturity ( $age_{mat}$ ), growth coefficient ( $k$ ), asymptotic size ( $L_{inf}$ ), natural mortality ( $M$ ) and steepness ( $h$ ). However, most of these LHT are correlated (Thorson et al., 2017). To avoid overweighting the PCA by strongly correlated LHT, only the less correlated parameters were selected to conduct the PCA:  $age_{mat}$ ,  $L_{inf}$ ,  $M$  and  $h$  (Table S3.1.3.1).

Table S3.1.3.1: Values of asymptotic size ( $L_{inf}$ ), growth coefficient ( $k$ ), maximum age ( $age_{max}$ ), age at maturity ( $age_{mat}$ ), natural mortality ( $M$ ) and steepness ( $h$ ) for the sub-list of marine species from STECF. Bold parameters and values were used for the PCA analysis.

N°	English name	$L_{inf}$	$k$	$a_{max}$	$a_{mat}$	$M$	$h$
1	European eel	71	0,15	13	5	0,26	0,34
2	Greater argentine	44	0,20	22	6	0,29	0,52
3	Redfish	26	0,25	10	3	0,53	0,86
4	Boarfish	14	0,29	13	3	0,44	0,87
5	Mediterranean horse mackerel	36	0,30	12	2	0,52	0,64
6	Chilean jack mackerel	82	0,12	24	5	0,24	0,68
7	Blue jack mackerel	59	0,17	18	3	0,32	0,68
8	Atlantic horse mackerel	39	0,21	14	3	0,40	0,75
9	Leafscale gulper shark	138	0,06	47	21	0,09	0,42
10	Basking shark	943	0,04	57	23	0,07	0,32
11	Atlantic herring	30	0,34	12	5	0,24	0,58



<b>12</b>	<b>European pilchard</b>	<b>20</b>	0,41	9	<b>3</b>	<b>0,44</b>	<b>0,77</b>
<b>13</b>	<b>European sprat</b>	<b>15</b>	0,52	6	<b>2</b>	<b>0,66</b>	<b>0,80</b>
<b>14</b>	<b>European anchovy</b>	<b>18</b>	0,48	5	<b>1</b>	<b>0,91</b>	<b>0,71</b>
<b>15</b>	<b>Atlantic cod</b>	<b>104</b>	0,17	15	<b>3</b>	<b>0,27</b>	<b>0,79</b>
<b>16</b>	<b>Haddock</b>	<b>67</b>	0,24	14	<b>2</b>	<b>0,33</b>	<b>0,66</b>
<b>17</b>	<b>Whiting</b>	<b>45</b>	0,29	11	<b>2</b>	<b>0,43</b>	<b>0,71</b>
<b>18</b>	<b>Blue whiting</b>	<b>36</b>	0,29	13	<b>3</b>	<b>0,41</b>	<b>0,55</b>
<b>19</b>	<b>Pollack</b>	<b>80</b>	0,21	13	<b>3</b>	<b>0,41</b>	<b>0,76</b>
<b>20</b>	<b>Saithe</b>	<b>115</b>	0,13	22	<b>5</b>	<b>0,23</b>	<b>0,79</b>
<b>21</b>	<b>Norway pout</b>	<b>22</b>	0,56	5	<b>1</b>	<b>1,17</b>	<b>0,74</b>
<b>22</b>	<b>Poor cod</b>	<b>25</b>	0,43	5	<b>1</b>	<b>0,98</b>	<b>0,86</b>
<b>23</b>	<b>Black marlin</b>	<b>153</b>	0,37	9	<b>2</b>	<b>0,56</b>	<b>0,47</b>
<b>24</b>	<b>Indo-Pacific sailfish</b>	<b>276</b>	0,34	7	<b>2</b>	<b>0,71</b>	<b>0,43</b>
<b>25</b>	<b>Atlantic white marlin</b>	<b>198</b>	0,42	9	<b>2</b>	<b>0,62</b>	<b>0,46</b>
<b>26</b>	<b>Blue marlin</b>	<b>428</b>	0,25	16	<b>4</b>	<b>0,34</b>	<b>0,37</b>
<b>27</b>	<b>Porbeagle</b>	<b>304</b>	0,09	30	<b>11</b>	<b>0,15</b>	<b>0,32</b>
<b>28</b>	<b>American angler</b>	<b>148</b>	0,07	17	<b>6</b>	<b>0,20</b>	<b>0,94</b>
<b>29</b>	<b>Blackbellied angler</b>	<b>88</b>	0,11	13	<b>4</b>	<b>0,32</b>	<b>0,93</b>
<b>30</b>	<b>Angler</b>	<b>138</b>	0,11	11	<b>4</b>	<b>0,36</b>	<b>0,92</b>
<b>31</b>	<b>Tusk</b>	<b>81</b>	0,13	21	<b>6</b>	<b>0,23</b>	<b>0,57</b>
<b>32</b>	<b>Blue ling</b>	<b>138</b>	0,12	21	<b>6</b>	<b>0,23</b>	<b>0,52</b>
<b>33</b>	<b>Ling</b>	<b>145</b>	0,12	21	<b>6</b>	<b>0,24</b>	<b>0,53</b>
<b>34</b>	<b>Roundnose grenadier</b>	<b>75</b>	0,09	48	<b>12</b>	<b>0,10</b>	<b>0,40</b>
<b>35</b>	<b>Roughhead grenadier</b>	<b>83</b>	0,08	46	<b>13</b>	<b>0,11</b>	<b>0,53</b>
<b>36</b>	<b>Roughsnout grenadier</b>	<b>47</b>	0,20	22	<b>6</b>	<b>0,24</b>	<b>0,50</b>
<b>37</b>	<b>European hake</b>	<b>80</b>	0,14	12	<b>3</b>	<b>0,31</b>	<b>0,56</b>
<b>38</b>	<b>Senegalese hake</b>	<b>87</b>	0,18	15	<b>4</b>	<b>0,33</b>	<b>0,52</b>
<b>39</b>	<b>European seabass</b>	<b>75</b>	0,17	8	<b>2</b>	<b>0,20</b>	<b>0,90</b>
<b>40</b>	<b>Surmullet</b>	<b>31</b>	0,29	8	<b>1</b>	<b>0,54</b>	<b>0,72</b>
<b>41</b>	<b>Capelin</b>	<b>21</b>	0,50	5	<b>2</b>	<b>1,09</b>	<b>0,64</b>
<b>42</b>	<b>Greater forkbeard</b>	<b>53</b>	0,28	8	<b>2</b>	<b>0,41</b>	<b>0,68</b>
<b>43</b>	<b>Witch flounder</b>	<b>43</b>	0,20	21	<b>5</b>	<b>0,21</b>	<b>0,63</b>
<b>44</b>	<b>Common dab</b>	<b>31</b>	0,31	12	<b>2</b>	<b>0,31</b>	<b>0,90</b>

<b>45</b>	<b>Lemon sole</b>	<b>40</b>	0,22	28	<b>6</b>	<b>0,20</b>	<b>0,73</b>
<b>46</b>	<b>European flounder</b>	<b>41</b>	0,25	14	<b>4</b>	<b>0,24</b>	<b>0,81</b>
<b>47</b>	<b>European plaice</b>	<b>53</b>	0,14	28	<b>4</b>	<b>0,14</b>	<b>0,82</b>
<b>48</b>	<b>Greenland halibut</b>	<b>132</b>	0,06	34	<b>10</b>	<b>0,10</b>	<b>0,89</b>
<b>49</b>	<b>Starry ray</b>	<b>87</b>	0,11	18	<b>8</b>	<b>0,20</b>	<b>0,51</b>
<b>50</b>	<b>Blue skate</b>	<b>244</b>	0,07	26	<b>14</b>	<b>0,12</b>	<b>0,44</b>
<b>51</b>	<b>Cuckoo ray</b>	<b>85</b>	0,14	18	<b>9</b>	<b>0,20</b>	<b>0,42</b>
<b>52</b>	<b>Blonde ray</b>	<b>130</b>	0,14	18	<b>8</b>	<b>0,23</b>	<b>0,35</b>
<b>53</b>	<b>Thornback ray</b>	<b>118</b>	0,13	18	<b>8</b>	<b>0,21</b>	<b>0,38</b>
<b>54</b>	<b>Small-eyed ray</b>	<b>130</b>	0,12	21	<b>10</b>	<b>0,19</b>	<b>0,39</b>
<b>55</b>	<b>Spotted ray</b>	<b>79</b>	0,19	14	<b>6</b>	<b>0,30</b>	<b>0,38</b>
<b>56</b>	<b>Undulate ray</b>	<b>111</b>	0,14	17	<b>8</b>	<b>0,25</b>	<b>0,40</b>
<b>57</b>	<b>Atlantic salmon</b>	<b>123</b>	0,27	6	<b>2</b>	<b>0,77</b>	<b>0,86</b>
<b>58</b>	<b>Sea trout</b>	<b>52</b>	0,25	7	<b>2</b>	<b>0,64</b>	<b>0,95</b>
<b>59</b>	<b>Skipjack tuna</b>	<b>82</b>	0,53	7	<b>2</b>	<b>1,04</b>	<b>0,62</b>
<b>60</b>	<b>Atlantic mackerel</b>	<b>40</b>	0,32	13	<b>3</b>	<b>0,30</b>	<b>0,64</b>
<b>61</b>	<b>Albacore</b>	<b>153</b>	0,18	14	<b>4</b>	<b>0,27</b>	<b>0,64</b>
<b>62</b>	<b>Yellowfin tuna</b>	<b>209</b>	0,31	8	<b>2</b>	<b>0,55</b>	<b>0,67</b>
<b>63</b>	<b>Bigeye tuna</b>	<b>214</b>	0,18	12	<b>4</b>	<b>0,35</b>	<b>0,63</b>
<b>64</b>	<b>Atlantic bluefin tuna</b>	<b>376</b>	0,10	27	<b>7</b>	<b>0,16</b>	<b>0,53</b>
<b>65</b>	<b>Longtail tuna</b>	<b>190</b>	0,22	14	<b>4</b>	<b>0,35</b>	<b>0,59</b>
<b>66</b>	<b>Four-spot megrim</b>	<b>37</b>	0,19	12	<b>3</b>	<b>0,35</b>	<b>0,87</b>
<b>67</b>	<b>Megrim</b>	<b>51</b>	0,15	15	<b>3</b>	<b>0,26</b>	<b>0,84</b>
<b>68</b>	<b>Turbot</b>	<b>56</b>	0,25	15	<b>3</b>	<b>0,33</b>	<b>0,86</b>
<b>69</b>	<b>Brill</b>	<b>41</b>	0,43	7	<b>1</b>	<b>0,67</b>	<b>0,86</b>
<b>70</b>	<b>Small-spotted catshark</b>	<b>71</b>	0,21	11	<b>4</b>	<b>0,32</b>	<b>0,34</b>
<b>71</b>	<b>Beaked redfish</b>	<b>46</b>	0,09	53	<b>12</b>	<b>0,08</b>	<b>0,65</b>
<b>72</b>	<b>Golden redfish</b>	<b>46</b>	0,10	56	<b>12</b>	<b>0,08</b>	<b>0,58</b>
<b>73</b>	<b>White grouper</b>	<b>91</b>	0,14	22	<b>8</b>	<b>0,22</b>	<b>0,72</b>
<b>74</b>	<b>Common sole</b>	<b>38</b>	0,32	12	<b>2</b>	<b>0,31</b>	<b>0,60</b>
<b>75</b>	<b>Bogue</b>	<b>31</b>	0,21	12	<b>3</b>	<b>0,41</b>	<b>0,89</b>
<b>76</b>	<b>Blackspot seabream</b>	<b>55</b>	0,14	14	<b>4</b>	<b>0,30</b>	<b>0,93</b>
<b>77</b>	<b>Common pandora</b>	<b>36</b>	0,19	12	<b>3</b>	<b>0,40</b>	<b>0,93</b>

