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# Modélisation du cycle de vie des ressources marines exploitées : une approche intégrée pour quantifier les effets relatifs des différentes pressions anthropiques et environnementales. Application à la sole commune de Manche Est

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# Avant-propos

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# Résumé

Les populations de poissons marins exploitées sont soumises à des pressions multiples d'origines humaines ou environnementales. L'impact de l'Homme sur ces ressources halieutiques ne se limite pas aux effets de la pêche ; la dégradation des habitats ainsi que le changement global affectent les espèces à tous les stades de leur cycle de vie. Ces effets se conjuguent à ceux de l'exploitation halieutique et perturbent la structure et le fonctionnement des écosystèmes et des populations. Il est primordial, en vue de la restauration ou du maintien du bon état des écosystèmes en accord avec les objectifs de la directive cadre européenne « stratégie pour le milieu marin », de pouvoir appréhender ces pressions multiples et de quantifier leurs impacts respectifs sur le renouvellement des ressources marines exploitées. Plus particulièrement, dans le cas des espèces de poissons marins nourriceries-dépendantes faisant l'objet de cette thèse, les conditions hydroclimatiques déterminent la survie des premiers stades (œufs puis larves). La qualité et la disponibilité des nourriceries vont ensuite impacter la survie des stades juvéniles, déterminant la capacité d'accueil de ces habitats essentiels, conditionnant *in fine* la taille maximale des populations. Enfin, la pêche cible principalement les individus adultes. Cette thèse a pour objectif d'analyser la dynamique de population de ces espèces par une approche de modélisation du cycle de vie intégrant ces différentes pressions. Les phases successives de ce travail ont largement fait appel aux outils de la modélisation Bayésienne hiérarchique, adaptés à l'intégration de modèles écologiques complexes dans une approche statistique visant à intégrer de multiples sources d'information (information *a priori* et données hétérogènes) en prenant en compte les différentes sources d'incertitude associées aux processus et aux données.

La première partie de la thèse s'attache à analyser la relation entre la biomasse féconde et le succès du recrutement chez un ordre représentatif des espèces nourriceries-dépendantes : les pleuronectiformes (poissons plats). Une approche de métanalyse (12 espèces ; 39

populations) de la variance du succès du recrutement est mise en œuvre. Les résultats montrent que (i) la variabilité interannuelle du recrutement est inférieure pour les poissons plats, comparativement aux principaux autres ordres de poissons exploités, (ii) chez les populations de pleuronectiformes, la variance du succès du recrutement diminue quand le niveau de biomasse féconde augmente, ce qui est en accord avec l'hypothèse d'une mortalité densité-dépendante durant la phase juvénile benthique (hypothèse de concentration).

Dans une deuxième partie, en valorisant les acquis de la première partie, les connaissances et les travaux existants, nous avons développé un modèle de cycle de vie de la sole de Manche Est, dans le but de décrire la dynamique de cette population et de quantifier l'effet des différentes pressions anthropiques. Ce modèle structuré en stades successifs permet la description du cycle de vie dans son intégralité en intégrant sa composante spatiale. Cette population présente en effet une ségrégation spatiale aux différents stades de vie : diffusion limitée et rétention larvaire lors de la vie pélagique, confinement des juvéniles dans des nourriceries côtières et estuariennes, et mouvements limités des adultes. Nous comparons deux hypothèses de connectivité induite par les mouvements des adultes. La première considère qu'une fois passée la phase juvénile sur des habitats spécifiques de nourricerie, marquée par une séggrégation spatiale forte, la population adulte forme un ensemble homogène au sein de la Manche Est. Cette hypothèse correspond à celle utilisée par le groupe de travail du CIEM chargée de l'évaluation de cette population. La deuxième considère que la forte séggrégation spatiale due à la phase juvénile sur nourriceries perdure aux stades adultes sous la forme de trois composantes spatialement et démographiquemnt distinctes. Le passage d'une hypothèse à l'autre impacte fortement l'estimation des paramètres clés (e.g. production de juvéniles par les différentes nourriceries). Considérer un fonctionnement sous la forme de trois composantes conduit à des dynamiques spécifiques pour chaque sous-composante, et renforce l'intérêt de considérer une gestion spatialisée de la ressource.

Enfin, dans la troisième partie, le modèle régional développé dans la deuxième partie de la thèse est utilisé pour simuler des scénarios sur les facteurs de pressions intégrés au modèle, à savoir la mortalité par pêche sur les adultes, la quantité et la qualité des habitats juvéniles, et les conditions hydroclimatiques rencontrées par les stades larvaires. Les résultats démontrent l'impact majeur de la pêche sur les populations marines exploitées, mais mettent également en avant l'importance de la conservation/restauration des habitats de nourriceries pour les espèces nourriceries-dépendantes En revanche, la variabilité issue des conditions hydroclimatiques semble de moindre ampleur mais l'impact de la variabilité des conditions hydroclimatiques et de modifications de l'habitat est accentué quand le niveau d'exploitation de la population augmente.

Au travers du cas d'étude de la population de sole de Manche Est, les travaux contribuent à la compréhension du fonctionnement des espèces nourriceries-dépendantes, et apportent une contribution en terme d'outil d'aide à la décision pour la gestion spatialisée des ressources marines exploitées dans un contexte multi-pressions.

# Abstract

Marine fish populations are subject to various environmental and anthropic pressures, from fishing mortality to habitat degradation and global change, that impact populations at different stages of their life cycle. Improving our knowledge of the different ecological processes and a fair assessment of consequences of the environmental and anthropic pressures associated with each life history stage is required to help the sustainable management of fish populations. In the case of nursery-dependant species, hydroclimatic conditions influence the survival and the dispersal of eggs then larvae. The quality and the availabilty of nursery grounds further impact juvenile survival, determining the carrying capacity of these essential habitats and *in fine* the maximum size of the population. Last, fishing activities target mostly adults. This thesis ultimately aims at investigating the functioning of these nursery-dependant species through a life cycle modeling approach that integrates the different pressures in their spatial dimensions along the life cycle. The methods largely rely on hierarchical Bayesian models, which are well adapted to integrate complex ecological models within a statistical approach, accounting for various sources of information (prior knowledge and data) together with the different sources of uncertainty in the process and the observations.

The first part of the thesis analyzes the relationship between the spawning biomass and the recruitment success for flatfish (Pleuronectiforms), known to concentrate in restricted nursery grounds during the juvenile stage. We propose a modeling approach which integrates two successives phases in the recruitment process: a density-independent phase corresponding to the pelagic eggs and larval stages followed by a benthic juvenile phase, where density-dependent processes occur. Using a metanalytical approach (39 populations for 12 flatfish species) centered on the analysis of the variance of this relation, we show that (i) flatfish display a lower interannual variance in the recruitment success compared to other exploited orders of marine fishes, (ii) the variance of recruitment success decreases with increasing stock level, which is consistent with the hypothesis of density-dependent process during the juvenile phase of the life cycle.

In the second part of the thesis, we rely on results from the the first stage (plus expert knowledge and existing work) to develop a life cycle model for the Eastern Channel common sole which accounts for both the stage-specific pressures described previously and the spatial functioning of the population at the successives stages. The population displays a consistent spatial segregation between pool of individuals along the whole life cycle, due to the combination of (i) moderate pelagic diffusivity and larval retention, (ii) juvenile containment in nurseries, and (iii) limited adults' movements. We compared two contrasted hypotheses about the spatial structure of the population. The first hypothesis considers that after the juvenile phase characterized by spatial segregation on specific nurseries, the adult population forms one single homogeneous pool in the Eastern Channel. This is the hypothesis used buy the ICES stock assessment Working Group. The second hypothesis considers that the spatial segregation persists after the juvenile phase, within three adults sub-components. Althought it is not possible to quantify the relative likelihood of those different hypotheses, we emphasize how changing from one hypothesis to the other impacts estimation of key population dynamics parameters. Considering these three sub-components with isolated dynamics emphasizes the importance of spatialized management scenarios.

Finally, in the third part of the thesis, we rely on the model developed previously to simulate realistic scenarios on the different pressures (i.e. hydroclimate, habitat, fishing) in order to quantify their respective and/or combined effects (e.g. climate and fishing pressure). Results emphasize the importance of nursery habitat availability and quality for these species. Realistic restoration scenarios of the Seine estuary lead up to an increase in biomass and catch potential. Fishing however remains the main source of population depletion and adapting fishing mortality to MSY levels leads to substantial increases in biomass and catches. We also show how hydroclimatic conditions are susceptible to interact with these two "manageable" pressures, e.g. overfishing increase the sensitivity to unfavorable hydroclimatic conditions.

Overall, the thesis provides insights towards the understanding of the population dynamics of nursery-dependent species, and provides a substantial contribution to develop tools to evaluate the performance of spatialized management scenarios in a multi-pressures context.

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# 1. Introduction générale

## Préambule

Le fonctionnement des écosystèmes marins exploités est complexe et sa compréhension constitue un défi permanent pour le monde scientifique. Cette complexité résulte en premier lieu de l'interaction dans l'espace et dans le temps d'un grand nombre de facteurs écologiques : conditions biophysiques du milieu soumises à une variabilité importante, biologie et comportement des espèces, interactions trophiques. A cette liste non exhaustive s'ajoute un facteur majeur sans équivalent dans le milieu terrestre : la pêche. Les activités de pêches affectent profondément les populations ciblées (Branch *et al.*, 2011; Worm and Branch, 2012) et leurs effets se répercutent sur les communautés (Coll *et al.*, 2008) et la biodiversité (Worm et al, 2009), au travers notamment d'une modification des interactions trophiques (Pauly *et al.*, 1998; Zeller and Russ, 2004). De plus, l'impact de l'Homme ne se limite pas à la pêche, les activités humaines ont d'autres effets perturbateurs sur les habitats et les écosystèmes, notamment en milieu côtier (Halpern *et al.*, 2008, 2012) où une partie importante de la population mondiale est concentrée (60% à moins de 100 km du rivage ; Brown, 2006).

Ces enjeux écosystèmiques requièrent une compréhension fine des processus agissant sur les écosystèmes et les populations de poissons qu'ils renferment (Mora *et al.*, 2009; Pitcher *et al.*, 2009 ; Brownman *et al.*, 2004) et de leurs possibles interactions. Ce travail de thèse propose d'apporter une pierre à cet édifice, en se concentrant particulièrement sur le cycle de vie des espèces nourriceries-dépendantes. Ces espèces présentent un intérêt halieutique majeur. En effet, les ressources halieutiques faisant l'objet d'une évaluation par le Conseil International pour l'Exploration de la Mer (CIEM), celles qui présentent une dépendance côtière et/ou estuarienne à un moment donné de leur cycle de vie (le stade juvénile pour une large majorité), représentent 44% des espèces et 77 % du tonnage des débarquements (Seitz *et al.*, 2014). Cette introduction mettra tout d'abord en avant trois questionnements clés relatifs à la complexité du cycle de vie de ces populations marines exploitées : (i) Quels sont les mécanismes du déterminisme du recrutement ? (ii) Quel est le rôle de la connectivité entre les différents habitats au cours du cycle de vie ? (iii) Quelle est l'influence des différentes pressions anthropiques et environnementales agissant à différentes échelles d'espace et de temps au cours du cycle de vie ? Ces questionnements seront explorés dans le cas particulier des espèces nourriceries-dépendantes et notamment de la sole commune, espèce modèle pour développer ce travail. Ensuite nous nous intéresserons aux outils de modélisation mis en oeuvre pour répondre aux questions de recherche soulevées par la prise en compte de ces trois concepts clés. Enfin nous introduirons le cas d'étude : la population de sole commune (*Solea solea*) de Manche Est.

## 1.1. Le déterminisme du recrutement et le cas particulier des espèces nourriceries-dépendantes

### 1.1.1. Des jeunes stades très sensibles aux fluctuations environnementales

La compréhension du déterminisme du recrutement, de par son influence sur les fluctuations des populations marines, en lien avec l'évaluation des niveaux d'exploitation durable et la capacité de reconstitution de populations surexploitées, constitue un enjeu majeur des sciences halieutiques. Il s'agit d'un des principaux sujets d'étude abordés durant les dernières décennies en écologie des ressources marines exploitées (Houde, 2008). De nombreux travaux sont menés pour analyser et quantifier le lien entre la biomasse féconde (proxy du nombre d'œufs) et le recrutement (Myers, 2001; Myers *et al.*, 2001; Minto *et al.*, 2008), et comprendre les processus écologiques sous-jacents (Petitgas *et al.*, 2013).

La plupart des espèces marines ont un cycle de vie caractérisé par de très faibles taux de survie de l'œuf à l'adulte, du fait de la mortalité très élevée des premiers stades œufs, larvaires et juvéniles (dans une moindre mesure). Ces taux sont variables d'une espèce à une autre. Ainsi, par exemple, si 10 millions d'œufs aboutiront à un adulte mature chez la morue (*Gadus morhua*) de mer du Nord, il en faudra « seulement » environ 100 000 pour la population de sole de Manche Est (Le Pape and Bonhommeau, *in press*). Cette survie est également fluctuante au sein d'une même population, avec une forte dépendance du succès annuel de la ponte et de la survie des jeunes stades aux conditions environnementales (Bakun, 1996; Houde, 2008). Les tous premiers stades (œufs et larves) subissant la majeure partie de cette mortalité (Levin et Stunz, 2005; Le Pape et Bonhommeau, *in press*), les grandes fluctuations de la survie larvaire sous l'influence des facteurs environnementaux sont la principale cause de la variabilité du recrutement (Cushing, 1995; Werner *et al.*, 1997; van der Veer *et al.*, 2000a). Les conditions hydroclimatiques (Cushing, 1995), la disponibilité en nourriture (Beaugrand *et al.*, 2003) et la pression de prédation (van der Veer *et al.*, 2000b) sont autant de facteurs à même de se cumuler et d'affecter la survie des jeunes stades (Rijnsdorp *et al.*, 1995; van der Veer *et al.*, 2000a). La température conditionne le développement ontogénique des œufs et larves et influence la durée de ces stades de vie vulnérables et la mortalité dans la colonne d'eau (Gerber *et al.*, 2014). Le vent et les courants entrainent une dispersion de ces stades pourvus de capacités de nage limitées vers des habitats propices à leur développement ultérieur ou au contraire vers des zones défavorables (Bakun, 1996). Cette stratégie de type « r » alliant fécondité élevée et forte fluctuation de la survie a plusieurs conséquences sur le cycle de vie des poissons marins et leur exploitation. Tout d'abord, la relation entre la quantité de reproducteurs (la biomasse féconde) et l'abondance des juvéniles qui en découle (le recrutement) est dominée par l'influence de multiples facteurs difficiles à prévoir donc souvent considérés comme densité-indépendants et aléatoires (Myers and Barrowman, 1996; Minto *et al.*, 2008; Archambault et al. 2014). De plus, contrairement à d'autres classes (e.g. mammifères), les populations de poissons marins sont, du fait de cette dynamique spécifique, souvent à même de supporter des taux d'exploitation relativement élevés. En effet, la très forte production d'œufs couplée avec l'occurrence de conditions environnementales très favorables certaines années entraîne l'apparition de pics d'abondance de jeunes recrues qui concourent à maintenir des niveaux d'abondance importants de la population et augmentent la résilience des populations suite à des déplétions importantes engendrées par la pêche (Myers *et al.*, 1995, 1999; Keith *et al.*, 2012). Ainsi, pour un certain nombre de populations marines exploitées, il est possible de prélever chaque année de l'ordre d'un tiers de la biomasse féconde en se maintenant à un niveau durable de prélèvement (contre moins de 2 % pour les dauphins et marsouins par exemple).

### 1.1.2. La spécificité des espèces nourriceries-dépendantes : une phase juvenile réalisée (exclusivement) sur des nourriceries restreintes

Si les caractéristiques des premiers stades du cycle de vie de l'œuf à la larve sont valables pour la plupart des espèces de poissons marins exploitées, les caractéristiques de la phase juvénile varient fortement selon les stratégies vitales.

En particulier, de nombreuses espèces d'intérêt halieutique des milieux tempérés sont dites nourriceries-dépendantes car elles réalisent la phase juvénile de leur cycle de vie dans des habitats restreints, aux caractéristiques biophysiques précises, le plus souvent situés en secteurs côtiers et estuariens : les habitats halieutiques essentiels de nourriceries (Beck *et al.*, 2001a; Le Pape *et al.*, 2003b; Rochette *et al.*, 2010; Vasconcelos *et al.*, 2014 ; Figure 1.1). C'est notamment le cas chez de nombreux pleuronectiformes (ordre des poissons plats auquel appartient la sole commune *Solea solea*) pour qui, suite à une phase pélagique, les larves atteignant les zones de nourriceries vont se métamorphoser pour coloniser des habitats de nourriceries côtières très spécifiques et aux surfaces restreintes. Ces aires de nourriceries sont caractérisées par des conditions favorables à la survie et la croissance des juvéniles, notamment des températures plus élevées, de fortes disponibilités alimentaires et une protection accrue contre les prédateurs (Miller *et al.*, 1984; Gibson, 1994, 1997, 2004). De nombreux travaux ont ainsi montré la préférence des juvéniles pour des caractéristiques d'habitats particulièrement représentées au sein des nourriceries, à savoir une bathymétrie réduite (<20 voire 10m) et des substrats meubles (vases et sables fins), chez la sole (Le Pape *et al.*, 2003b; Rochette *et al.*, 2010) mais également chez d'autres espèces de poissons plats (Trimoreau *et al.*, 2013) ou d'autres espèces d'importance commerciale (Vasconcelos *et al.*, 2010). La réalisation du cycle de vie de la sole, comme des nombreuses autres espèces présentant cette dépendance (Seitz *et al.*, 2014), dépend ainsi directement de la capacité d'accueil de ces nourriceries qui va conditionner la production d'individus adultes et donc *in fine* la taille (maximale) de la population (Rijnsdorp *et al.*, 1992; Schmitt and Holbrook, 2000; Le Pape and Bonhommeau, *in press*).

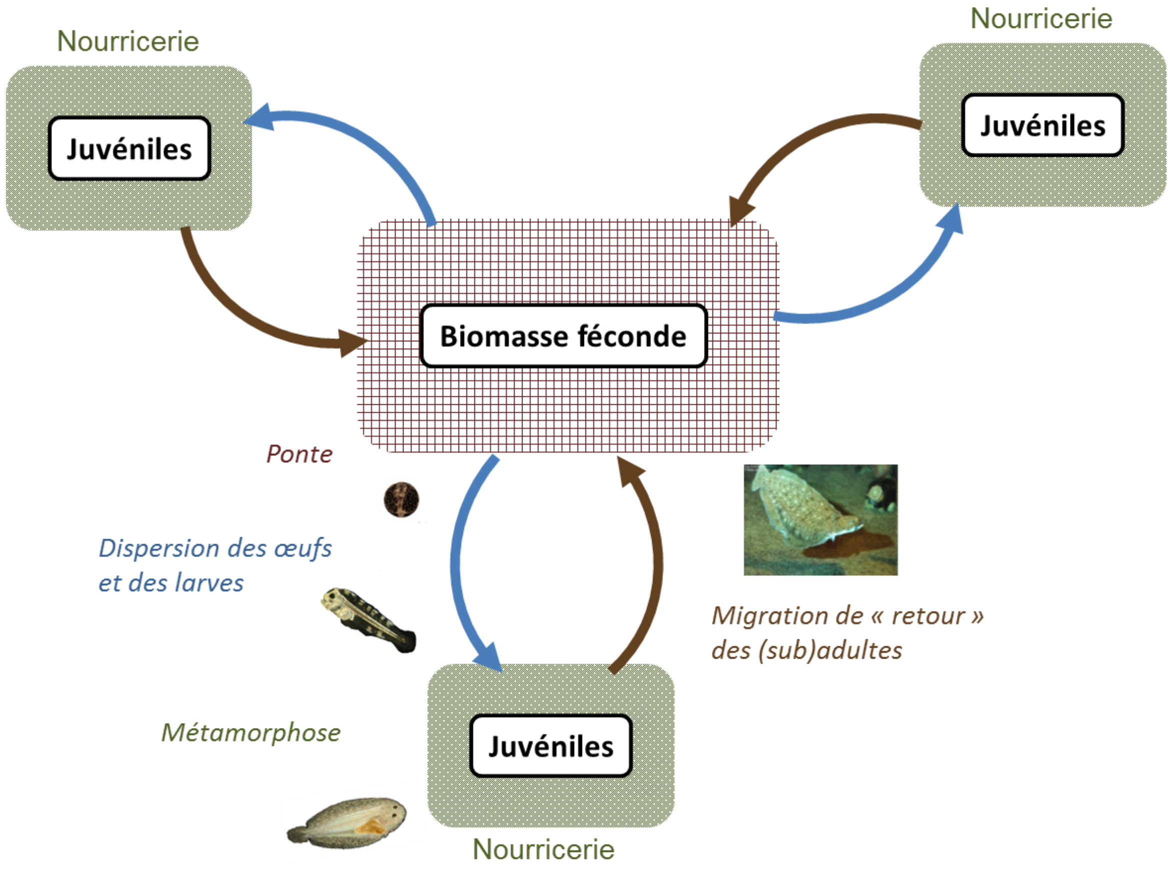

Figure 1.1 - Cycle de vie des espèces nourriceries-dépendantes

### 1.1.3. Conséquences pour la dynamique du recrutement des espèces nourriceries-dépendantes

Pour les espèces nourriceries-dépendantes, les premiers stades (œufs et larves/juvéniles) présentent des caractéristiques écologiques contrastées : une production abondante d'œufs et de larves caractérisés par une mortalité très élevée et fortement contrôlée par des phénomènes densité-indépendants sous l'influence des fluctuations environnementales (stratégie « r »), suivie d'une phase juvénile dans des zones de nourriceries bien délimitées où les phénomènes de densité-dépendance (compétition pour l'espace, la nourriture ; Le Pape and Bonhommeau, *in press*) sont à même de se manifester en raison de la capacité restreinte de ces habitats.

Ces caractéristiques écologiques forgent une dynamique du recrutement particulière pour les populations de poissons plats. La variabilité engendrée par les stades pélagiques (œufs et larves), à la mortalité à la fois forte et fluctuante (Chambers and Trippel, 1997; Gallego *et al.*, 2012), devrait être tamponnée par l'existence d'un recrutement maximum défini par la capacité d'accueil des nourriceries (Levin and Stunz, 2005; Juanes, 2007). Cette capacité est elle-même susceptible de varier annuellement, notamment en raison de la fluctuation des apports terrigènes conditionnés par les débits des fleuves en milieu estuarien (Le Pape *et al.*, 2003a; Kostecki *et al.*, 2010), mais la variabilité qui en découle demeure inférieure à celle engendrée par l'influence des fluctuations environnementale sur les premiers stades pélagiques (van der Veer *et al.*, 2000a). Ainsi, au-delà d'un certain seuil d'apport larvaire, la densité-dépendance au sein des nourriceries conduit au plafonnement de la production de juvéniles, le recrutement devenant ainsi relativement indépendant du nombre de larves ayant atteint la métamorphose sur les sites de nourriceries (Le Pape and Bonhommeau, *in press*). Il s'agit de l'hypothèse de concentration formulée par Iles et Beverton (2000). Ce phénomène de concentration doit logiquement conduire à un recrutement « modérément » variable pour les espèces nourriceries-dépendantes (Le Pape *et al.*, 2003b), au regard de la variabilité plus forte du recrutement des autres espèces de poissons marins (Houde, 2008).

Ce cycle de vie engendre par ailleurs une sensibilité de ces espèces aux pressions anthropiques affectant leurs habitats côtiers et estuariens de nourriceries (Le Pape and Bonhommeau, *in press*; Vasconcelos *et al.*, 2014), la dégradation de ces habitats diminuant la capacité de renouvellement de ces espèces (cf. 1.3.2.).

## 1.2. La connectivité et le fonctionnement spatial des populations d'espèces nourriceries-dépendantes

La connectivité permet aux individus d'interagir au sein d'entités allant de concentrations locales de groupes limités à des méta-populations à large échelle (Palmer *et al.*, 2014). L'étude de la connectivité constitue un thème majeur de l'écologie, aussi bien en milieu terrestre que marin. Dans le milieu marin, cette thématique révèle toute sa complexité en raison du caractère ouvert du milieu, de la mobilité des individus et des difficultés d'observations : « *Counting fish is like counting trees, except they are invisible and they move* » (J. Shepherd).

### 1.2.1. Importance de la structure spatiale pour les (méta)populations de poissons marins exploités

Les taux d'échanges entre populations locales, leur échelle et leur structure spatiale conditionnent la capacité de renouvellement et la résilience des populations (Figueira and

Crowder, 2006; Cianelli *et al.*, 2013), de par leur implication en termes de dynamique de population et/ou d'échange de matériel génétique (Palumbi, 2003; Cowen *et al.*, 2006).