<b>78</b>	<b>Gilthead seabream</b>	<b>56</b>	0,25	12	<b>3</b>	<b>0,42</b>	<b>0,85</b>
<b>79</b>	<b>Picarel</b>	<b>20</b>	0,40	6	<b>1</b>	<b>0,80</b>	<b>0,91</b>
<b>80</b>	<b>Picked dogfish</b>	<b>117</b>	0,08	25	<b>13</b>	<b>0,13</b>	<b>0,36</b>
<b>81</b>	<b>Brusetooth lizardfish</b>	<b>38</b>	0,54	6	<b>2</b>	<b>0,79</b>	<b>0,75</b>
<b>82</b>	<b>Orange roughy</b>	<b>60</b>	0,07	24	<b>9</b>	<b>0,18</b>	<b>0,83</b>
<b>83</b>	<b>Tope shark</b>	<b>172</b>	0,12	44	<b>13</b>	<b>0,11</b>	<b>0,25</b>
<b>84</b>	<b>Black scabbardfish</b>	<b>126</b>	0,19	12	<b>3</b>	<b>0,27</b>	<b>0,35</b>
<b>85</b>	<b>Grey gurnard</b>	<b>36</b>	0,33	13	<b>3</b>	<b>0,37</b>	<b>0,59</b>
<b>86</b>	<b>Swordfish</b>	<b>261</b>	0,14	15	<b>4</b>	<b>0,26</b>	<b>0,65</b>

The two first dimension of the PCA explained 79% of the total inertia (e.g., the total variance of the dataset). Regarding axis construction,  $age_{mat}$  and  $h$  are mostly correlated with the first axis, while  $M$  is more correlated with the second one. Finally,  $L_{inf}$  is correlated with both axis (Fig. S3.1.3.1). We can notice that steepness and asymptotic length are negatively correlated and nearly uncorrelated with natural mortality.

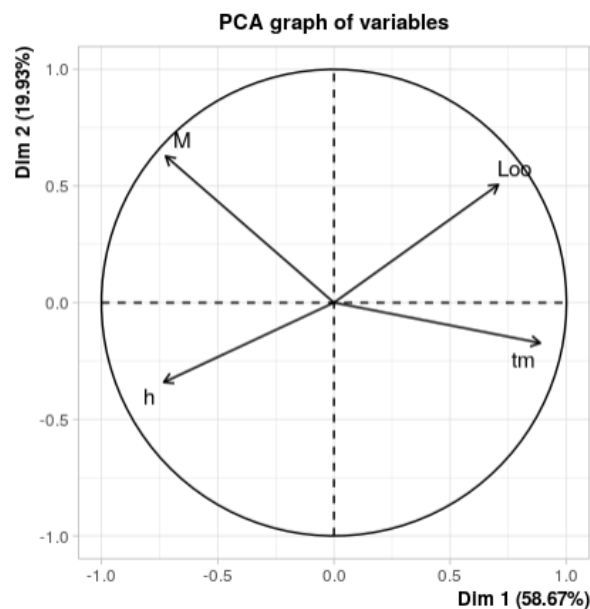


Figure S3.1.3.1: Variable graph of the Principal component analysis

Individuals are not uniformly scattered on the two axes (Fig. S3.1.3.2). Finally, we selected three species that respect the tradeoff between:

- 1) a high contrast in LHT;
- 2) data availability (especially, fecundity, larval mortality) were missing for some species, for example deep sea species (distributed on the edge of the bottom right quarter) or basking shark (far up right point);
- 3) respect of some key population dynamics hypotheses (we considered that our model could not capture the population dynamic of great migrators as anadromous fish or big pelagic (tunas...)).

Finally, we selected European anchovy (*Engraulis encrasicolus*, Engraulidae), European plaice (*Pleuronectes platessa*, Pleuronectidae) and cuckoo ray (*Leucoraja naevus*, Rajidae) both for their data availability and consistence with our modelling framework. Parameter values and source for the four species are provided in Table 3.1.1 and Table S3.1.3.2.

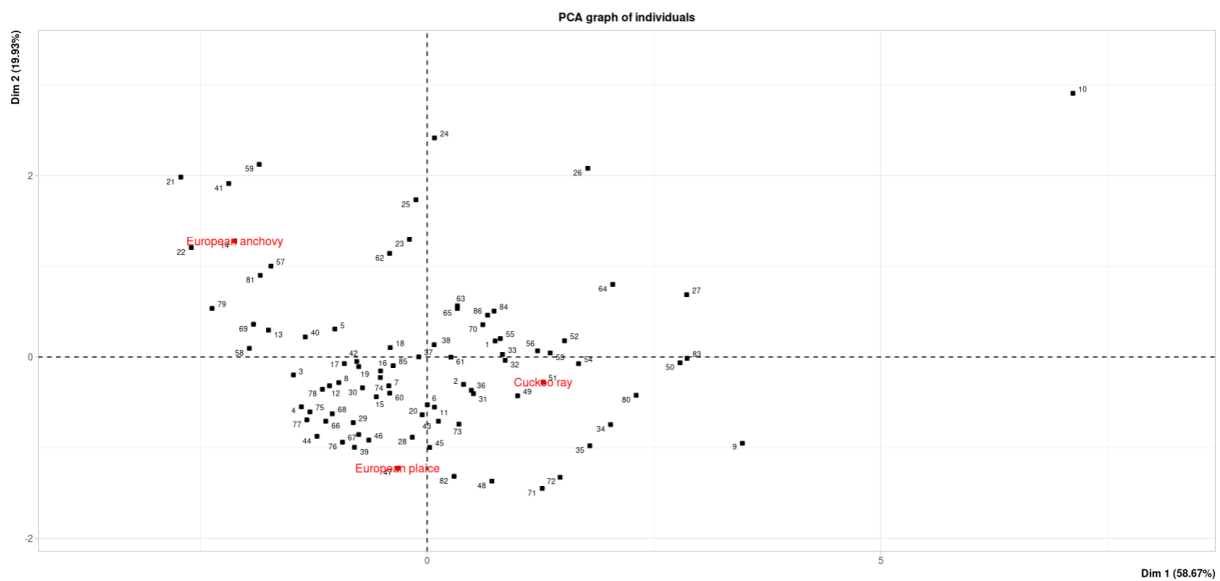


Figure S3.1.3.2: Individual graph of the Principal component analysis. Each point is a species, numbers are detailed in Table S3.1.3.1. The three selected species are coloured in red and labelled.

Table S3.1.3.2: Length-weight parameters (Froese et al., 2014) and fecundity data for the three-example species.

Biological process	Length-weight relationship		Fecundity estimate		
	Species	<i>b</i>	<i>c</i>	Estimate	Source
European anchovy		0.0047	3.1	$550 \times W_a \times 30$	(Pethybridge et al., 2013; Sanz and Uriarte, 1989)
Cuckoo ray		0.0026	3.2	All ages: 80	(Frisk et al., 2001)
European plaice		0.0081	3.05	$2.33 \times L_a^{3.10}$	(Carpentier et al., 2009)

#### 7.2.4 Supp. Mat. 3.1.4. Analytical exploration of the sensitivity analysis of h and K to habitat multipliers

Our simulations of habitat scenario relied on the modification of the stock-recruitment parameters (carrying capacity  $K$  and steepness  $h$ ) according to multipliers. A surface multiplier ( $\lambda_{surface}$ ) is applied directly to the nursery surface parameter. Quality multipliers ( $\lambda_{quality}$ ) impact both the density-dependent and -independent mortality rates. We use  $\frac{1}{\lambda_{surface}}$  as a multiplier of surface so as  $\lambda_{quality} > 1$  and  $\lambda_{surface} > 1$  both interpreted as habitats degradation.

Carrying capacity and steepness can then be directly expressed as function of surface and quality multiplier:

$$K(\lambda_{surface}, \lambda_{quality}) = \frac{M_{DI}}{M_{DD}} \times \frac{S}{\lambda_{surface}} \times \frac{1}{(e^{M_{DI} \times \lambda_{quality} \times a_{rec}} - 1)} \quad (\text{eq. S4.1})$$

$$h(\lambda_{quality}) = \frac{e^{-M_{DI} \times \lambda_{quality} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}{4 + e^{-M_{DI} \times \lambda_{quality} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}} \quad (\text{eq. S4.2})$$

The sensitivity of carrying capacity and steepness to habitat scenarios can then be analytically assessed through the first order partial derivative.

First, it is straightforward to see that steepness is independent of surface multiplier.

$$\frac{\partial h}{\partial \lambda_{surface}} = 0 \quad (\text{eq. S4.3})$$

Similarly, the partial derivative of carrying capacity with respect to the surface multiplier is a simple function of the surface multiplier and the carrying capacity itself:

$$\frac{\partial K}{\partial \lambda_{surface}} = -\frac{M_{DI} \times S}{M_{DD}} \times \frac{1}{(e^{M_{DI} \times \lambda_{quality} \times a_{rec}} - 1)} \times \frac{1}{\lambda_{surface}^2} = -\frac{K}{\lambda_{surface}} \quad (\text{eq. S4.4})$$

The partial derivative given in eq. S4.4 highlights that the sensitivity of  $K$  to surface multiplier will be the same for all species, because  $K$  was set equal for all.

The partial derivative of steepness relative to quality multiplier is a combination of  $M_{DI}$ , larval mortality and number of eggs produced on average by a recruit during its lifetime:

$$\frac{\partial h}{\partial \lambda_{quality}} = \frac{-4 \times M_{DI} \times a_{rec} \times e^{-M_{DI} \times \lambda_{quality} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}{(4 + e^{-M_{DI} \times \lambda_{quality} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}})^2} \quad (\text{eq. S4.5})$$

The value of this derivative according to combinations of the product  $e^{-M_{larvae}} \times \bar{W}$  and  $M_{DI}$  (Fig. S3.1.4.1) highlighted that Anchovy differentiates with a much lower derivative value associated with a with a low  $M_{DI}$  value. But the differentiation of the derivative values was not only determined by  $M_{DI}$  value. Cuckoo ray, has a medium  $M_{DI}$  value but a low  $e^{-M_{larvae}} \times \bar{W}$ , leading to the strongest derivative value. Plaice exhibited high values of  $M_{DI}$  and  $e^{-M_{larvae}} \times \bar{W}$  resulting into a lower derivative value than ray.