Les patrons de connectivité conditionnent la structure spatiale des populations et sont à la base même de la définition du *stock* en sciences halieutiques : un regroupement d'individus capable de se reproduire et considéré comme une population exploitée indépendante des autres populations de la même espèce (Cushing, 1968; Hilborn and Walters, 1992). La définition de stocks distincts homogènes en leur sein et sans interrelations s'avère utile pour la gestion opérationnelle des ressources halieutiques qui nécessite de définir des contours pour les entités de gestion. C'est sur la base de ces contours que sont réalisées les évaluations des stocks et les synthèses sur l'état des ressources (FAO, 2014; Gascuel *et al.*, 2014; Lassen *et al.*, 2014). La délimitation des stocks comporte toutefois une part d'arbitraire et est guidée tout autant par des questions de gestion que par des réalités écologiques. La définition des stocks est donc souvent simplificatrice et peut dissimuler une complexité en terme de structure et d'échanges entre différentes composantes de méta-populations (Cianelli *et al.*, 2013). La compréhension des patrons de connectivité existant au sein de ces méta-populations est essentielle pour comprendre leur dynamique (Pittman *et al.*, 2014). La connaissance des niveaux de mouvements et d'échanges entre les composantes de méta-populations est par ailleurs essentielle pour mettre en place des mesures de gestion spatialisées efficaces pour la gestion durable des ressources halieutiques (Grüss *et al.*, 2011b; Abecasis *et al.*, 2014), notamment des aires marines protégées (Lockwood *et al.*, 2002; Sale *et al.*, 2005; Planes *et al.*, 2009).

### 1.2.2. Le rôle de la connectivité dans le cycle de vie des populations de poissons nourriceries-dépendants

Du fait que les stades successifs de leur cycle de vie se déroulent dans des habitats spatialement distincts (Figure 1.1), la prise en compte de la connectivité spatiale entre les différents habitats et stades associés au cours du cycle de vie conditionne le fonctionnement des populations des espèces nourriceries-dépendantes.

En effet, l'influence des conditions hydroclimatiques sur les apports de larves aux différentes nourriceries depuis les aires de ponte conditionne le degré d'isolement de différentes composantes spatiales des populations au cours des jeunes stades (Rochette *et al.*, 2012). Les mouvements des juvéniles depuis les nourriceries jusqu'aux aires de distribution des adultes, puis des adultes au sein de leurs zones de vie et de reproduction peuvent ensuite générer une structure spatiale complexe.

### Connectivité au cours des premiers stades

La plupart des espèces marines benthiques, et notamment l'ensemble des pleuronectiformes, présentent un stade pélagique pourvu d'un fort potentiel de dispersion (Scheltema, 1986; Cowen and Sponaugle, 2009) en comparaison avec l'absence (espèces sessiles) ou la forte limitation de mouvements qui les caractérisent au cours de leur vie benthique (Pittman *et al.*, 2014). En conséquence, la majeure partie des travaux portant sur la connectivité des populations benthiques marines s'est focalisée sur les stades œufs et larves (Frisk *et al.*, 2013). Les approches de couplage entre modèles de circulation océanique et modèles biologiques (Miller, 2007), développées sur de nombreux cas d'étude (Huret *et al.*, 2010; Savina *et al.*, 2010; Rochette *et al.*, 2012; Lacroix *et al.*, 2013), ont fortement contribué à affiner la compréhension des processus gouvernant la dispersion de ces premiers stades en relation avec les paramètres environnementaux. Il apparait toutefois que les périmètres de dispersion restent modestes (Cowen *et al.*, 2000; Rochette *et al.*, 2012) et que les cas de rétention spatiale des larves dans des zones limitées sont courants (Cowen *et al.*, 2006; Cuif *et al.*, 2014).

### Une vie juvénile sédentaire

Les juvéniles des espèces nourriceries-dépendantes sont généralement peu mobiles (Sheaves, 2009; Pittman *et al.*, 2014). Notamment, à l'instar des autres pleuronectiformes, la capacité de dispersion des juvéniles de sole est très restreinte (Burrows *et al.*, 1994; Le Pape *et al.*, 2003b; Rochette *et al.*, 2010), et induit un phénomène de rétention des juvéniles au sein d'aires de nourriceries spatialement distinctes.

### Les mouvements des adultes : le chaînon manquant ?

La majeure partie des travaux portant sur la connectivité dans le milieu marin s'est focalisée sur les premiers stades (Frisk *et al.*, 2013). S'ils peuvent avoir une influence forte sur les patrons de connectivité, l'influence des mouvements des stades sub-adultes et adultes a reçu beaucoup moins d'attention (Frisk *et al.*, 2013). Les individus (sub)adultes, pourvus de capacité de déplacement actif, peuvent potentiellement migrer assez loin de leur aire de recrutement (Darnaude et Hunter, 2008) et étendre l'aire de distribution de la population au-delà des limites de l'aire de dispersion des premiers stades (Frisk *et al.*, 2008). Au contraire, un comportement très sédentaire (Abecasis *et al.*, 2014) amplifiera la structuration spatiale engendrée par la rétention larvaire (Rochette *et al.*, 2012). Par ailleurs, les mouvements des géniteurs ont une influence cruciale en raison de leur impact sur la distribution des œufs dans les aires de ponte, en interaction avec la connectivité frayère-nourricerie générée par la dispersion pélagique des premiers stades sous l'influence des conditions hydroclimatiques.

Ainsi, une bonne compréhension du fonctionnement spatial des populations nécessite de prendre en compte les processus de dispersion et de déplacement à tous les stades du cycle de vie. Dans le cas des espèces nourriceries-dépendantes, alors que les juvéniles demeurent confinés dans les aires de nourricerie, cela implique de coupler les connaissances liées à la dérive des premiers stades (de l'œuf jusqu'aux nourriceries) à celles sur les mouvements des (sub)adultes pour prendre en compte l'intégralité du fonctionnement spatial des populations. L'analyse des patrons de connectivité au cours du cycle de vie devrait ouvrir la voie à une gestion spatialisée adaptée aux différents stades et aux pressions qui les affectent (e.g. pêche et adultes, protection des habitats et juvéniles).

## 1.3. De multiples facteurs de pression sur les populations de poissons exploitées

### 1.3.1. Trois pressions principales : la pêche, le climat et la dégradation de la qualité des habitats

Les populations marines sont exposées, au cours de leur cycle de vie, à diverses pressions d'origines environnementale (Bakun, 1996) et anthropique (Halpern *et al.*, 2007, 2008). Nous décrivons ici trois sources majeures de pression qui seront abordées dans le cadre de ce travail : la pêche, la variabilité et le changement climatiques, et les dégradations de l'habitat. Cette analyse n'est pas exhaustive et d'autres facteurs de pression affectent les communautés marines. Leur influence reste toutefois hors du champ de la présente approche.

**Prélèvements par la pêche**

La pêche constitue le premier facteur de pression retenu lorsque l'on évoque l'impact de l'Homme sur les écosystèmes marins (Hutchings, 2000; Jackson *et al.*, 2001b) ; elle est considérée comme principal responsable du déclin des populations marines (Christensen *et al.*, 2003; Myers and Worm, 2003; Pauly, 2005). Une proportion importante de stocks demeure surexploitée (environ 30% à l'échelle planétaire ; FAO, 2014). Les effets de la pêche sur les écosystèmes sont multiples et se cumulent (Jennings and Kaiser, 1998). La capture répétée de géniteurs (ou futurs géniteurs) impacte directement le potentiel reproducteur des populations (Hilborn and Walters, 1992). La diminution du nombre et de la taille des classes d'âge affecte la capacité de résilience des populations (Jackson *et al.*, 2001a). En plus de ces effets directs s'ajoutent des effets induits à moyen/long termes sur les populations exploitées. Sont ainsi mis en avant la diminution de la variabilité génétique (Smith *et al.*, 1991; Conover, 2007), la pression de sélection et l'évolution induite, avec des conséquences sur la résilience des stocks (Trippel, 1995; Olsen *et al.*, 2004). Par ailleurs, les effets de la pêche ne se limitent pas aux seules espèces exploitées ; aux captures ciblées s'ajoutent des captures accessoires

(Alverson, 1994) et des rejets (Kelleher, 2005). De plus, les prélèvements à différents niveaux de la chaine alimentaire conduisent à l'altération des réseaux trophiques (Pauly *et al.*, 1998; Österblom *et al.*, 2007) susceptible de mener à des changements profonds et irréversibles des écosystèmes (Baum and Worm, 2009). Enfin, selon les techniques employées, la pêche est également susceptible d'altérer directement la structure des habitats (Thrush *et al.*, 1998; Auster and Langton, 1999; Turner *et al.*, 1999).

### Influences du climat, fluctuations et tendances

Il est possible de distinguer au sein de l'« effet du climat » des effets à long terme liés aux changements globaux, des effets à moyen terme liés aux régimes océaniques et enfin des impacts à court terme, telle la variabilité interannuelle des conditions hydroclimatiques affectant la survie des premiers stades.

Le changement global affecte les écosystèmes terrestres et marins (Walther *et al.*, 2002) et il est prévu que ses conséquences aillent en augmentant (Solomon, 2007). Ce changement affecte en premier lieu les caractéristiques physiques du milieu marin : élévation du niveau des mers, augmentation de la température, modification de la circulation océanique, changement de la stratification verticale, acidification des océans (Bakun, 1990; Sarmiento *et al.*, 2004). Ces changements engendrent à leur tour un certain nombre de conséquences sur la vie marine parfois difficiles à prédire ou tout au moins à quantifier. Ils modifient la biologie (physiologie, croissance, mortalité, fécondité ; Pörtner, 2012) et également les aires de distribution (Cheung *et al.*, 2009) ou les routes de migration (Gerber *et al.*, 2014) des espèces marines exploitées (Perry *et al.*, 2010; Rijnsdorp *et al.*, 2010). Ces perturbations ont des conséquences à l'échelle des écosystèmes (Drinkwater *et al.*, 2010) : apparition de nouvelles espèces et fort *turnover* taxonomique (diversité β ; Rahel and Olden, 2008; Cheung *et al.*, 2009), modification de la production primaire (Behrenfeld *et al.*, 2006) et des interactions trophiques (Preston *et al.*, 2008).

Les oscillations des régimes océaniques sont susceptibles d'entrainer une modification périodique des conditions hydroclimatiques ayant des effets en cascade sur les écosystèmes marins (Alheit *et al.*, 2014). Ces phénomènes relativement bien connus affectent tous les compartiments de ces écosystèmes (Hays, 1986; Chavez *et al.*, 2003).

Si les effets du climat décrits précédemment ont une action à moyen/long terme, la variabilité des conditions climatiques a également un impact à une échelle de temps beaucoup plus réduite et sans doute plus structurante dans le cadre d'une gestion à court/moyen terme des populations exploitées. Plus particulièrement, les conditions hydroclimatiques sont susceptibles d'engendrer une réponse rapide de la part des populations (à l'échelle de la cohorte) notamment en raison de leur impact sur la survie des premiers stades (Planque and Frédou, 1999; Hermant *et al.*, 2010 ; cf. 1.1.1).

**Dégradation des habitats halieutiques essentiels**

Plus encore que la pêche, aux conséquences abordées précédemment, les autres activités humaines affectant les écosystèmes marins sont concentrées sur la frange littorale (Halpern *et al.*, 2008). Cette pression anthropique côtière va encore s'intensifier au cours des prochaines décennies (Brown, 2006). Ces activités ont des conséquences néfastes sur les écosystèmes et les habitats, tout particulièrement en milieu côtier et estuarien qui abritent notamment les nourriceries pour de nombreuses espèces (Lotze *et al.*, 2006). Ces impacts peuvent être structurels, de par la destruction physique des habitats : extensions portuaires, construction de digues (Rochette *et al.*, 2010), extractions de granulat, éolien *offshore*. Ils peuvent également se manifester sous la forme d'une dégradation de la qualité du milieu : présence de substances xénobiotiques (Budzinski *et al.*, 1997), eutrophisation (Paerl *et al.*, 1998; Kemp *et al.*, 2005; Diaz and Rosenberg, 2008), pollutions diverses. La dégradation des habitats est susceptible de perturber le cycle de vie des espèces marines (Peterson *et al.*, 2003; Le Pape *et al.*, 2007) via une perte de surface d'habitat essentiel à la réalisation du cycle de vie (e.g. nourriceries côtières), ou une dégradation de leur qualité engendrant une augmentation de la mortalité « naturelle » (i.e. hors exploitation halieutique) ou encore la diminution de la croissance, de la condition, de la fécondité et *in fine* de la *fitness* des individus. Il faut souligner l'ampleur, souvent négligée au regard des autres pressions, des conséquences de cette dégradation des habitats côtiers et estuariens sur les ressources halieutiques. Ainsi, on estime aujourd'hui que du fait des pressions multiples, la fonctionnalité de nourricerie de ces milieux a été réduite d'un facteur au moins égal à 2 à l'échelle planétaire (Worm *et al.*, 2006; Barbier *et al.*, 2011).