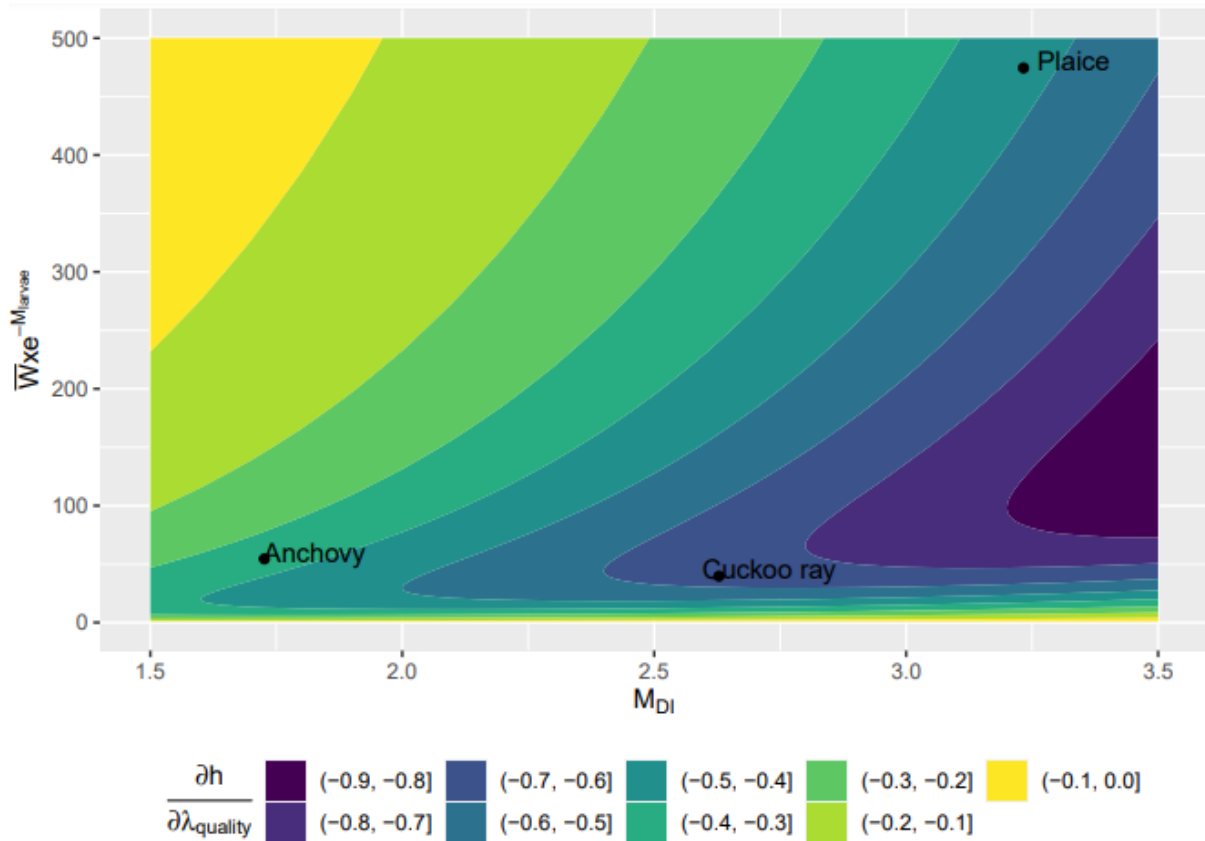


Figure S3.1.4.1: Value of the partial derivative of the steepness with respect to quality multiplier in relation to density-independent ( $M_{DI}$ ) mortality rate and number of eggs produced on average by an egg  $e^{-M_{larvae}} \times \bar{W}$ . The points indicate where a specie lie in the ( $M_{DI}$ ,  $e^{-M_{larvae}} \times \bar{W}$ ) space.

The partial derivative of the carrying capacity with respect to quality multiplier is a combination of  $M_{DI}$  and  $M_{DD}$ :

$$\frac{\partial K}{\partial \lambda_{\text{quality}}} = -\frac{M_{DI}^2 \times a_{rec} \times S \times e^{M_{DI} \times \lambda_{\text{quality}} \times a_{rec}}}{M_{DD} \times (e^{M_{DI} \times \lambda_{\text{quality}} \times a_{rec}} - 1)^2} \quad (\text{eq. S4.6})$$

The value of this derivative according to combinations of  $M_{DD}$  and  $M_{DI}$  (Fig. S3.1.4.1) highlights that plaice differentiates from the three other species. Indeed, with a lower  $M_{DD}$  and a higher  $M_{DI}$  leading to a higher absolute (but negative) value of this derivative relative to the

other species, meaning a higher sensitivity of the carrying capacity of plaice to quality multiplier relative to the other species. By contrast, cuckoo ray and anchovy have higher  $M_{DD}$  and lower  $M_{DI}$  values, resulting in lower derivative values.

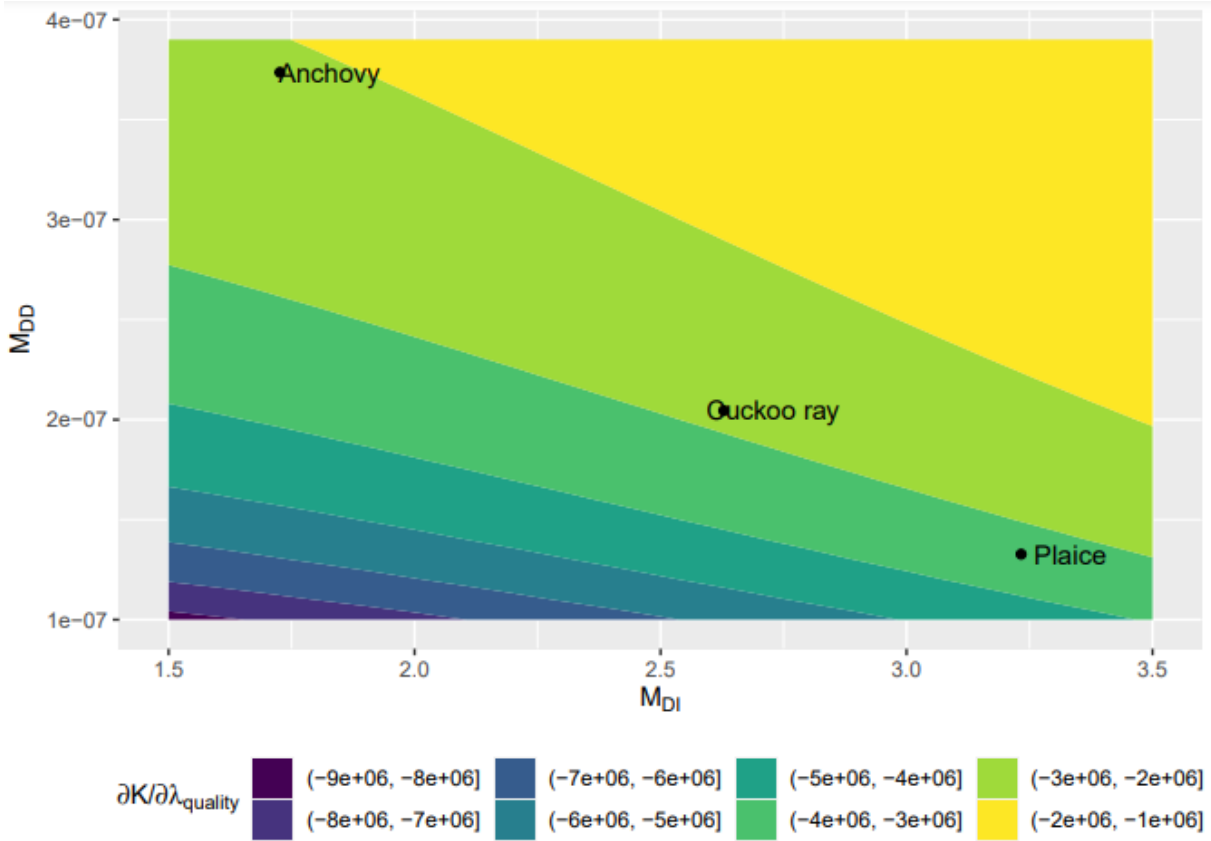


Figure S3.1.4.2: Value of the partial derivative of the carrying capacity with respect to quality multiplier in relation to density-dependent ( $M_{DD}$ ) and -independent ( $M_{DI}$ ) mortality rates. The points indicate where a specie lie in the ( $M_{DD}$ ,  $M_{DI}$ ) space.

We also compute the sensitivity of the steepness relative to habitat multiplier as  $\frac{1}{h} \times \frac{\partial h}{\partial \lambda_{quality}}$ :

$$\frac{1}{h} \times \frac{\partial h}{\partial \lambda_{quality}} = \frac{-4 \times M_{DI} \times a_{rec}}{4 + e^{-M_{DI} \times \lambda_{quality} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}} \quad (\text{eq. S4.7})$$

The value of this sensitivity  $\frac{1}{h} \times \frac{\partial h}{\partial \lambda_{quality}}$  according to combinations of  $M_{DI}$  and  $e^{-M_{larvae}} \times \bar{W}$  highlights that only a small number of combinations of low  $e^{-M_{larvae}} \times \bar{W}$  and large  $M_{DI}$  values will results in a strong response of  $h$ . Consequently, cuckoo ray displayed the highest derivative value while plaice and anchovy exhibited lower values.

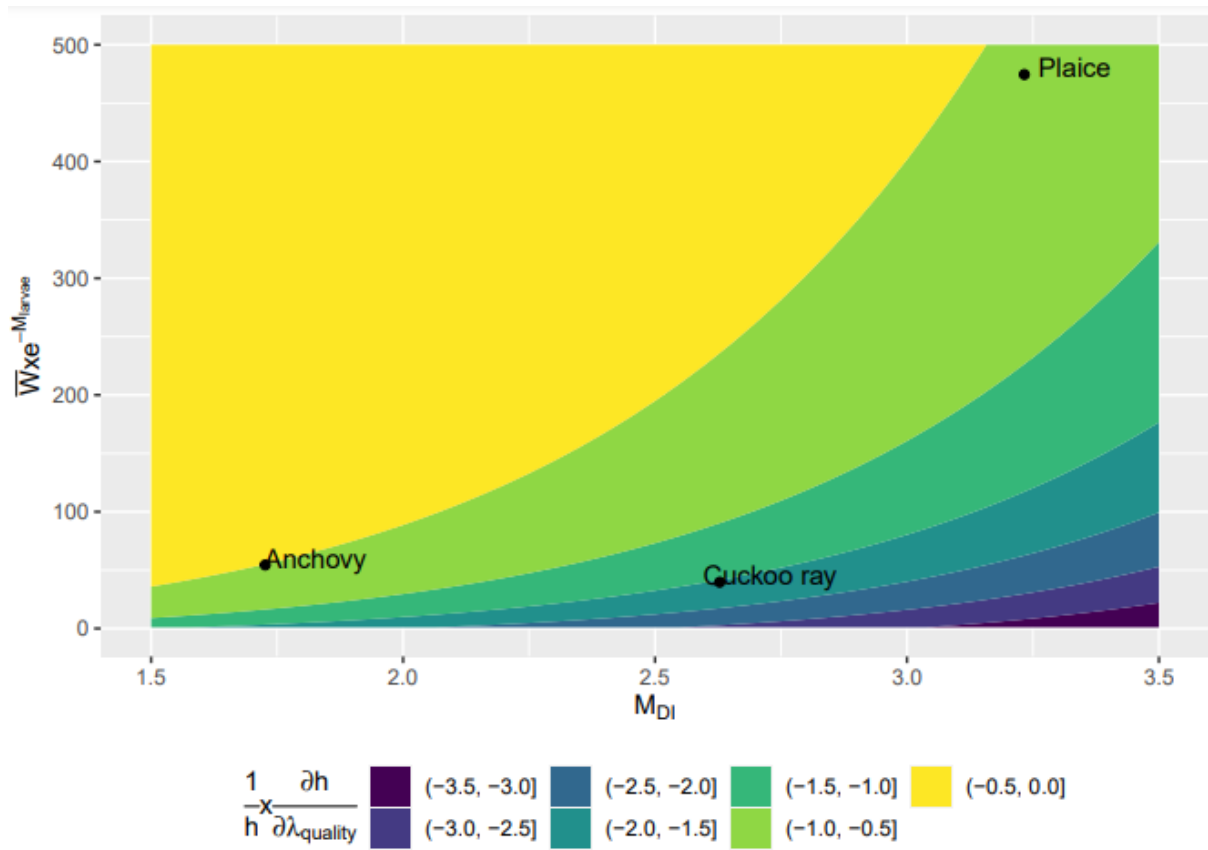


Figure S3.1.4.3: Value of the sensitivity of the steepness with respect to quality multiplier in relation to density-independent ( $M_{DI}$ ) mortality rate and number of eggs produced on average by an egg  $e^{-M_{larvae}} \times \bar{W}$ . The points indicate where a specie lie in the  $(M_{DI}, e^{-M_{larvae}} \times \bar{W})$  space.



7.2.5 Références Supp. Mat. Chapitre 3.1

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### 7.3 Annexes du chapitre 3.2

#### 7.3.1 Supp. Mat. 3.2.1: Age structured model

The description of this model comes from Champagnat et al., (sub.).

Population dynamics is simulated by a deterministic life cycle model structured by age ( $a$ ) with a year time step ( $y$ ).

Fish are supposed to recruit at age  $a_{rec}$ . For all ages classes  $a_{rec} < a < a_{max}$ , population abundance ( $N$ ) is described by:

$$\text{Eq. (A.1)} \quad N_{a+1,y+1} = N_{a,y} \times e^{-(M_{a,y}+F_{a,y})}$$

And for  $a = a_{max}$ , population abundance is described by:

$$\text{Eq. (A.2)} \quad N_{a_{max},y+1} = N_{a_{max},y} \times e^{-(M_{a_{max},y}+F_{a_{max},y})} + N_{a_{max}-1,y} \times e^{-(M_{a_{max}-1,y}+F_{a_{max}-1,y})}$$

with  $M$  and  $F$  the natural and fishing mortality rates, respectively.

Fishing mortality at age is defined as the product of selectivity at age and a maximum fishing mortality value:

$$F_{a,y} = sel_a \times F_y$$

with  $sel_a$  a logistic function of age specified for each stock.

Catches in weight are computed based on Baranov equation:

$$\text{Eq. (A.3)} \quad C_y = \sum_{a=a_{rec}}^{a_{max}} \frac{F_{a,y}}{F_{a,y}+M_{a,y}} \times N_{a,y} \times (1 - e^{-(F_{a,y}+M_{a,y})}) \times SW_{a,y}$$

with  $SW_{a,y}$  the stock weights at age, available in appendix B.

Spawning Stock Biomass (SSB) is computed according to the equation:

$$\text{Eq. (A.4)} \quad SSB_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times SW_a \times pf_a \times Mat_a$$

with  $SW_a$ , the stock weights at age,  $pf_a$  the female proportion, and  $Mat_a$  the maturity ogive, all available in appendix B.

The number of eggs spawned in year  $y$  is computed based on adult abundance:

$$\text{Eq. (A.5)} \quad \omega_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times Mat_a \times pf_a \times Fec_a$$

with  $Mat_a$  the probability of being mature,  $pf_a$  the female proportion and  $Fec_a$  the fecundity (number of eggs per female). All values used are available in appendix B.

Eggs are supposed to first survive to the larval drift with density-independent survival before settling in nursery areas. The larval mortality during larval drift,  $M_{larvae}$ , are available in appendix B.

The number of recruits for year  $y$  is computed with a Beverton-Holt relationship based on eggs numbers of the previous year:

$$\text{Eq. (A.6)} \quad N_{a_{rec},y} = \frac{4 \times h \times \omega_{y-1}}{\bar{W} \times (1-h) + \frac{4 \times h \times \omega_{y-1}}{K}}$$

with  $h$  the steepness,  $\bar{W}$  the number of eggs produced on average by a recruit during its lifetime in the absence of any fishing and  $K$  the carrying capacity of the nursery.

The number of eggs produced on average by a recruit during its lifetime in the absence of fishing,  $\bar{W}$ , is defined as:

$$\text{Eq. (A.7)} \quad \bar{W} = \sum_{a=a_{rec}}^{a_{max}} S_a \times Mat_a \times pf_a \times Fec_a$$

with  $S_a$  the cumulative survival at age  $a$  without fishing, as defined according to the equation:

$$\text{Eq. (A.8)} \quad S_a = \prod_{i=a_{rec}}^{a-1} e^{-M_i}$$

The parameters  $h$  and  $K$  of the Beverton-Holt relation are related to density-independent and density-dependent mortality ( $M^{di}$  and  $M^{dd}$  respectively, Quinn & Deriso, 1999) according to the equations:

$$\text{Eq. (A.9)} \quad h = \frac{e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}{4 + e^{-M^{di} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}$$

$$\text{Eq. (A.10)} \quad K = \lim_{\omega \rightarrow +\infty} N_{a_{rec}} = \frac{M^{di}}{M^{dd}} \times \frac{1}{e^{M^{di} \times a_{rec}} - 1} \times S$$

$M^{di}$  and  $M^{dd}$  can therefore be derived as:

$$\text{Eq. (A.11)} \quad M^{di} = -\log\left(\frac{4 \times h}{e^{-M_{larvae} \times \bar{W}} \times (1-h)}\right)$$

$$\text{Eq. (A.12)} \quad M^{dd} = \frac{M^{di}}{K \times (e^{M^{di}} - 1)}$$

### 7.3.2 Supp. Mat. 3.2.2: Data and equations to calculate fecundity and associated values for each species

The larval mortality rate during larval drift,  $M_{larvae}$ , was set to  $3 \times \log(10)$  for each species (Le Pape and Bonhommeau, 2015) so as the resulting survival  $e^{-M_{larvae}}$  is  $10^{-3}$ . For the female proportion ( $pf$ ) we assumed a value at 0.5 for each species. Other parameters and equations are species-specific and are presented in the following tables with their references.

Table S3.2.2.1. Sole (*Solea solea*)

Parameters	Value	Source
Stock weights-at-age ( $SW_a$ )	Matrix	ICES, 2021a
Maturity ogive ( $Mat$ )	Age 1: 0; Age 2: 0.53; Age 3: 0.92; Age 4: 0.96; Age 5: 0.97; Age 6: 1; Age 7: 1; Age 8: 1; Age 9: 1; Age 10: 1; Age 11: 1	ICES, 2021a
Cumulative survival to age ( $S_a$ )	Age 1: 1; Age 2: 0.905; Age 3: 0.819; Age 4: 0.741; Age 5: 0.670; Age 6: 0.606; Age 7: 0.549; Age 8: 0.497; Age 9: 0.449; Age 10: 0.407; Age 11: 0.368	Computed from Eq. (A.9)
Fecundity ( $Fec$ )	$e^{(5.619+1.17 \times \log(SW_a \times 1000))}$	Anon, 1992
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ( $\bar{W}$ )	732502.8	Computed from Eq. (A.8)

Table S3.2.2.2 Plaice (*Pleuronectes platessa*)

Parameters	Value	Source
Stock weights-at-age ( $SW_a$ )	Matrix	ICES, 2021a
Maturity ogive ( $Mat$ )	Age 1: 0; Age 2: 0.15; Age 3: 0.53; Age 4: 0.96; Age 5: 1; Age 6: 1; Age 7: 1	ICES, 2021a
Cumulative survival to age ( $S_a$ )	Age 1: 1, Age 2: 0.702; Age 3: 0.514; Age 4: 0.383; Age 5: 0.291; Age 6: 0.225; Age 7: 0.175	Computed from Eq. (A.9)
Length at age ( $L_a$ )	$71.65 \times (1 - e^{(-0.23 \times (a+0.83)})$	ICES, 2021a
Fecundity ( $Fec$ )	$2.33 \times L_a^{3.10}$	ICES, 2021a
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ( $\bar{W}$ )	323551.1	Computed from Eq. (A.8)

Table S.3.2.2.3. Whiting (*Merlangius merlangus*)

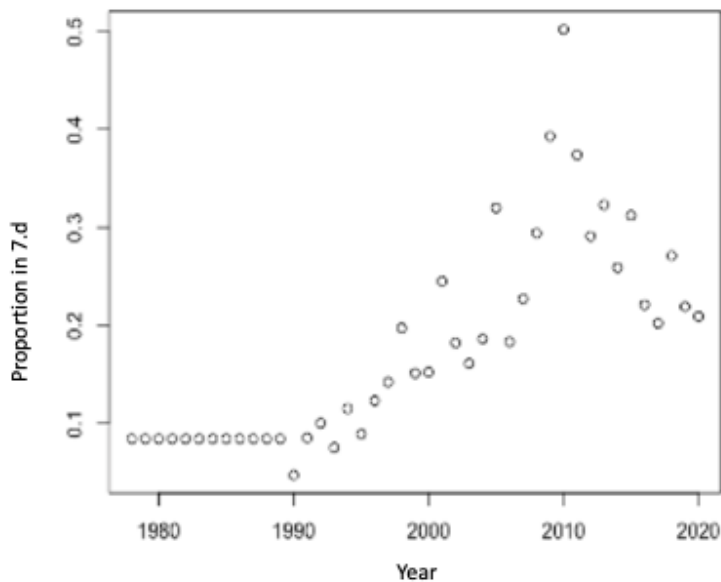
Parameters	Value	Source
Stock weights-at-age ( $SW_a$ )	Matrix	ICES, 2021a
Maturity ogive ( $Mat$ )	Age 0: 0; Age 1: 0.262; Age 2: 0.807; Age 3: 0.973; Age 4: 0.995; Age 5: 0.999; Age 6: 1; Age 7: 1; Age 8: 1	Mean from ICES, 2021a
Length at age ( $L_a$ )	$\left(\frac{SW_a \times 1000}{0.00621}\right)^{\frac{1}{3.10286}}$	Dorel, 1986
Cumulative survival to age ( $S_a$ )	Age 0: 1; Age 1: 0.141; Age 2: 0.039; Age 3: 0.020; Age 4: 0.012; Age 5: 0.008; Age 6: 0.005; Age 7: 0.003; Age 8: 0.002	Computed from Eq. (A.9)
Fecundity ( $Fec$ )	$0.0065 \times L_a^{5.28}$	Mestorff, 1959
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ( $\bar{W}$ )	15783.5	Computed from Eq. (A.8)

Table S3.2.2.4. Seabass (*Dicentrarchus labrax*)

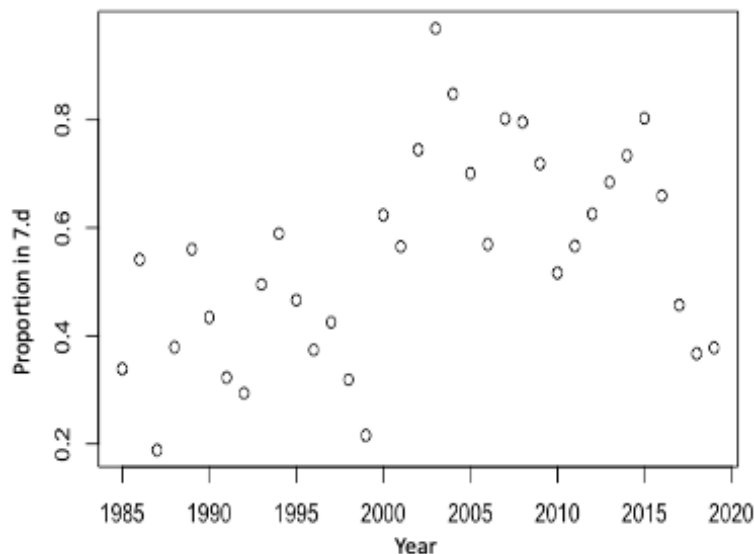
Parameters	Value	Source
Stock weights-at-age ( $SW_a$ )	Age 0: 0.003; Age 1: 0.024; Age 2: 0.097; Age 3: 0.210; Age 4: 0.369; Age 5: 0.571; Age 6: 0.807; Age 7: 1.071; Age 8: 1.357; Age 9: 1.655; Age 10: 1.962; Age 11: 2.272; Age 12: 2.579; Age 13: 2.882; Age 14: 3.176; Age 15: 3.460; Age 16: 4.176	ICES, 2021b
Maturity ogive ( $Mat$ )	Age 0: 0; Age 1: 0; Age 2: 0; Age 3: 0; Age 4: 0.186; Age 5: 0.419; Age 6: 0.638; Age 7: 0.792; Age 8: 0.885; Age 9: 0.937; Age 10: 0.965; Age 11: 0.980; Age 12: 0.989; Age 13: 0.993; Age 14: 0.996; Age 15: 0.998; Age 16: 0.998	ICES, 2021b
Cumulative survival to age ( $S_a$ )	Age 0: 1; Age 1: 0.787; Age 2: 0.619; Age 3: 0.487; Age 4: 0.383; Age 5: 0.301; Age 6: 0.237; Age 7: 0.186; Age 8: 0.147; Age 9: 0.115; Age 10: 0.091; Age 11: 0.071; Age 12: 0.056; Age 13: 0.044; Age 14: 0.035; Age 15: 0.027; Age 16: 0.021	Computed from Eq. (A.9)
Fecundity ( $Fec$ )	$557.12 \times SW_a \times 1000 - 226020$	Mayer et al., 1988
Number of eggs produced by a recruit during its lifetime in the absence of any fishing ( $\bar{W}$ )	332645.7	Computed from Eq. (A.8)

### 7.3.3 Supp. Mat. 3.2.3: Proportion of catches in division 7.d for whiting (4 and 7.d) and seabass (4.b–c, 7.a, and 7.d–h)

The SSB and catches for whiting (ICES, 2021a) and seabass (ICES, 2021b) were derived from stock assessments covering a wider area. They were scaled to the EEC proportionally to the average proportion of landings in division 7.d with respect to total landing. Proportions of catches in division 7.d are presented for whiting (figure C.1) and for seabass (figure C.2).