### 1.3.2. Le cas des espèces nourriceries-dépendantes : des facteurs de pression associés à différents stades et à différentes échelles spatiales au cours du cycle de vie

Dans la suite, nous nous intéressons uniquement aux effets de ces pressions à court terme sur la démographie des populations, en mettant de côté les impacts à plus long terme (cf. 1.3.1) liés aux effets de la pêche, comme la sélection génétique (*fishing induced evolution*) ou les modifications des réseaux trophiques, ou aux changements climatiques globaux.

Dans le cas des espèces nourriceries-dépendantes, les effets majeurs des trois facteurs de pression principaux – la variabilité climatique, la dégradation des habitats et les prélèvements par la pêche – peuvent être principalement associés à des stades spécifiques au cours du cycle de vie.

Par exemple, dans le cas de la sole commune, les variations hydroclimatiques affectent principalement les premiers stades pélagiques (œufs et larves ; Hermant *et al.*, 2010), conditionnant leur survie mais également l'allocation spatiale des œufs et des larves depuis les zones de ponte vers les secteurs de nourricerie (Rochette *et al.*, 2012). La qualité des habitats des nourriceries côtières et estuariennes détermine ensuite le succès de la métamorphose, du développement et de la croissance des stades suivants (post-larves et juvéniles ; Le Pape et Bonhommeau, *in press*). La qualité de l'habitat et la surface disponible associée seront prépondérantes dans la détermination des capacités d'accueil des nourriceries et détermineront le succès de la phase juvénile (recrutement) et *in fine* le potentiel reproducteur des populations. Enfin, la pêche affecte quasi-exclusivement les stades ultérieurs (subadultes et adultes), les juvéniles étant confinés dans les secteurs de nourricerie et donc spatialement séparés des adultes et *a fortiori* des zones de pêche.

Au-delà de ce schéma simplificateur associant trois couples distincts pressions-stades (i.e. climat – premiers stades, habitat – juvéniles, pêche - (sub)adultes), il faut noter l'existence d'interactions entre les différentes pressions ainsi que la complexité (Petitgas *et al.*, 2013) et l'imbrication des effets induits. Ainsi, du fait notamment de ses conséquences sur les structures démographiques des stocks, la pêche est susceptible d'accentuer la sensibilité des ressources aux fluctuations climatiques (Brander, 2005; Planque *et al.*, 2010). Par ailleurs, l'effet de la pêche interagit aussi avec la saturation de la capacité des nourriceries, une biomasse féconde fortement réduite conduisant à réduire la saturation en apports larvaires et donc à diminuer le recrutement tout en augmentant sa variabilité (cf. 1.1.3).

## 1.4. Une approche intégratrice de modélisation du cycle de vie pour mieux comprendre le fonctionnement des populations sous multiples pressions et répondre aux enjeux de gestion

La prise en compte de ces différentes pressions, et non plus de la seule exploitation par la pêche, propose de nouveaux défis aux scientifiques en charge de l'analyse du fonctionnement des populations marines. Il apparait nécessaire d'intégrer les facteurs de pression dans des approches de modélisation spatialisées pour comprendre le fonctionnement de ces populations sous contraintes naturelles et anthropiques, évaluer et déconvoluer les impacts respectifs des différents facteurs de stress et prédire les évolutions des systèmes sous différents scénarios et options de gestion dans une optique d'aide à la décision. Ces différentes pressions doivent être intégrées dans les modèles d'aide à la décision pour la gestion, afin de les minimiser (dégradation des habitats), les optimiser (pêche) ou les prendre en compte (variabilité climatique). S'il est envisageable de prendre des mesures de préservation/restauration des habitats essentiels ou de contrôler l'impact de la pêche, les aléas climatiques doivent être pris en compte dans les modèles sous la forme de variabilité additionnelle.

Les caractéristiques particulières du cycle de vie des espèces nourriceries-dépendantes plaident pour une gestion spatialisée de ces ressources. Celle-ci peut se concrétiser sous la forme de zones soumises à des mesures particulières (e.g. Aires Marines Protégées permettant de stimuler l'alimentation de la population depuis les nourriceries ; Nagelkerken *et al.*, 2012) telle la « Plaice Box » établie en Mer du Nord en 1989 (Pastoors *et al.*, 2000), ou encore par une gestion spatialisée de la pêche en établissant des quotas régionaux en fonction de la production locale des différentes composantes isolées d'un point de vue démographique. Concernant les pressions sur les habitats, des mesures spatialisées visant la préservation voire la restauration des nourriceries et donc l'augmentation de leur capacité d'accueil peuvent se révéler efficaces dans une optique de bonne gestion des populations d'espèces nourriceries-dépendantes, parfois davantage que des mesures régulant la pêche des adultes (Levin and Stunz, 2005; van de Wolfshaar *et al.*, 2011). Ces mesures visant la bonne santé des habitats essentiels peuvent cibler une restauration passive (Elliott *et al.*, 2007), si la suppression des facteurs de stress existants est suffisante pour que l'écosystème retrouve un état satisfaisant (Klein *et al.*, 1998; Elliott *et al.*, 2007). Il est également possible de mener une restauration active, par exemple au travers de mesures de réhabilitation d'habitats perdus (Elliott *et al.*, 2007; Benayas *et al.*, 2009; Moreno-Mateos *et al.*, 2012; Irving, 2013).

Les modèles de dynamique de population de type « analyse de cohortes » (Shepherd, 1999), largement utilisés pour l'évaluation des stocks (Conseil International pour l'Exploration de la Mer ; CIEM), sont résolument tournés vers l'analyse de l'influence de la pêche sur la fraction exploitable (i.e. adulte) du stock et n'abordent donc pas de manière explicite la dynamique des populations sous l'angle du cycle de vie. La pêche y est considérée comme le principal impact anthropique sur la mortalité et la dimension spatiale est généralement occultée. S'ils permettent de retro-calculer le recrutement *a posteriori*, la dynamique du renouvellement des populations et les spécificités du processus de recrutement liées au fonctionnement des espèces nourriceries-dépendantes (e.g. phénomène de concentration) ne sont pas prises en compte. Les approches abordant la dynamique associée à d'autres stades du cycle de vie prennent rarement en compte l'intégralité du cycle. Dans le cas des espèces nourriceries-dépendantes, de nombreux travaux ont porté sur les premiers stades, notamment sur la variabilité des apports larvaires vers les secteurs de nourriceries (Savina *et al.*, 2010;

Rochette *et al.*, 2012; Comerford *et al.*, 2013; Lacroix *et al.*, 2013), ou sur les relations entre l'habitat et les stades juvéniles (Eastwood *et al.*, 2003; Le Pape *et al.*, 2003b; Rooper *et al.*, 2004; Nash *et al.*, 2007; Rochette *et al.*, 2010; Trimoreau *et al.*, 2013). Peu de travaux (Stelzenmüller *et al.*, 2011; van de Wolfshaar *et al.*, 2011) ont intégré ces différents stades au sein d'une approche commune (Rochette et al. 2013).

Ainsi, la modélisation intégrée des cycles de vie apparait comme une approche permettant d'appréhender la complexité inhérente au fonctionnement des populations marines, en intégrant notamment la complexité du processus de recrutement, la dynamique spatiale liée à la connectivité entre les différents stades de développement, et l'influence conjointe des pressions environnementales et anthropiques.

## 1.5. Apports de la modélisation hiérarchique Bayesienne

Le développement de modèles de cycle de vie fait face à d'importants obstacles méthodologiques, notamment la pauvreté et l'hétérogénéité des données disponibles (Schnute, 1987; Hilborn and Walters, 1992; Hilborn, 1997), l'incertitude sur les processus ou encore la difficulté d'intégrer l'ensemble des échelles (spatiales, temporelles) dans un cadre de modélisation unifié.

La modélisation hiérarchique Bayesienne (Clark, 2005; Cressie *et al.*, 2009; Parent and Rivot, 2012) apparait comme un outil utile qui permet de lever certains de ces verrous méthodologiques.

### 1.5.1. Le théorème de Bayes : un processeur d'information intégrant de la connaissance *a priori*

Les statistiques Bayesiennes reposent sur le théorème introduit par Bayes (1702-1761), lui-même basé sur les propriétés des probabilités conditionnelles. Ce théorème (1) peut être considéré comme un « processeur d'information » : la connaissance subjective *a priori* sur un paramètre, décrite sous la forme d'une distribution de probabilité $\mathrm{P}(\theta)$, est mise à jour par l'information contenue dans les données via la vraisemblance $L(y_{obs}|\theta)$ pour donner une distribution *a posteriori* $P(\theta|y_{obs})$. Cette « philosophie » du traitement de l'information et de l'inférence statistique (Figure 1.2) reflète la démarche scientifique (Clark, 2005), où les connaissances sur le fonctionnement des systèmes se précisent au fur et à mesure des expérimentations et de l'acquisition d'informations.

$$(1)\quad P(\theta|y_{obs}) = \frac{P(\theta).L(y_{obs}|\theta)}{\int L(y_{obs}|\theta)P(\theta)d\theta}$$

La vraisemblance traduit la crédibilité des données conditionnellement aux paramètres et est directement définie par le modèle probabiliste pour les données. Deux propriétés se détachent de ce théorème (i) l'approche Bayesienne permet d'introduire de la connaissance (selon le principe du *« Standing on the shoulders of giants »* ; Hilborn and Liermann, 1998) via l'utilisation de *priors informatifs* traduisant ce niveau de connaissance et d'expertise *a priori*, c'est-à-dire avant de disposer des données à analyser ; (ii) l'incertitude autour de l'estimation des paramètres est décrite par des distributions de probabilité (*a posteriori*) qui s'interprètent directement comme des degrés de crédibilité associés à différentes valeurs des paramètres.

Le dénominateur de l'équation (1) est un facteur de normalisation aussi appelé constante d'intégration (probabilité marginale des données) qui ne modifie pas la forme de la distribution *a posteriori*. L'équation (1) est souvent notée sous sa forme non normalisée (2) :

(2) $P(\theta|y_{obs}) \propto P(\theta).L(y_{obs}|\theta)$

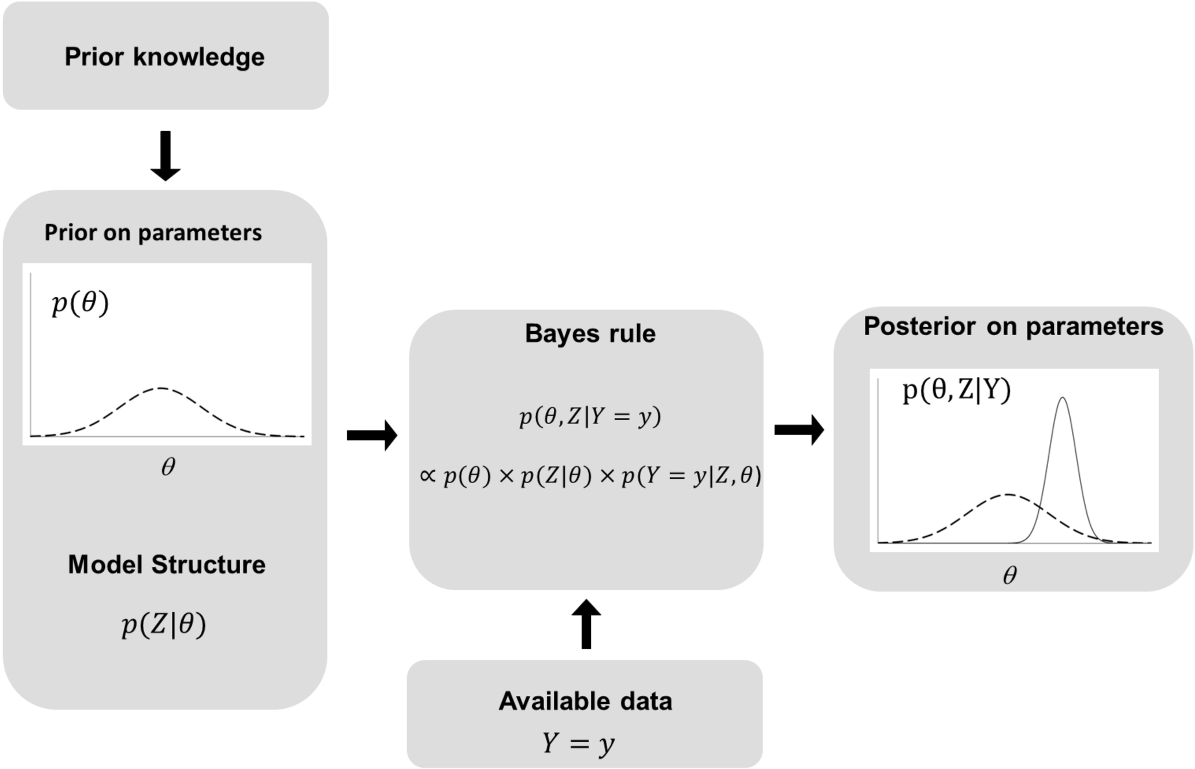

Figure 1.2 - Représentation schématique du mécanisme d'inférence Bayesienne. Adapté de Parent et Rivot (2012).