*Figure S3.2.3.1. Proportion of catches in division 7.d for whiting (ICES, 2021a). Landings data by area were not available for the first twelve years of the stock assessment period. For this period, the proportion of catches was calculated as the average proportion for the first 5 years with spatialised data.*



*Figure S3.2.3.2. Proportion of catches in division 7.d for seabass (ICES, 2021b)*



### 7.3.4 Supp. Mat. 3.2.4. Estimation of nursery surface losses

The habitat surface scenario was based on estimation of surface losses since 1870, derived from bathymetry data in three coastal sectors of the French EEC coastline in 1870 (Bay of Veys, Seine Estuary, Somme and Canche) available on the EMODnet website. To build bathymetric maps from these data, the sampled points were transformed into maps using a universal kriging method. In a first step, a semi-variogram was constructed with a spherical model, without nugget effect. Then, spatial interpolation by kriging was realised on the area covered by the sampling.

These maps in 1870 were compared with the 2020 bathymetry map, directly provided by EMODnet, on the same spatial coverage. The loss of habitats above a bathymetry of 5 meters, including intertidal area, was then estimated in each sector. This limit was chosen because it integrates almost all of surfaces loss in CE nursery areas (Rochette et al., 2010; Stamp et al., 2022).

The loss of the surface areas above 5 m between 1870 and 2020 was estimated to 26.86% for the Bay of Veys, 66.42% for the seine estuary, and 19.56% for the bay of Somme and Canche estuary, (figure D.1). These estimates were used to build a surface restoration scenario for the shallow habitats of the Eastern Channel, on average these habitats have lost 37.61% of their area.

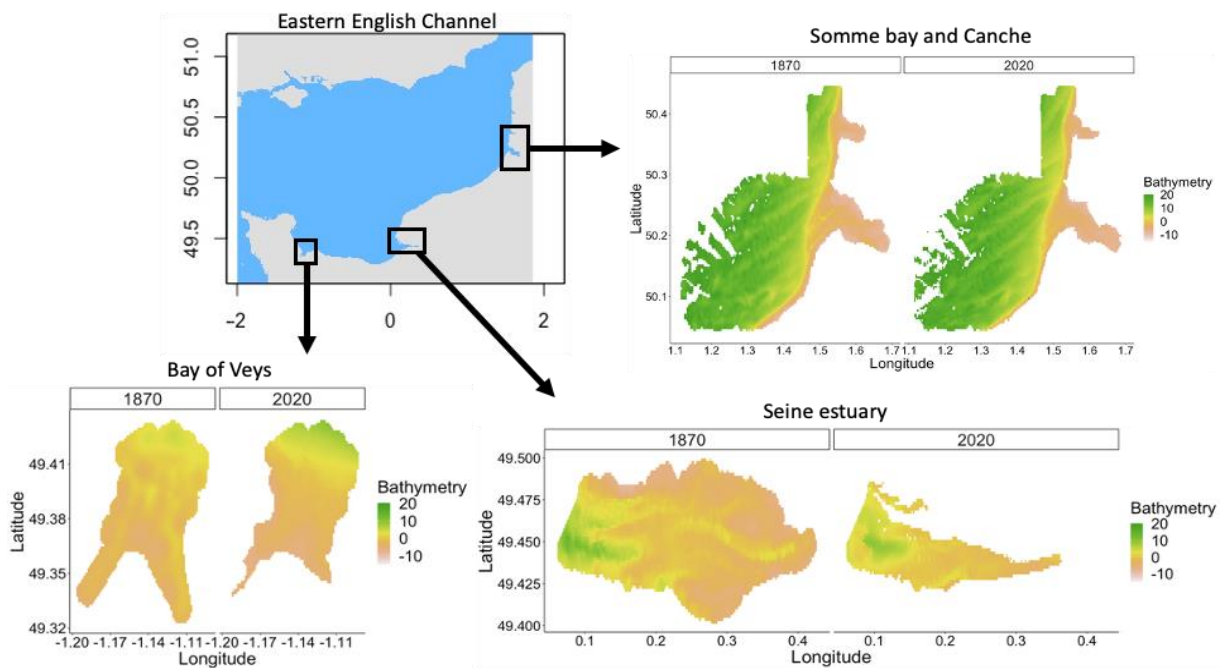


Figure 3.2.4.1. Habitat loss in the three areas of interest since 1870.

### 7.3.5 Supp. Mat. 3.2.5: Estimation of the species-specific proportion of juvenile concentrated above the 5m limit of bathymetry

In a first step, nursery maps for each species were extracted from the Sextant website (references of each map are given on Fig. 3.2.5.1-4), and a fine-scale bathymetric map of the EEC was downloaded from the EMODnet website. The resolution of the bathymetry map was first degraded, with bilinear interpolation method, to match that of the nursery. The species-specific proportion of juveniles present in habitats above 5 meters was estimated from both bathymetric and nursery maps. This proportion for sole, plaice, whiting and seabass is 49.7, 16.7, 4.1, and 80.2 respectively.

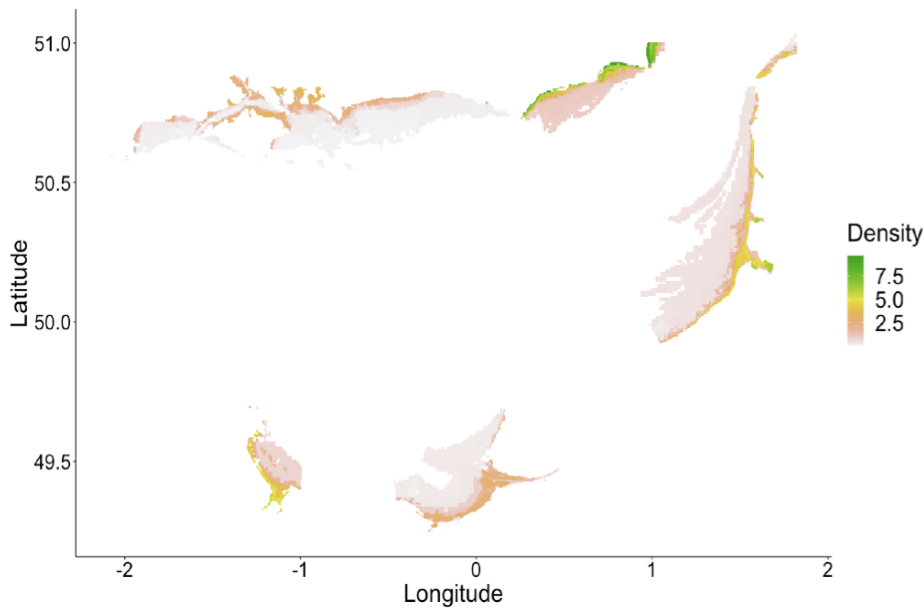


Figure 3.2.5.1. Map of Eastern English Channel nursery areas for sole (in juveniles/m<sup>2</sup>). Source: Rochette et al., 2010. (Modified)

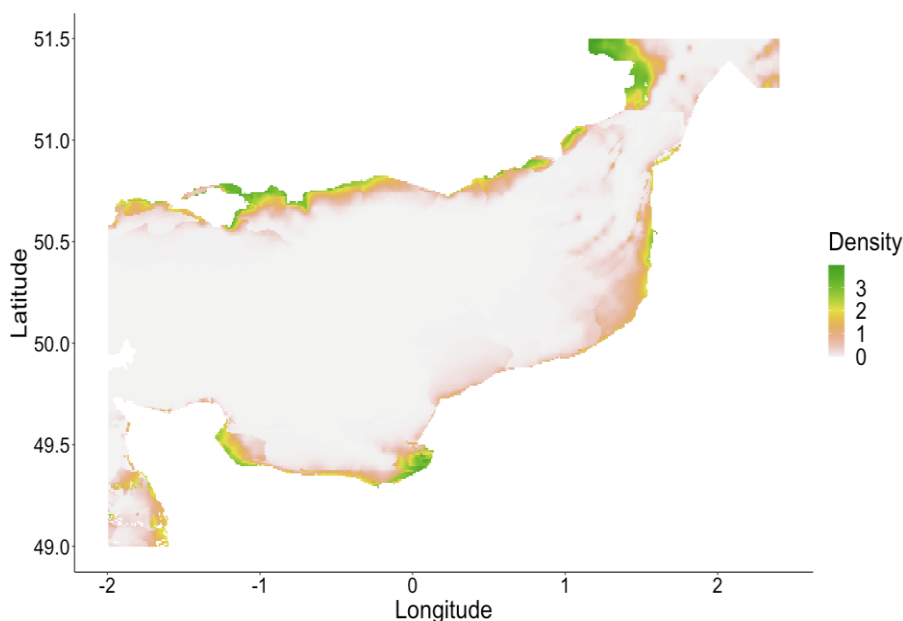


Figure 3.2.5.2. Map of Eastern English Channel nursery areas for plaice (in juveniles/m<sup>2</sup>). Source: Carpentier et al., 2009. (Modified)

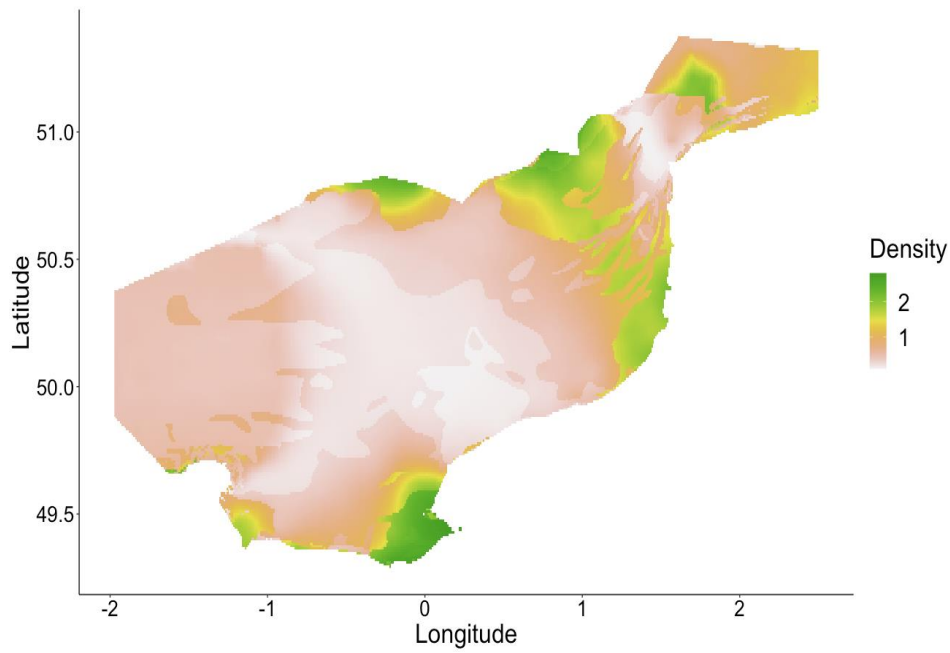


Figure S3.2.5.3. Map of Eastern English Channel nursery areas for whiting (in juveniles/m<sup>2</sup>). Source: Carpentier et al., 2009. (Modified)

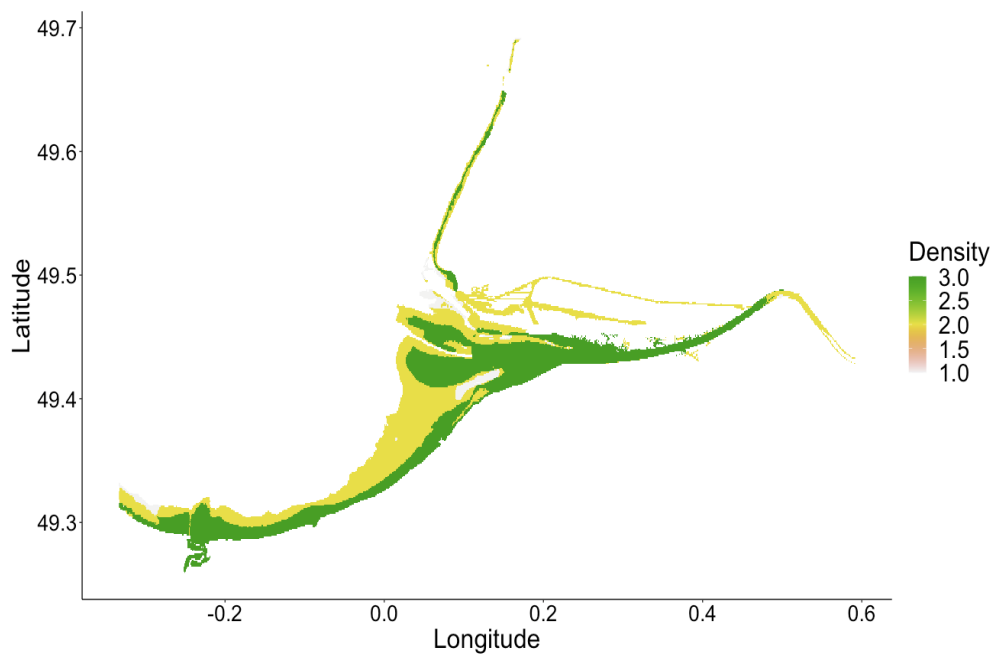


Figure S3.2.5.4. Map of Seine nursery areas for seabass (in juveniles/m<sup>2</sup>). Used as an estimator of the distribution of juveniles across the EEC nurseries. Source : Bacq et al., 2013. (Modified)

7.3.6 Supp. Mat. 3.2.6: Complementary equations for parameterization of quality multipliers

The density independent mortality ( $M^{di}$ ) is described in equation F.1:

$$\text{Eq. (F.1)} \quad M^{di} = \frac{-\log\left(\frac{4 \times h}{e^{-M_{larvae} \times \bar{W} \times (1-h)}}\right)}{\text{delta}T}$$

with  $\text{delta}T = 1$

The density dependent mortality ( $M^{dd}$ ) is dependent to  $M^{di}$  according to equation F.2:

$$\text{Eq. (F.2)} \quad M^{dd} = \frac{M^{di}}{K \times e^{(M^{di} \times \text{delta}T) - 1}}$$

The values of  $M^{di}$  and  $M^{dd}$  calculated from the parameters  $h$ ,  $K$  and the value of  $M_{larvae}$  and  $\bar{W}$ , allows to calculate a multiplier to simulate a quality restoration.

7.3.7 Supp. Mat.3.2.7: Fit plot for each species

The SSB and catches estimates from our model are presented and compared with the ICES data (ICES, 2021ab) for each species.

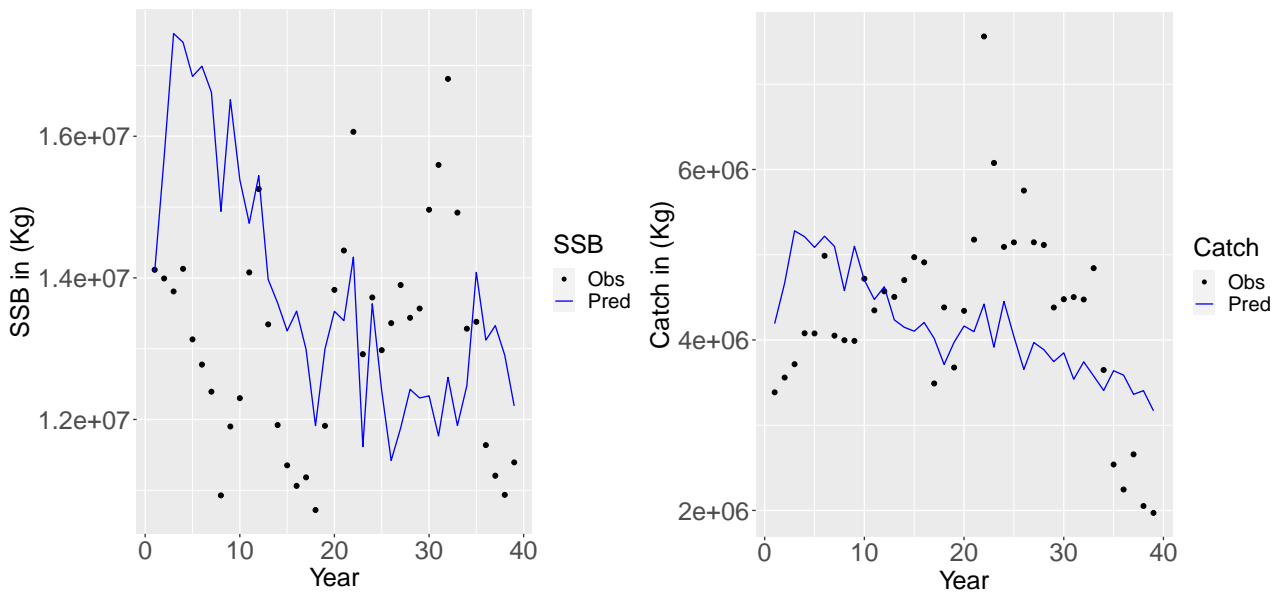


Figure 3.2.7.1. Sole case study. Fit between data (Obs black points) and model prediction (Pred blue line) for SSB (left) and catch (right).

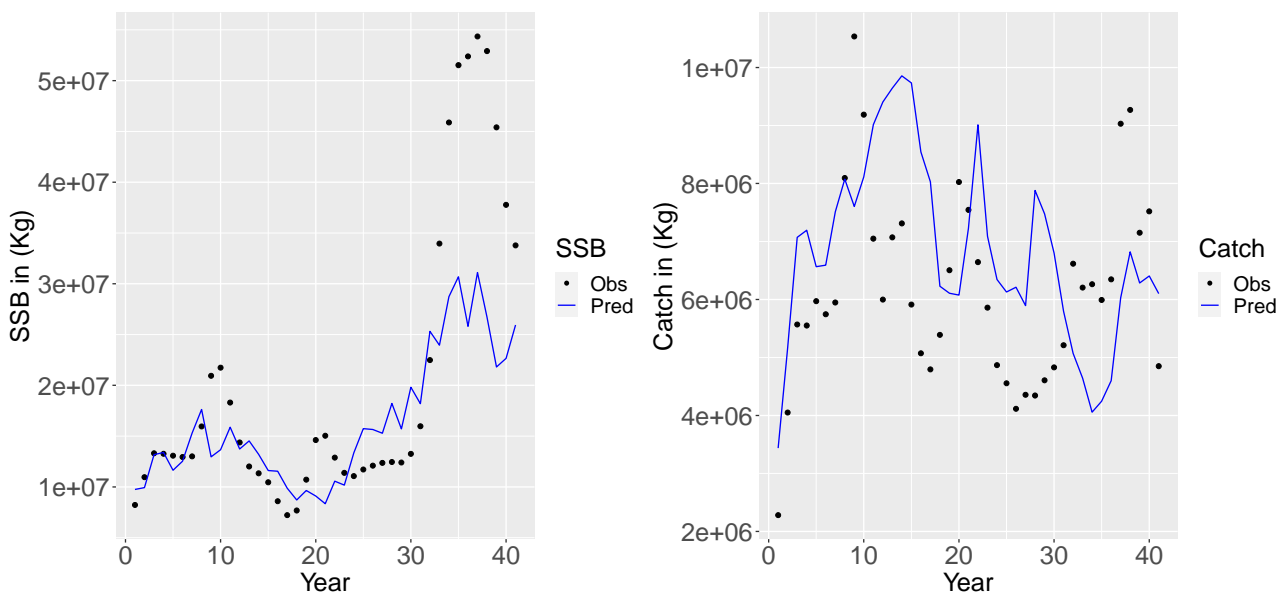


Figure S3.2.7.2. Plaice case study. Fit between data (Obs black points) and model prediction (Pred blue line) for SSB (left) and catch (right).

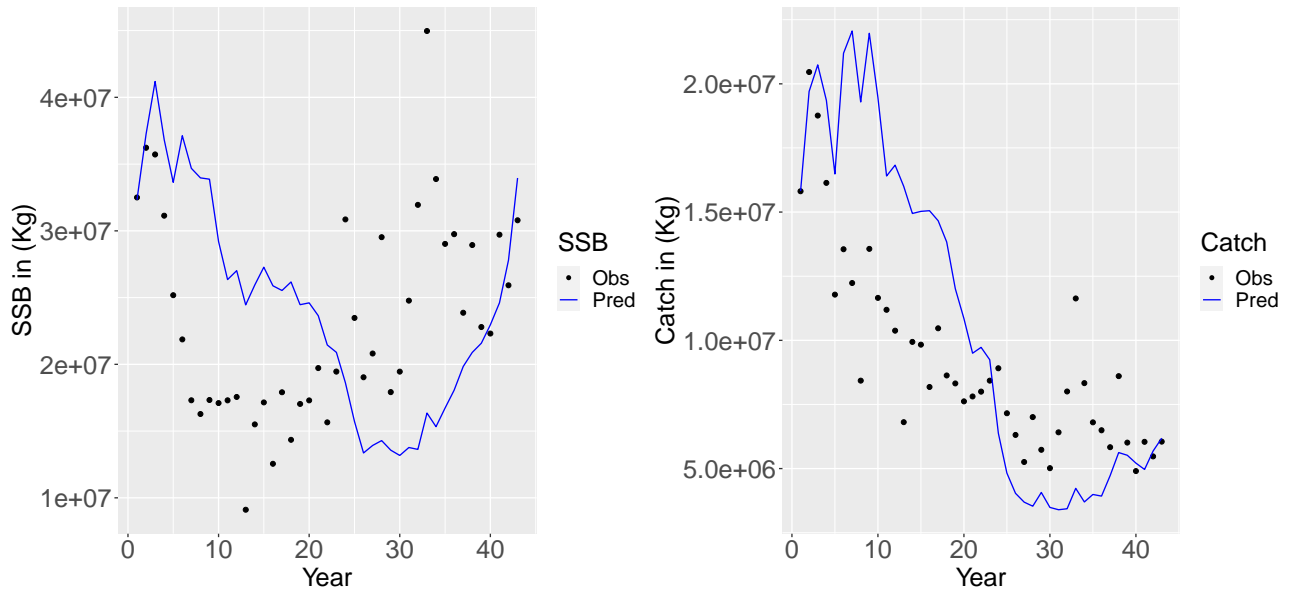


Figure S3.2.7.3. Whiting case study. Fit between data (Obs black points) and model prediction (Pred blue line) for SSB (left) and catch (right).