### 1.5.2. Modélisation hiérarchique : articulations entre observations et processus

Une démarche de modélisation consiste avant tout à proposer une (ou plusieurs) représentation(s) du fonctionnement du système. S'il comporte des termes aléatoires, le système peut être décrit sous la forme *d'une équation stochastique de processus* : les différentes variables d'état du système, notées $Z$ (e.g. abondances aux années $t$ et $t+1$ dans le cas d'un modèle de dynamique de population), aussi appelées *états cachés* car généralement non directement observées, sont reliées par des équations aux paramètres inconnus (e.g. mortalité), notés ici $\theta$. Ces équations comportent généralement des termes stochastiques pour représenter l'incertitude inhérente à la simplification du processus sous la forme d'un modèle. Ainsi, le processus des états cachés du modèle peut s'écrire sous une forme compacte qui traduit la distribution des états cachés conditionnellement aux paramètres :

(3) $P(Z|\theta)$

Si une distribution *a priori* $P(\theta)$ est définie sur l'ensemble des paramètres du modèle, la distribution *a priori* jointe $P(\theta, Z)$ synthétise toute la connaissance *a priori* sur la structure du modèle ($P(Z|\theta)$) et ses paramètres ($P(\theta)$) :

(4) $P(\theta, Z) = P(\theta) \cdot P(Z|\theta)$

Par ailleurs, le modélisateur a à sa disposition des données, notées $y_{obs}$, qui l'informent sur l'état du système (e.g. captures aux années $t$ et $t+1$). Ces données peuvent être reliées aux états cachés du système par une *équation stochastique d'observation*, qui traduit les sources d'incertitude inhérentes au processus d'observation du système (erreur d'échantillonnage, de mesure etc.) :

(5) $P(y_{obs}|\mathrm{Z}, \theta)$

Dans le cadre Bayesien, les équations du processus et d'observation peuvent être articulées pour obtenir la *distribution jointe a posteriori* des paramètres $\theta$ et des états cachés du système $Z$ (notée ici sous sa forme non normalisée, i.e. sans la constante d'intégration) :

(6) $P(\theta, Z|y_{obs}) \propto P(\theta) \cdot P(Z|\theta) \cdot P(y_{obs}|\mathrm{Z}, \theta)$

Ainsi, la modélisation hiérarchique permet de séparer la modélisation des processus des états cachés, de celles des observations, ainsi que les incertitudes associées.

Dans la pratique, la distribution *a posteriori* jointe est rarement accessible analytiquement mais doit être estimée par des méthodes numériques d'échantillonnage. Les méthodes de Monte Carlo par Chaînes de Markov (MCMC) (Robert, 1996 ; Gelman *et al.*, 2004) sont les plus couramment utilisées. L'estimation de modèles Bayesiens complexes est aujourd'hui facilitée par l'existence d'outils informatiques dédiés tels que les plateformes WinBUGS (Lunn *et al.*, 2000), OpenBUGS (Lunn *et al.*, 2009) ou JAGS (Plummer, 2003), même si les simulations MCMC peuvent encore se révéler très coûteuses en temps de calcul (Bolker *et al.*, 2013).

### 1.5.3. Intégration d'échelles multiples, transfert d'information entre différentes unités

La modélisation hiérarchique permet aussi d'organiser le transfert de l'information au sein de différentes unités (Figure 1.3) qui peuvent être spatiales (e.g. secteurs géographiques), temporelles (e.g. années d'observations) ou même liées à la nature des objets biologiques modélisés (e.g. populations d'espèces semblables ou différentes). Dans ces cas de figures fréquemment rencontrés, et plus particulièrement dans un contexte d'informations et de données lacunaires (contexte « *data poor* »), il est courant de vouloir faire circuler l'information au sein de ces différentes unités afin de transférer l'information des unités riches en données (« *data rich* ») vers les unités plus pauvres (« *Robin Hood Approach* » ; Punt *et al.*, 2011).

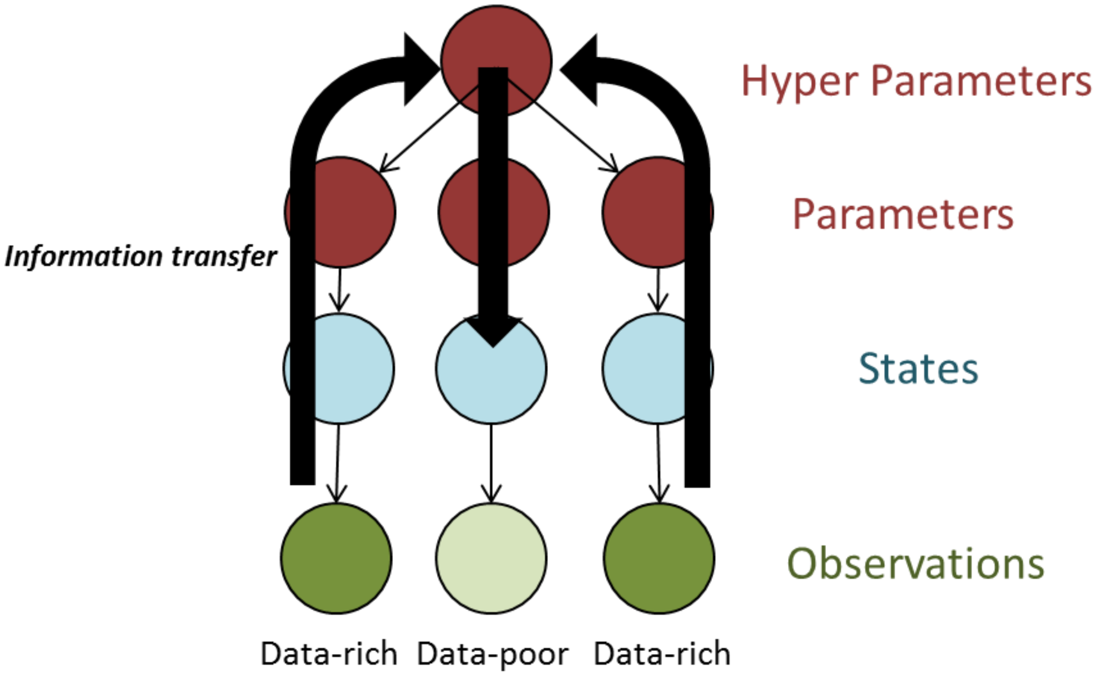

Figure 1.3 - Transfert de l'information au sein d'un modèle hiérarchique

### 1.5.4. Modélisation Hiérarchique Bayesienne (MHB) et modélisation du cycle de vie

Les modèles hiérarchiques Bayesiens permettent : (i) l'introduction de connaissance *a priori* sur des paramètres parfois difficiles à estimer à partir des seules données disponibles ; (ii) l'assimilation de sources de données multiples en prenant en compte les différents niveaux d'incertitude (données, processus) ; (iii) l'organisation du transfert d'information au sein de strates hiérarchiques.

Ces propriétés font de la MHB un outil d'intérêt pour la modélisation des cycles de vie des populations marines exploitées (Rivot *et al.*, 2004; Ruiz *et al.*, 2009; Rochette *et al.*, 2013; Massiot-Granier *et al.*, 2014).

## 1.6. Questions de recherche abordées dans la thèse

La confrontation du cycle de vie caractéristique des espèces nourriceries-dépendantes aux trois questionnements clés abordés dans cette introduction, à savoir le déterminisme du recrutement, la connectivité au sein et entre les différents stades de vie et l'exposition aux facteurs de pressions, soulève de nouvelles questions de recherche. Ce travail tâchera d'y répondre via des approches de modélisation successives faisant très largement appel à la MHB.

### 1.6.1. Un recrutement en deux phases chez les espèces nourriceries-dépendantes ?

Avant de développer un modèle spécifique, il apparait nécessaire de confronter les hypothèses écologiques que nous avons formulées sur le recrutement des espèces nourriceries-dépendantes aux données existantes. Nous nous sommes intéressés plus particulièrement aux espèces de poissons plats, emblématiques de cette dépendance aux nourriceries (Iles and Beverton, 2000). Nous avons testé les hypothèses formulées en 1.1.3 posant la base d'un recrutement s'effectuant en deux phases : une première phase génératrice de variabilité où s'exercent principalement des phénomènes de mortalité densité-indépendants liés aux conditions hydroclimatiques dans lesquelles évoluent les premiers stades pélagiques, suivie d'une phase benthique (juvénile) où interviennent des phénomènes de densité-dépendance (i.e. compétition pour l'espace, les ressources). Les acquis de cette première phase devront permettre également de préciser la formalisation des processus de mortalité densité-dépendante affectant les juvéniles au sein des aires de nourriceries dans des modèles intégrés de cycle de vie.

Une démarche de méta-analyse (mobilisant un outil de modélisation hiérarchique Bayesienne) est mise en œuvre pour tester cette hypothèse. Les données stock-recrutement (traditionnellement les couples biomasse féconde (poids) – nombre de recrues (nombre)) disponibles sont généralement peu informatives (Minto *et al.*, 2008) et ne permettent pas de déterminer une relation fiable sur la base d'une série de données stock-recrutement provenant d'une population unique (Lee *et al.*, 2012; Burrow *et al.*, 2013). Nous avons donc eu recours à une démarche de méta-analyse visant à extraire des tendances communes à partir des données stock-recrutement disponibles sur l'ensemble des populations de poissons plats évaluées au niveau planétaire. Cette première phase de la thèse fera l'objet du second chapitre intitulé "Modélisation du processus de recrutement chez les espèces nourriceries-dépendantes" (Publication 2014 dans l'*ICES Journal of Marine Science* ; édition speciale "*Hjort 1914 commemorative issue*").

### 1.6.2. Quels sont les impacts de la rétention larvaire et de la faible mobilité des adultes sur le fonctionnement spatial des populations ?

Les présomptions de l'existence d'une forte rétention larvaire et d'une faible mobilité des stades adultes et subadultes soulèvent des questions quant au fonctionnement spatial des populations de poissons nourriceries-dépendantes. Nous avons vu que les oeufs et larves pouvaient être soumis à une forte dispersion liée à la vie pélagique sous l'influence des courants marins. Cette capacité de dispersion ne signifie en aucun cas une diffusion uniforme des individus au sein de la zone de répartition et il apparait au contraire que les phénomènes de rétention larvaire locaux sont très courants (Sheaves and others, 2009; Gerber *et al.*, 2014). Afin d'appréhender pleinement le fonctionnement spatial des populations il convient de poser également la question de la connectivité des stades plus âgés, et notamment le stade adulte (Frisk *et al.*, 2013). En effet, les patrons spatiaux de connectivité (ou le cas échéant d'absence de connectivité) résultant de la dynamique des premiers stades, couplés à la ségrégation spatiale des juvéniles, donnent une importance toute particulière aux conséquences des capacités de mouvements des adultes (Abecasis *et al.*, 2014; Pittman *et al.*, 2014) sur la distribution spatiale des géniteurs et les échanges entre sous–entités spatiales.