Figure S3.2.7.4. Seabass case study. Fit between data (Obs black points) and model prediction (Pred blue line) for SSB (left) and catch (right).

7.3.8 Supp. Mat. 3.2.8: Comparison between  $K$  value, reference points, MSY related indicators from the estimation of our model and ICES prediction

Values of reference points and MSY related indicators from estimation of our model as compared to the ICES (ICES, 2021ab) prediction.

Table S3.2.8.1.  $K$  values, reference points, MSY related indicators.

	$K^*$ (in number of juveniles)	$\frac{SSB_{MSY}^*}{SSB_0}$	$F_{MSY}$	Average SSB (in Kg) (ICES values)	Average Catches (in Kg) (ICES values)
Sole	$4.0 \times 10^7$	0.25	0.16 (ICES=0.19)	$1.4 \times 10^7$ ( $1.3 \times 10^7$ )	$4.2 \times 10^6$ ( $4.3 \times 10^6$ )
Plaice	$7.1 \times 10^7$	0.21	0.29 (ICES= 0.25)	$1.6 \times 10^7$ ( $2 \times 10^7$ )	$6.8 \times 10^6$ ( $6.1 \times 10^6$ )
Whiting	$5.3 \times 10^9$	0.30	0.39 (ICES=0.37)	$2.4 \times 10^7$ ( $2.3 \times 10^7$ )	$11 \times 10^6$ ( $9.2 \times 10^6$ )
Seabass	$1.1 \times 10^7$	0.28	0.15 (ICES=0.17)	$5.6 \times 10^6$ ( $5.8 \times 10^6$ )	$1.2 \times 10^6$ ( $1.4 \times 10^6$ )

\* not available in the ICES

7.3.9 Supp. Mat. 3.2.9: Production curves for each species

The model was used to simulate equilibrium catch curves obtained under different scenarios of nursery quality and surface restoration for the four species.

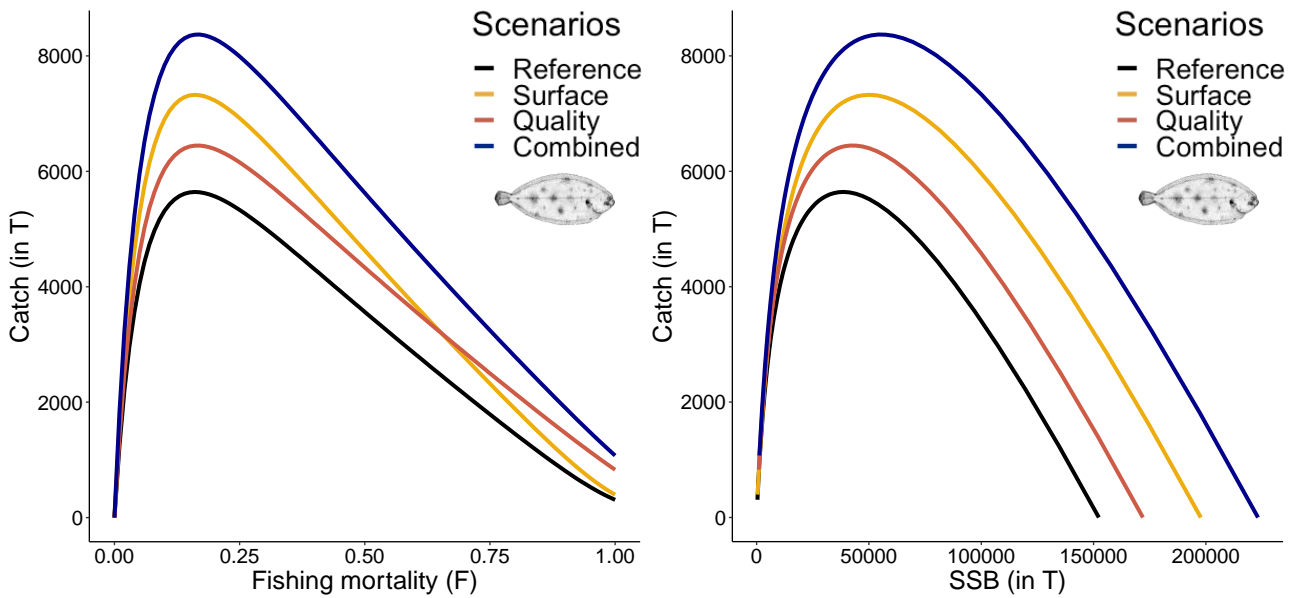


Figure S3.2.9.1. Sole case study. Production curves according to habitat scenarios as function of fishing mortality or SSB.

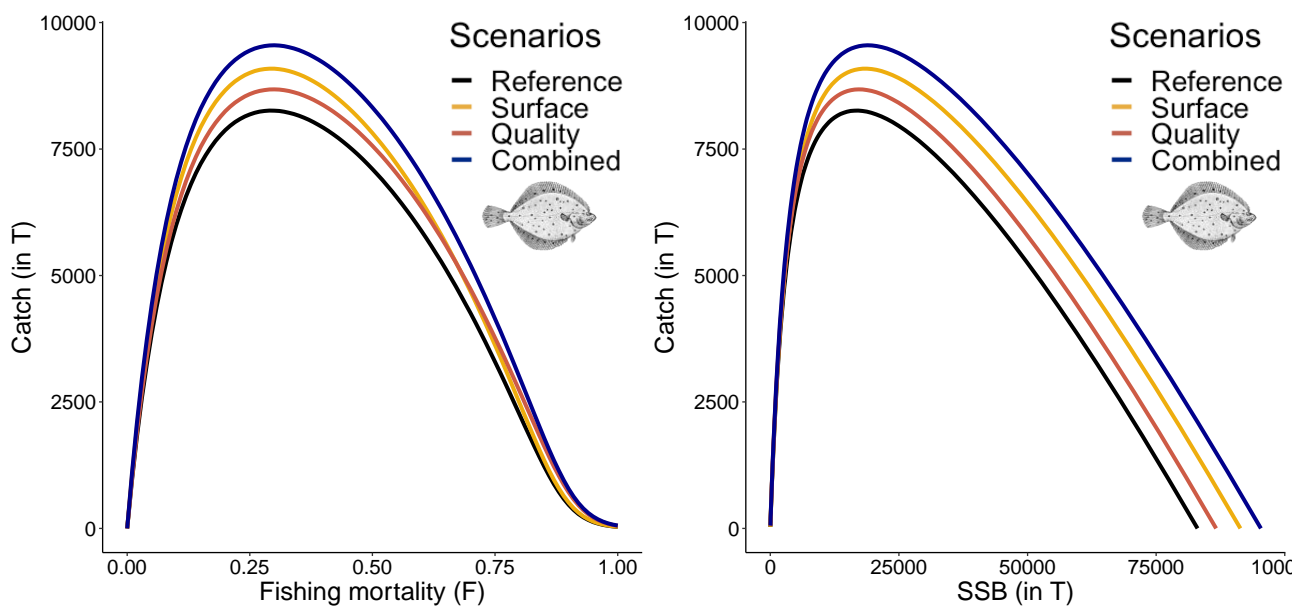


Figure S3.2.9.2. Plaice case study. Production curves according to habitat scenarios as function of fishing mortality or SSB.



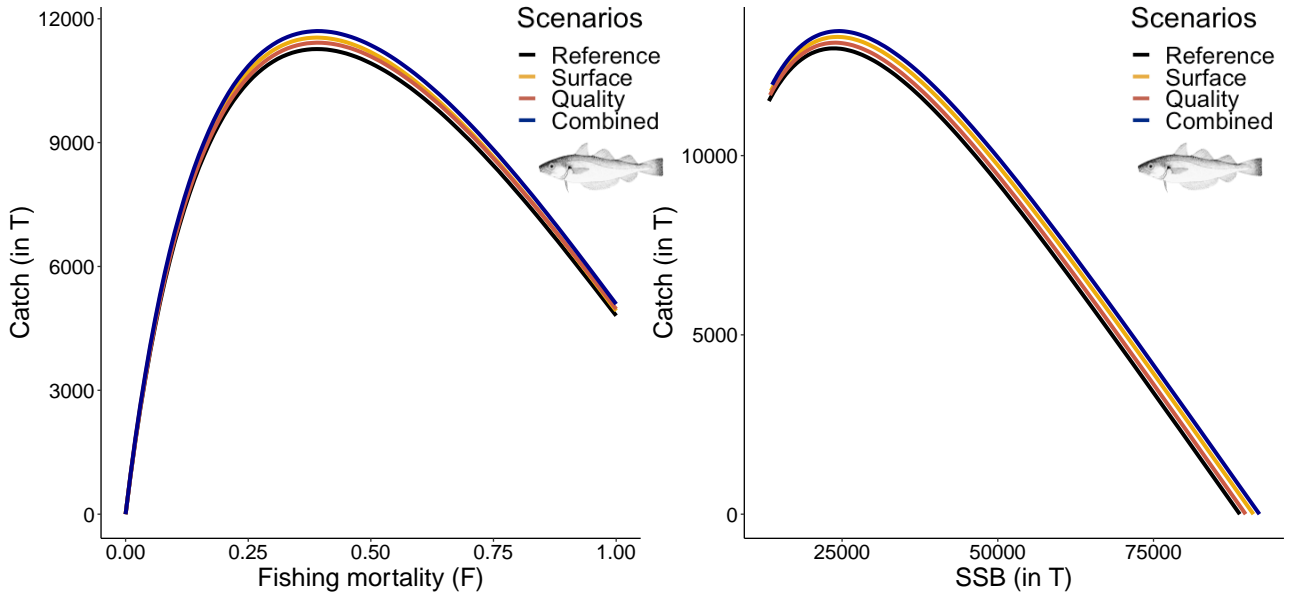


Figure S3.2.9.3. Whiting case study. Production curves according to habitat scenarios as function of fishing mortality or SSB.

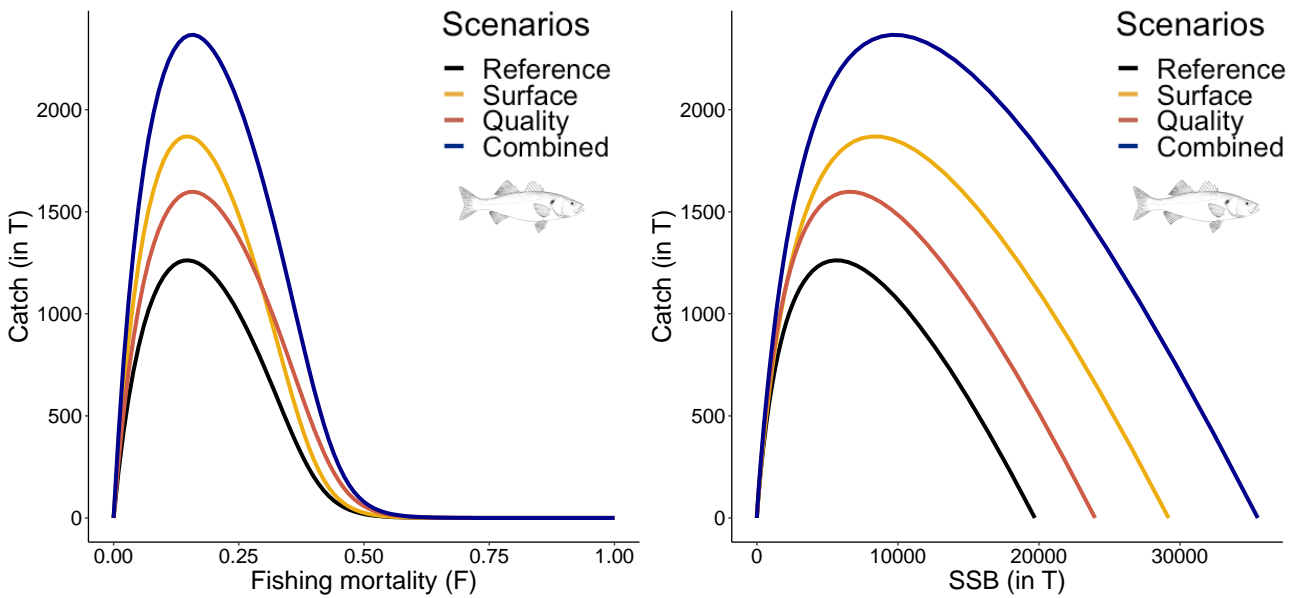


Figure S.3.2.9.4. Seabass case study. Production curves according to habitat scenarios as function of fishing mortality or SSB.