Pour aborder cette question, nous évaluons, via un modèle de cycle de vie intégrant la composante spatiale des stades successifs, l'impact de différentes hypothèses sur la structuration spatiale d'une population de sole commune. Nous discutons des conséquences de diverses hypothèses sur le fonctionnement spatial de la population sur des indicateurs pour une gestion spatialisée de la population. Cette partie fait l'objet du troisième chapitre de la thèse intitulé "Quantifier l'impact de la connectivité aux différents stades du cycle de vie sur la perception du fonctionnement de la population de sole en Manche Est" (Article soumis au *Canadian Journal of Fisheries and Aquatic Sciences*)

### 1.6.3. Quels sont les effets des différentes pressions s'exerçant au cours du cycle de vie ?

L'analyse de l'influence relative des différents facteurs de pression au cours du cycle de vie des espèces nourricerie-dépendante est essentielle afin de fournir une aide à la décision pour hiérarchiser l'influence des facteurs et aider à fixer des priorités d'action de gestion.

L'approche de modélisation intégrée du cycle de vie (et la paramétrisation qui découle de la démarche d'inférence Bayesienne) développée dans la deuxième phase de la thèse est ici valorisée afin de prendre en compte, par une approche de simulation basée sur des scénarios, l'influence de différents facteurs de pression associés à différents stades du cycle de vie et les possibles interactions (e.g. pêche et climat). Le caractère spatial du modèle est valorisé via l'exploration de scénarios de gestion spatialisée. Cette partie fait l'objet du quatrième chapitre de la thèse intitulé "Quantifier l'impact des pressions agissant au cours du cycle de vie de la sole en Manche Est " (Article en cours de préparation pour un numéro spécial du projet européen VECTORS, dans un journal à définir).

## 1.7. Cas d'étude : le stock de sole commune de Manche Est

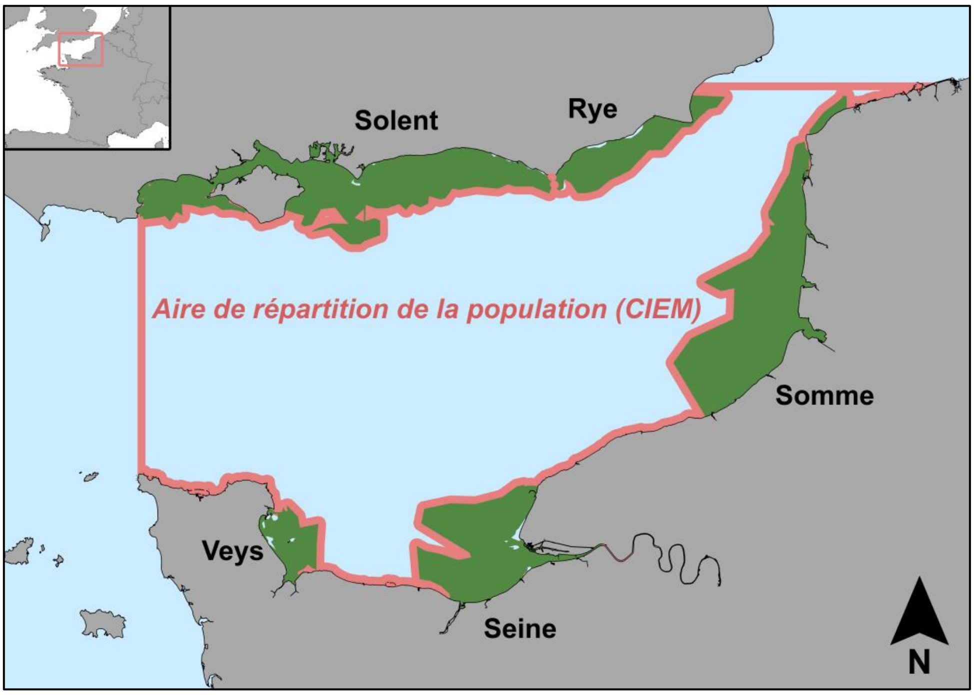

Figure 1.4 - Stock de sole de Manche Est, limites géographiques et secteurs de nourriceries

A l'issue du second chapitre, qui prend en compte l'ensemble des populations évaluées de pleuronectiformes, les questions de recherche sont développées en s'appuyant principalement sur le cas d'étude de la population de Sole commune de la Manche Est. Le cycle de vie bien connu de cette population est emblématique de la complexité du fonctionnement des ressources marines exploitées et fait largement échos aux trois points clés mis en avant dans cette introduction :

*(i) Un processus de recrutement caractéristique des espèces nourriceries-dépendantes.*

Les œufs sont pondus entre février et juin dans des aires de pontes bien identifiées sur des fonds de plus de 20 mètres. Suite à la ponte, les œufs/larves dérivent de manière passive puis active (à l'approche des côtes) durant 6 semaines environ pour éventuellement s'établir sur les secteurs de nourriceries côtiers et estuariens. Cette phase présente un succès (i.e. taux de survie) faible, variable en fonction des conditions hydroclimatiques. Suite à la métamorphose (i.e. passage d'un mode de vie pélagique à benthique), les stades juvéniles effectuent leur croissance durant environ 2 ans au sein de secteurs côtiers et estuariens de nourriceries. Le succès du recrutement est donc la résultante de l'enchaînement de la phase pélagique des tout premiers stades suivie de cette phase de croissance des juvéniles dans des nourriceries aux capacités d'accueil limitées. Il n'existe pas, dans l'évaluation réalisée par le CIEM (ICES, 2013), de relation stock-recrutement établie pour cette population (Figure 1.6), ce qui nuit à sa performance (Punt, 1997) et empêche le calcul d'une biomasse au Rendement Maximum Durable (RMD) recommandée par l'approche écosystémique des pêches. Ainsi le recrutement futur n'est pas prédit par l'évaluation mais est considéré comme étant une moyenne géométrique des recrutements des années passées (ICES, 2013).

(ii) *Connectivité et fonctionnement spatial*

Le fonctionnement de cette population se caractérise par l'absence potentielle de connectivité aux différents stades. Le stock de sole de Manche Est (zone CIEM VIId) est soutenu par cinq nourriceries côtières et estuariennes bien identifiées (Rochette *et al.*, 2010), disposées le long des côtes françaises et anglaises (Figure 1.4) qui concentrent l'intégralité des juvéniles (i.e. rétention juvénile). A l'issue de deux années de vie au sein de ces secteurs, les subadultes rejoignent les zones de distribution plus au large, opèrent leur maturation sexuelle et rentrent dans la phase d'exploitation ciblée par la pêche. Les mouvements des individus adultes entre les différentes régions de la zone sont vraisemblablement limités (Rochette *et al.*, 2012). Par ailleurs, il ressort des modèles biophysiques de derive larvaire que les patrons de connectivité entre les différentes zones de ponte et les nourriceries côtières sont très limités (i.e. rétention larvaire) (Rochette *et al.*, 2012). Ainsi, l'hypothèse d'un fonctionnement de type meta-population avec une connectivité très limitée entre plusieurs composantes entretenues par des nourriceries spécifiques se révèle réaliste.

### (iii) *Une exposition à de multiples facteurs de pression*

Cette population est soumise à différentes pressions anthropiques et environnementales (Le Pape *et al.*, 2007; Figure 1.5). Elle est tout d'abord fortement exploitée (Figure 1.6) avec une mortalité par pêche évaluée bien au-dessus de $F_{RMD}$ (facteur de 1.6 en 2012 ; ICES, 2013). Les pays exploitant ce stock sont en ordre décroissant d'importance la France, la Belgique et le Royaume-Uni (respectivement 62, 23 et 16 % des débarquements en 2012 ; ICES, 2013). Les nourriceries sont fortement exposées aux activités humaines qui ont entrainé une réduction de leur surface (e.g. diminution drastique de la surface de l'estuaire de la Seine suite à des aménagements portuaires ; Delsinne, 2005; Rochette *et al.*, 2010) et de leur qualité (présence de substances xénobiotiques ; Le Pape *et al.*, 2007; Courrat *et al.*, 2009) avec un impact sur la survie, le développement et la croissance des stades juvéniles (Gilliers *et al.*, 2006; Amara *et al.*, 2007).

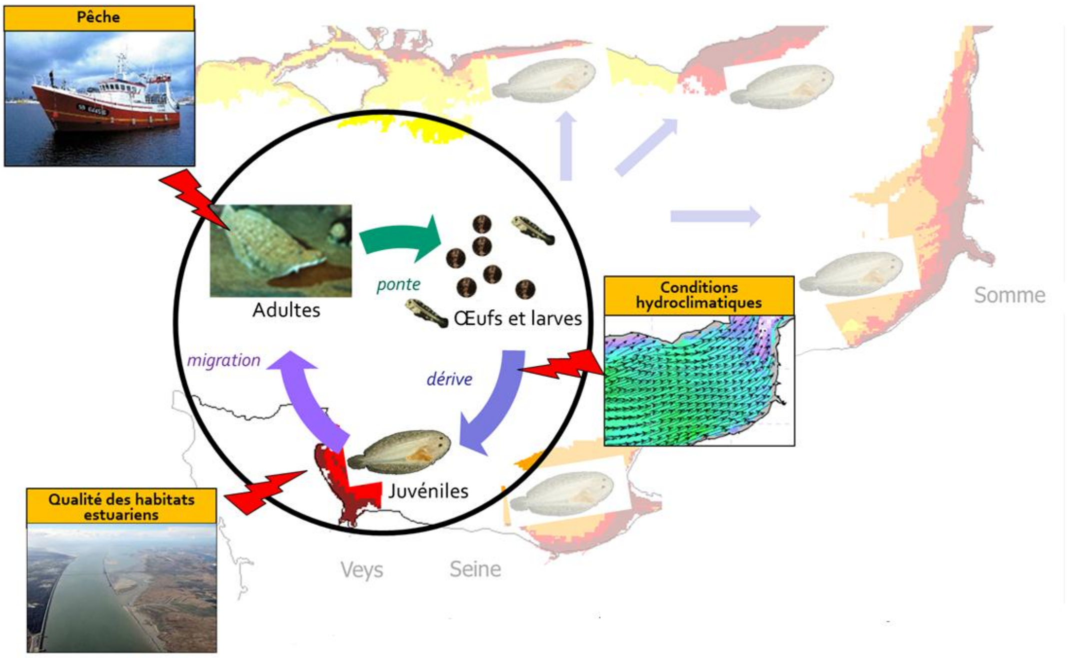

Figure 1.5 - La sole de Manche Est : un cycle de vie soumis à différentes pressions

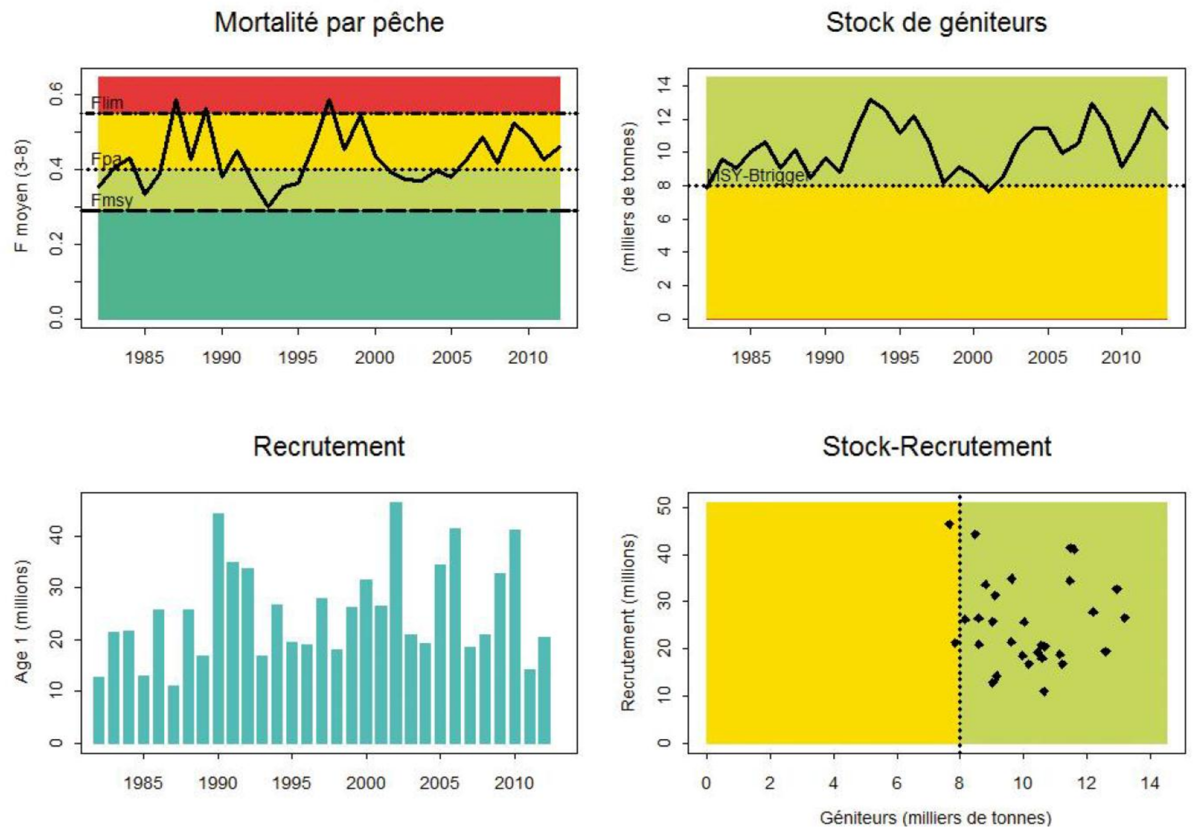

Figure 1.6 - Diagnostic (ICES, 2013) pour la sole de Manche Est en 2013. Source : Ifremer

## 1.8. Démarche de modélisation

La population de sole de Manche Est a fait l'objet de nombreux travaux scientifiques, apportant les connaissances requises à l'exploration d'une approche de modélisation du cycle de vie (Rochette *et al.*, 2013). Le travail réalisé dans cette thèse est essentiellement basé sur ce cas d'étude, objet exclusif des chapitres 3 et 4 également intégré à la méta-analyse réalisée au chapitre 2. Il s'intéresse aux processus de recrutement, à l'influence de la connectivité spatiale au cours du cycle de vie sur la dynamique de la popualtion et à la quantification des conséquences des pressions naturelles et anthropiques.

Ainsi la démarche de modélisation suivie au cours de cette thèse se structure en trois chapitres successifs chacun centré sur une de ces questions en lien avec le cycle de vie des espèces nourriceries-dépendantes (Figure 1.7) :

- le deuxième chapitre explore la relation stock-recrutement chez les populations de poissons plats;
- le troisième chapitre explore l'impact de la ségrégation spatiale entre pools d'individus au long du cycle de vie de la population de soles de Manche Est ;

- le quatrième explore l’effet respectif des différentes pressions agissant au cours du cycle de vie de cette population, via une approche de scénarios.

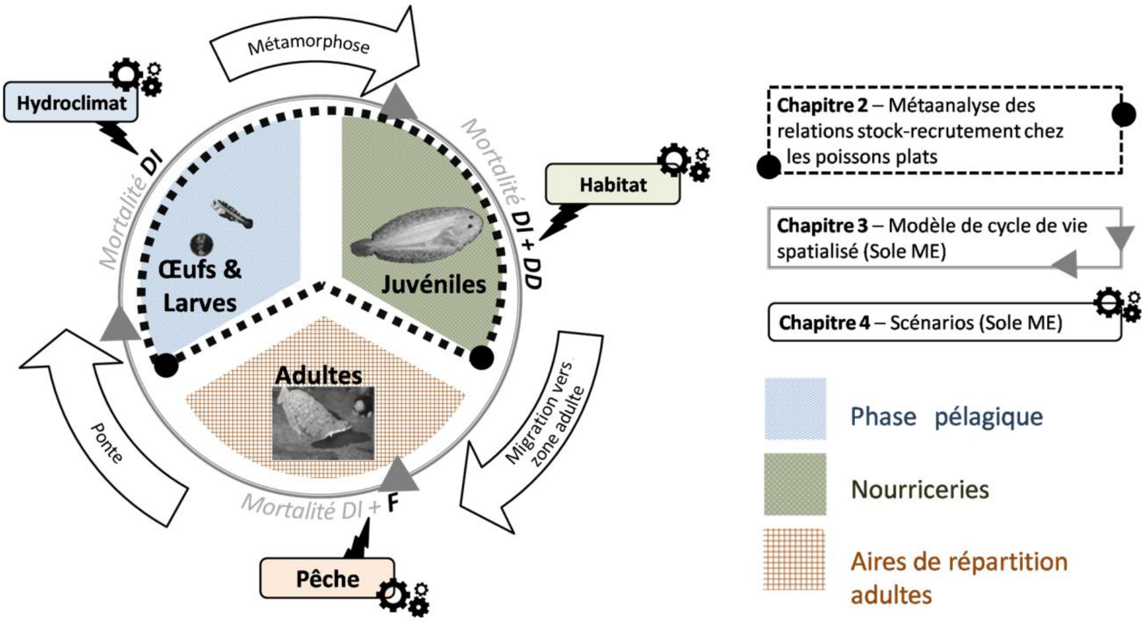

Figure 1.7 - Cycle de vie des espèces nourriceries-dépendantes et démarche de modélisation suivie au cours de la thèse

# 2. Modélisation du processus de recrutement chez les éspeces nourriceries-dependantes

## Introduction du chapitre

Le recrutement des espèces nourriceries-dépendantes se caractérise par une combinaison de deux phases (cf. portion du cycle en pointillés de la Figure 1.7) : (i) une première phase pélagique (œufs et larves) largement dominée par des processus de mortalité densité indépendants et exhibant une forte variabilité (interannuelle) liée aux conditions hydroclimatiques; (ii) une seconde phase benthique suite à la métamorphose et l'installation des individus dans des nourriceries à la capacité d'accueil limitée. Les connaissances biologiques et écologiques suggèrent que cette seconde phase est caractérisée par l'existence de phénomènes de mortalité densité-dépendants générés par la compétition pour l'espace et les ressources. Ainsi, l'hypothèse de concentration (Iles et Beverton, 2000) prévoit un « tamponnement » durant la seconde phase de la variabilité générée durant la première (Le Pape et Bonhommeau, *in press*).

Dans ce chapitre, nous confrontons cette hypothèse écologique d'un recrutement en deux phases aux données « stock-recrutement » (SR) existantes, à partir d'une méta-analyse compilant les séries historiques issues d'évaluations de stocks disponibles. Ces données associent chaque année un couple biomasse féconde-recrutement. Deux constats majeurs ressortent de l'observation des données stock-recrutement et de l'abondante littérature ayant abordé ce sujet : (i) les modèles de relations stock-recrutement sont traditionnellement largement dominés par une forte variabilité à même de masquer la relation sous-jacente ; (ii) le faible nombre de données disponibles à l'échelle d'une seule population permet rarement d'extraire un signal clair et informatif. Face à ces deux écueils nous avons choisi d'aborder cette question via (i) un focus sur la variance autour de la relation SR plutôt que sur la relation moyenne, (ii) une approche consistant à analyser conjointement, par le biais de MHB, les données disponibles pour l'ensemble des populations de poissons plats évaluées pour en extraire des signaux communs.

Ainsi, dans un premier temps, nous réalisons une comparaison « inter-ordres » pour comparer la variabilité du succès du recrutement des poissons plats (pleuronectiformes) avec celle des autres ordres. Dans un second temps nous nous appuyons sur le cadre des modèles hiérarchiques Bayesiens pour proposer une méta-analyse des relations SR des populations de poissons plats évaluées (39 populations ; 12 espèces) par une modélisation explicite de la variance autour de ces relations. Les signaux extraits de cette modélisation sont ensuite comparés aux traits d'histoire de vie des différentes espèces.

# Density dependence can be revealed by modeling the variance in the stock-recruitment process. An application to flatfish

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## Abstract

Recruitment success in marine species is mostly driven by the high and variable mortality of first life stages, and the relationships between stock and recruitment are then largely dominated by residual variability. We show that analyzing the residual variability may provide insights on the density-dependence process occurring during the recruitment. Following the seminal formulation of Minto et al. (Minto *et al.* Survival variability and population density in fish populations. Nature, 2008), we show that when recruitment is considered as a sequence of a pelagic stage with stochastic density independent mortality followed by a second stage with stochastic density dependent mortality, then the variability of the recruitment rate per spawning biomass (RPSB) should be a decreasing function of the spawning biomass. Using stock-recruit data of 148 stocks from the RAM-legacy database, we provide a test of this hypothesis by showing that the variability of RPSB is lower for fish species with the higher concentration during juvenile stages. Second, a Hierarchical Bayesian model (HBM) is built to derive a meta-analysis of stock-recruit data for 39 flatfish stocks, characterized by a high concentration of juveniles in coastal nursery habitats. Results of the HBM show that variance of the RPSB decreases with the spawning biomass for almost all

stocks, thus providing strong evidence of density-dependence during the recruitment process. Finally, we attempt to relate patterns in recruitment variance to relevant life history traits of flatfish species.

## 2.1. Introduction

Understanding the relationship between the spawning potential and the recruitment (*i.e.*, the Stock-Recruitment process, hereafter denoted SR) is pivotal for fisheries ecology and fisheries management (Hilborn and Walters, 1992; Walters and Martell, 2004; Houde, 2008). The recruitment process of marine fish species is one of the main drivers of fluctuation in population abundance and critically depends upon the high and fluctuating mortality of early life stages (Chambers and Trippel, 1997; Levin and Stunz, 2005; Juanes, 2007; Gallego *et al.*, 2012). In particular, the recruitment rate per unit of spawning biomass (hereafter denoted $RPSB$) at low population size determines the resilience to exploitation and environmental disturbance (Mangel *et al.*, 2010; Keith *et al.*, 2012; Lee *et al.*, 2012). SR relationships are primordial for estimating biological and management reference points, and constitute key components of forward simulations and management strategies evaluation (Punt *et al.*, 2001).

Analyzing and modeling SR relationships is both a statistical and an ecological challenge. Several statistical difficulties such as the lack of long time series of SR data, the poor contrast in stock and spawning potential levels, the presence of observation errors and/or time correlation in the data hinder the identification of SR relationships and the estimation of associated parameters (Hilborn and Walters, 1992; Needle, 2001; Hinrichsen, 2001; Walters and Martell, 2004). Beyond these statistical issues, the complexity of the mechanisms involved in recruitment variability is also poorly represented by SR models as many factors (*e.g.,* hydroclimate, food availability, competition and predation) influence the survival at young stages and the recruitment, in addition to spawning biomass. The high and unpredictable fluctuating levels of mortality in early life stages (May, 1974; Koslow, 1992; Chambers and Trippel, 1997; Daewel *et al.*, 2011) reduces or even totally suppress the correlation between the spawning biomass and the subsequent year class (Hilborn and Walters, 1992; Myers and Barrowman, 1996; Hinrichsen, 2001; Rochette *et al.*, 2012). The recruitment process is thus rarely well described by classical SR models and the residual stochastic variance often largely dominates the signal (Minto *et al.*, 2008).

Motivated by the paucity of data and the difficulty to identify an average signal from a single SR data set, interest in meta-analysis has grown considerably over the past two decades. Meta-analysis allows to combine information from several fish stocks to help unraveling general patterns that could not be detected with only few data, and thus provide a better understanding of the recruitment process (Myers and Barrowman, 1996; Myers and Mertz, 1998; Myers *et al.*, 1999). Open data bases such as the RAM Legacy Stock Assessment Data Base, developed by Myers and its successors, has opened new horizons to explore a variety of question related to the recruitment process (Myers and Cadigan, 1993; Minto *et al.*, 2008; Ricard *et al.*, 2011). Although not the only tool for meta-analysis, Hierarchical Bayesian Models (HBM) have revealed as a comprehensive and flexible framework for “borrowing strength” between SR data sets (Liermann and Hilborn, 1997; Chen and Holtby, 2002; Prévost *et al.*, 2003; Michielsens and McAllister, 2004; Forrest *et al.*, 2010; Hillary *et al.*, 2012).

In this extensive literature, a large body of work has concentrated on unraveling the expected mean SR relationship to test for the existence of density-dependence such as compensation (Myers and Barrowman, 1996; Hillary *et al.*, 2012) or depensation (Liermann and Hilborn, 1997; Keith *et al.*, 2012). However, although the variance often dominates SR process, relatively poor attention has been paid to examining how the pattern of residual variability in the RPSB can provide insights to the existence of density dependence mechanisms (Myers, 2001; Minto *et al.*, 2008). According to the seminal concentration hypothesis (Rijnsdorp *et al.*, 1992; Iles and Beverton, 2000), when considering recruitment as a sequence of stochastic process, the variability of the $RPSB$ should be dampened if density dependence occurs at some latter stages in the sequence. This results in two hypotheses that can be challenged against data. First, when comparing various species, an interspecific pattern showing lower relative variance of the $RPSB$ for species with strong density dependence regulation during the early life stages should emerge. Second, in the context of SR modeling for one single stock, the variability of the $RPSB$ should be lower at higher stock levels (heteroscedasticity). Based on a meta-analysis of 147 stocks of exploited fish of various species, Minto et al. (2008) already inferred the existence of such a heteroscedasticity pattern for many stocks. This contrasts with classical statistical hypotheses, *e.g.,* logNormal or Gamma random variation with constant relative (Jiao *et al.*, 2004), and may have non negligible influence on estimates of the $RPSB$ at low stock size or of management reference points such as the Maximum Sustainable Yield (Burrow *et al.*, 2013).