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## 7.4 Annexes du chapitre 4

### 7.4.1 Supp. Mat. 4.1: Age structured model based on life history data

The description of this model is based on (Champagnat et al., sub.).

Population dynamics is simulated by a deterministic life cycle model structured by age ( $a$  subscript) and stage with a year time step ( $y$  subscript).

Fish are supposed to recruit at age  $a_{rec}$ . For all ages classes  $a_{rec} < a \leq a_{max}$ , population abundance ( $N$ ) is described by:

$$N_{a+1,y+1} = N_{a,y} \times e^{-(M+F_{a,y})} \quad (\text{eq. S1.1})$$

with  $M$  and  $F$  the natural and fishing mortality rates, respectively.

Fishing mortality at age is defined as the product of selectivity at age and a maximum fishing mortality value:  $F_{a,y} = sel_a \times F_y$ .

For simplicity we assumed a knife edge formulation for maturity and selectivity:

$$sel_a = mat_a = \begin{cases} 0 & \text{if } a < a_{mat} \\ 1 & \text{if } a \geq a_{mat} \end{cases} \quad (\text{eq S1.2})$$

thus supposing that the age fish start to be caught by the fishery is also the age at maturity.

Catches in weight are computed based on Baranov equation:

$$C_y = \sum_{a_{mat}}^{a_{max}} N_{a,y} \times \frac{F_{a,y}}{F_{a,y}+M} \times (1 - e^{-(F_{a,y}+M)}) \times W_a \quad (\text{eq. S1.3})$$

Weight at age ( $W_a$ ) is then computed as a simple power function of length at a given age:

$$W_a = b \times L_a^c \quad (\text{eq. S1.4})$$

with  $b$  and  $c$  being the proportion and shape parameters estimated with a hierarchical Bayesian model (Froese et al, 2014).

Length at age is computed based on Von Bertalanffy equation:

$$L_a = L_{inf} \times (1 - e^{-k \times (a - a_0)}) \quad (\text{eq. S1.5})$$

with  $L_{inf}$  the asymptotic length and  $k$  the growth coefficient both extracted from FishLife.  $a_0$  is the theoretical age at size 0 which was assumed to be equals to -0.1 (Thorson, 2020).

Stock spawning biomass is computed as:

$$SSB_y = \sum_{a=a_{rec}}^{a_{max}} N_{a,y} \times W_a \times pfa \times Mat_a \quad (\text{eq. S1.6})$$

with  $W_a$ , the stock weights at age,  $pfa$  the female proportion, and  $Mat_a$  the maturity ogive.

The number of eggs spawned any year  $y$  is computed based on adult abundance:

$$\omega_y = \sum_a N_{a,y} \times e^{-ts(M_{a,y}+F_{a,y})} \times pfa \times mat_a \times fec_a \quad (\text{eq. S1.7})$$

with  $mat_a$  the probability of being mature as defined in equation S1.2,  $fec_a$  the fecundity (number of eggs per female),  $pfa$  is the female proportion set at 0.5 for all age (time invariant variables).  $ts$  is a time scaling factor considering the mortality happening before spawning, it was set similarly for all species at 0.27.

Eggs are supposed to first survive to the larval drift with density-independent survival  $e^{-M_{larvae}}$  before settling in the nurseries area where they suffer density dependent mortality before recruiting. The larval mortality during larval drift was set at  $10^3$  for plaice and herring fish and  $10^5$  for cod (Le Pape & Bonhommeau, 2015).

The age at recruitment,  $a_{rec}$ , was set a 1 for all species, which implies a hypothesis of density dependent processes impacting only the survival from larval to age 1. The number of recruits for year  $y$  is computed with a Beverton-Holt relationship based on eggs numbers of the previous year:

$$N_{a_{rec},y} = \frac{e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \omega_{y-a_{rec}}}{1 + \frac{1}{S} \times \frac{M_{DD}}{M_{DI}} \times (e^{M_{DI} \times a_{rec}} - 1) \times e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae}} \times \omega_{y-a_{rec}}} \quad (\text{eq. S1.8})$$

Equation S1.8 is a logistic Beverton-Holt relationship (Quinn & Deriso, 1999) parameterised in terms of instantaneous mortality rates  $M_{DD}$  and  $M_{DI}$ , and the total surface area of the nursery  $S$ . It can be reparametrised in terms of steepness  $h$  and its asymptote,  $K$  interpreted as the carrying capacity of the nursery (the maximum number of juveniles that a nursery area can produce; (Del Monte-Luna et al., 2004). Under the hypothesis that habitat quality is homogeneous in space,  $K$  writes as the product of a carrying capacity per unit of surface  $K^*$ , that denotes the quality of habitat (and that is function of the rates  $M_{DI}$  and  $M_{DD}$ ) and  $S$  the surface area of the nursery. Hence equation S1.8 can also be written as:

$$N_{a_{rec},y} = \frac{4h \times \omega_{y-a_{rec}}}{\bar{W}(1-h) + \frac{1}{S} \times \frac{4h}{K^*} \times \omega_{y-a_{rec}}} \quad (\text{eq. S1.9})$$

The number of eggs produced on average by a recruit during its lifetime in the absence of any fishing,  $\bar{W}$ , is defined as:

$$\bar{W} = \sum_{a=a_{rec}+1}^{a_{max}} S_a \times p_{f_a} \times p_{mat,a} \times fec_a \quad (\text{eq. S1.9})$$

with  $S_a$  the cumulative survival to age  $a$  as:

$$S_a = \prod_{i=a_{rec}}^{a-1} e^{-M_i} \quad (\text{eq. S1.10})$$

The parameters  $h$  and  $K$  of the Beverton-Holt relation are related to density-independent and density-dependent mortality ( $M_{DI}$  and  $M_{DD}$  respectively), (Quinn and Deriso, 1999) according to the equations:

$$K^* = \frac{M_{DI}}{M_{DD}} \times \frac{1}{(e^{M_{DI} \times a_{rec}} - 1)} \quad (\text{eq. S1.11})$$

$$h = \frac{e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}}{4 + e^{-M_{DI} \times a_{rec}} \times e^{-M_{larvae} \times \bar{W}}} \quad (\text{eq. S1.12})$$

#### 7.4.2 Supp. Mat. 4.2: Model parametrisation for each species

*Table S4.2.1: Equations for computation of length at age ( $L_a$ ), weight at age ( $W_a$ ), and fecundity at age ( $fec_a$ ) for the three-example species.*

<b>Species</b>	<b>Length at age (Thorson 2020)</b>	<b>Weight at length (Froese et al, 2014)</b>	<b>Fecundity at age</b>
<b>Atlantic cod</b>	$104.5 \times (1 - e^{-0.17(a+0.1)})$	$0.0069 \times L_a^{3.08}$	$7.13 \times L_a^{3.03}$ (Chrzan, 1949)
<b>Atlantic herring</b>	$30.4 \times (1 - e^{-0.34(a+0.1)})$	$0.0056 \times L_a^{3.09}$	$3.41 \times L_a^{2.9}$ (Raid et al., 2010)
<b>European plaice</b>	$52.7 \times (1 - e^{-0.14(a+0.1)})$	$0.0081 \times L_a^{3.05}$	$2.33 \times L_a^{3.10}$ (Carpentier et al., 2009)

7.4.3 Références Supp. Mat Chapitre 4

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**Titre :** Modéliser l'impact des pressions anthropiques au niveau des habitats halieutiques sur la dynamique des populations de poissons marins exploités.

**Mots clés :** Modèle de population, Zone fonctionnelle halieutique, Nourriceries, Frayères, Dégradation/Restauration côtière

**Résumé :** Les nourriceries et frayères sont des zones fonctionnelles halieutiques d'importance (ZFHI) qui abritent des phases clés du cycle de vie des poissons marins. Ces ZFHI subissent de multiples pressions anthropiques dont l'impact sur la dynamique des populations est rarement quantifié.

Cette thèse vise à combler ces lacunes par une approche de modélisation de dynamique de population structurée en âge et en stades, où les phases critiques du cycle de vie sur les ZFHI sont explicitement représentées. Dans une première partie, le cas d'étude précis de la sole commune en Manche Est est examiné par une approche statistique hiérarchique bayésienne. Dans une deuxième phase, un modèle de population générique est développé pour représenter des populations de poissons aux histoires de vie

contrastées. Le modèle intègre une relation stock-recrutement paramétrée en fonction de la qualité et de la quantité des habitats juvéniles. Cette approche est d'abord utilisée pour mettre en évidence l'impact de scénarios de dégradation/restauration de surface et de qualité des nourriceries sur la dynamique des populations, et la sensibilité des réponses aux variations interspécifiques des paramètres démographiques. Puis, il est appliqué pour évaluer le bénéfice de la restauration des nourriceries estuariennes pour quatre espèces commerciales de Manche Est. Finalement le modèle est étendu pour intégrer l'impact de pressions anthropiques au niveau des frayères. Les hypothèses et limites des approches sont discutées, tout comme les perspectives d'utilisation du cadre générique et son intérêt en appui à la gestion.

**Title:** Modelling the impact of anthropogenic pressures on essential fish habitats for population dynamics of marine exploited fish.

**Keywords:** Population model, Fish habitat, Nurseries, Spawning grounds, Coastal degradation/restoration.

**Abstract:** Spawning and juvenile habitats are Critical Essential Fish Habitats (CEFH) that support key phases of the life cycle, when fish aggregate on restricted areas. These CEFH face numerous anthropogenic pressures that impact fish locally. Yet, these impacts are poorly quantified at population scale.

This PhD aims to fill this knowledge gap using age- and stage-structured modelling approaches, with explicit representation of the critical life stages on CEFH. A first approach aims to assess the impact of Seine estuary restoration for the common sole in the Eastern English Channel. It uses a hierarchical Bayesian modelling framework integrating a great amount of data and expertise to perform simulations of juvenile habitat restoration. The second one develops a generic mechanistic model to represent marine fish population with contrasted

fish population with contrasted life histories. It integrates a comprehensive steepness-based parameterization of the stock-recruitment relationship that directly depends upon juvenile habitat quality and surface area. This model is used to explore population response to juvenile habitat degradation/restoration and its sensitivity to interspecific variability in demographic rates. Then the approach is applied to assess the potential impact of restoring estuarine nursery grounds for four species of main fisheries interest in the Eastern English Channel. Finally, the model is extended to integrate anthropogenic pressures affecting spawning grounds. The main hypothesis and limits of the approaches are discussed; this outlined the large venues of the generic model, for both further scientific investigation and help for management.