In the present study, we use flatfish species as ideal candidates to elaborate more on these two hypotheses. Flatfish are widely distributed species with high commercial interest (Gibson, 2005), and providing insights on their recruitment process is of major interest for both scientific and management purposes (Iles, 1994). Most of the flatfish are typically nursery dependent species, whose juvenile stages concentrate on coastal nurseries habitat after a pelagic phase, and thus constitute an ideal case study to analyze how density dependent regulation in the latter stage can modulate the recruitment variability (Iles and Beverton, 2000). The drift of early life stages (eggs to post-larvae) determines their survival and transport from spawning grounds to nursery habitat (Miller, 2007; Nash *et al.*, 2007). This first phase of the recruitment process is characterized by high and highly fluctuating mortality rates (van der Veer *et al.*, 2000a; Daewel *et al.*, 2011; Rochette *et al.*, 2012), mainly driven by density independent factors such as temperature effects on growth and survival during eggs and larvae drift. Although the underlying driving process are still under debate, density dependent mechanisms such as growth limitation and mortality related to food deprivation or increased competition for space occur after metamorphosis and settlement on nurseries (Iles and Beverton, 2000; van der Veer *et al.*, 2000a; Le Pape *et al.*, 2003a; Rooper *et al.*, 2004; Juanes, 2007; Johnson, 2007; Nash and Geffen, 2012).

Our objective is to quantitatively assess how the variance of the survival can be analyzed to test for the existence of density dependent regulation at the juvenile stage for flatfish species. We first rely on Minto et al. (2008) to highlight why a recruitment process resulting from the combination of two sequential stochastic phases with density dependence occurring only in the second one results in a dampened variance of the $RPSB$ that varies with stock level. Second, we use 148 stocks from the RAM Legacy Stock Assessment Data Base to test for the hypothesis that the relative variance of the $RPSB$ is lower for flatfish (Pleuronectiforms) than for 3 other well documented orders (Clupeiforms, Perciforms and Gadiforms) for which early life stages are suspected to be less subject to concentration than flatfish. Third, we focus on the SR data series compiled for 39 flatfish stocks and develop a HBM to jointly analyze the 39 data sets to test for the existence of heteroscedasticity in the variance of the $RPSB$ due to density dependent regulation in the latter stage of the recruitment process. Last, we examined whether some life history traits suspected to influence the recruitment process (pelagic larval stage duration, level of dependence to restricted nursery grounds) were correlated with the patterns of heteroscedasticity in the $RPSB$ variance.

## 2.2. Materials and methods

### 2.2.1. A theoretical model for the variance of a two-stage recruitment process

As a generic template for the recruitment process in demersal marine fishes, we combine an egg/larval pelagic phase between stage $S$ ($S$ being a measure of the spawning stock size) and early juvenile $J$ (just after the end of larval stages), with mortality driven by stochastic density-independent processes, followed by a second phase between $J$ and recruits $R$ where both density-dependent mortality and environmental stochasticity occur. Let us denote $\alpha_1$

the average survival rate in the first stage with independent and identically distributed (*iid*) logNormal errors $e^{\varepsilon_1}$ with $\varepsilon_1 \sim N(0, {\sigma_1}^2)$:

(1) $$J = \alpha_1 \cdot S \cdot e^{\varepsilon_1}$$

Considering that both density dependence and stochasticity occur between larvae and recruits, the abundance of recruits $R$ is:

(2) $$R = \alpha_2 \cdot J \cdot f(J) \cdot e^{\varepsilon_2}$$

with $f(J)$ a function (defined latter) modeling how the survival $R/J$ depends upon $J$, and $e^{\varepsilon_2}$ *iid* logNormal errors with $\varepsilon_2 \sim N(0, {\sigma_2}^2)$. Combining the two sequential phases (1) and (2), the $RPSB$ in the log scale is:

(3) $$\log(\mathrm{RPSB}) = \log\left(\frac{R}{S}\right) = \log(\alpha_1 \cdot \alpha_2) + \log(f(\alpha_1 S e^{\varepsilon_1})) + \varepsilon_1 + \varepsilon_2$$

Considering that the random processes during the two stages are independent, the variance of log(RPSB) is:

(4) $$Var(\log(\mathrm{RPSB})) = {\sigma_1}^2 + {\sigma_2}^2 + Var(\log(f(\alpha_1 S e^{\varepsilon_1})) + 2 \cdot Cov(\log(f(\alpha_1 S e^{\varepsilon_1})), \varepsilon_1)$$

At this step, eq. (4) already shows that even if the two sequential phases have independent random variations, the variance of the whole survival process is not simply additive because, as shown in the covariance term, the stochasticity in the first phase will interplay with the density dependence of the second stage.

Let us now make the density dependent function $f(J)$ explicit by introducing the general Deriso-Schnute SR model (Quinn and Deriso, 1999):

(5) $$f(J) = (1 - \beta_2 \cdot \gamma \cdot J)^{1/\gamma}$$

with $\beta_2 \geq 0$, and the two classical compensatory Beverton-Holt (BH) and over-compensatory Ricker forms obtained as particular cases when $\gamma = -1$ and $\gamma \to 0$ respectively.

Following the same line of reasoning than Minto et al. (2008) (using Delta method to approximate the variance and covariance terms in eq. (4)), $Var(\log(\mathrm{RPSB}))$ can be approximated by:

(6) $$Var(\log(\mathrm{RPSB})) \approx \left(1 - \frac{\beta_2 \cdot \alpha_1 \cdot S}{1 - \gamma \cdot \beta_2 \cdot \alpha_1 \cdot S}\right)^2 {\sigma_1}^2 + {\sigma_2}^2$$

which simplifies under the special Beverton-Holt (eq. 7a) and Ricker (eq. 7b) cases to:

$$\text{(7) a} \qquad Var(\log(\text{RPSB})) \approx \left(1 - \frac{\beta_2 \cdot \alpha_1 \cdot S}{1 + \beta_2 \cdot \alpha_1 \cdot S}\right)^2 {\sigma_1}^2 + {\sigma_2}^2$$

$$\text{(7) b} \qquad Var(\log(\text{RPSB})) \approx (1 - \beta_2 \cdot \alpha_1 \cdot S)^2 \cdot {\sigma_1}^2 + {\sigma_2}^2$$

Equation (6) and particular declinations (7ab) highlight how the variance of the density independent stochastic phase (${\sigma_1}^2$) is modulated by the intensity of the density dependence, here parameterized by $\beta_2$ and the shape parameter $\gamma$. According to eq. (7a), when considering a compensatory BH density-dependent form, $Var(\log(\text{RPSB}))$ is a monotonous decreasing function of the stock size $S$, between ${\sigma_1}^2 + {\sigma_2}^2$ and the minimum value ${\sigma_2}^2$. When considering a Ricker form (*i.e.*, with over-compensation), $Var(\log(\text{RPSB}))$ decreases until $S < 1/\beta_2\alpha_1$, and then increases for higher $S$. As stated by Minto et al. (2008), such a domed-shaped relationship is general for over-compensatory SR models such as Ricker or Shaefer. Nevertheless, the pivotal stock value $(1/\beta_2\alpha_1)$ is generally rather high, and, for exploited stocks, most of the values of $S$ are likely to occur in the range where the variance decreases with the stock size (Minto *et al.*, 2008).

Even if considering the recruitment process as a sequence of two phases as in (1)-(2) could fit well to many fish species (flatfish in particular), such a two-stage model is over parameterized for classical SR analysis for which no data about the intermediate stage $J$ is available. However, the theoretical construction developed above shows that when considering classical SR models under the hypothesis of LogNormal random variations as in eq. (8):

$$\text{(8)} \qquad \log(RPSB) = \log(\alpha) + \log(f(\mathrm{S}, \beta, \gamma)) + \varepsilon$$

with $f(\cdot)$ the generalized Deriso-Schnute form in eq. (5) and *iid* logNormal errors $e^{\varepsilon}$, with $\varepsilon \sim N(0, \sigma^2)$, the following patterns in the variance of $\log(RPSB)$ ($\sigma^2$ in eq. (8)) should be expected:

(i) First, eqs. (7ab) show that the variance should be lower for species (or orders) with concentration mechanisms occurring at a later stage in the recruitment process. In particular, eq. (7a) highlights that when considering a BH form, all things being equal, the higher the density dependence in the second stage (*i.e.*, the higher $\beta_2$), the lower the ultimate variance. The asymptotic minimum values of $Var(\log(RPSB))$ is ${\sigma_2}^2$, *i.e.* the variance of the first phase ${\sigma_1}^2$ is fully dampened by density dependence.

(ii) Second, when considering the resulting patterns of stochasticity for a single stock, $\sigma^2$ should be a function of the stock, as soon as density dependence occurs in the second phase of the recruitment process (*i.e.*, $\beta_2$ is non-null). For realistic parameters and most of the observed stock values, and especially largely exploited flatfish, $\sigma^2$ is expected to be a decreasing function of $S$, whatever the density dependence form.

### 2.2.2. Stock-recruits data

The data (Table 2.1) included 148 stocks: 39 stocks of 17 flatfish species (Pleuronectiforms) and 109 stocks of 44 non-flatfish species (Clupeiforms, Perciforms and Gadiforms). All data were derived from statistical catch-at-age models (*e.g.*, VPA, XSA, ADAPT) to ensure homogeneity. Most of the stock-recruitment series were obtained from the RAM legacy database (Ricard *et al.*, 2011). The data from RAM database was completed with three additional flatfish stocks, and by adding the most recent data gathered from flatfish stock assessment reports published by regional working groups. This corresponds to 1237 SR flatfish observations (Table 2.2), constituting an increment of 15% with reference to suitable flatfish data found in the RAM legacy database (Ricard *et al.*, 2011).

Table 2.1 - Synthesis of the dataset used for the inter orders analysis (RAM legacy database supplemented by additional data for Pleuronectiforms).

| Order | Species | Populations | Observations<br>total (min,mean,max per population) |
|---|---|---|---|
| Clupeiformes | 9 | 30 | 1052 (16,35,54) |
| Perciformes | 25 | 33 | 1288 (9,39,79) |
| Gadiformes | 10 | 46 | 1518 (12,33,77) |
| Pleuronectiformes | 19 | 39 | 1237 (10,32,55) |
| Total | 63 | 148 | 5095 |

### 2.2.3. Comparing the variance of the survival process between fish orders

The 148 stocks were included in a first analysis designed to compare the variance of recruitment process between the four fish orders. For each of the 148 stocks, $Var(\log(RPSB))$ was estimated independently by fitting BH or Ricker models as in eq. (8) with a simple least-square procedure. No standardization of the data was required, as $\sigma^2$ in eq. (8) is independent of the unit of $S$ and $R$. The estimates of $\sigma$ were then compared across orders, and a multiple comparison Tukey test was used to test for the between orders difference.

Table 2.2 - Synthesis of Stock-Recruitment data (upgraded from RAM legacy database) and life history traits for Pleuronectiforms. SPRF=0 is the cumulative biomass produced per Recruit over its lifetime in the scenario of no fishing mortality (see text for details).

| Species/Stock | SPR$_{F=0}$ | Time series range | Nursery type | Pelagic stage duration (days) | Uncertainty (CV in %) | |
|---|---|---|---|---|---|---|
| | | | | | *S* | *R* |
| Alaska plaice (*Pleuronectes quadrituberlatus*) | | | | | | |
| Bering Sea – Aleutian Islands | 2.51 | 1975 – 2005 | 2 | NA | | |
| American plaice (*Hippoglossoides platessoides*) | | | | | | |
| NAFO 3LNO | 2.53 | 1960 – 2002 | 4 | 75 | | |
| NAFO 3M | 2.77 | 1988 – 2006 | | | | |
| NAFO 5YZ | 1.40 | 1980 – 2007 | | | | |
| Gulf of Maine – Georges banks | 2.18 | 1980 – 2004 | | | | |
| West Greenland | 2.09 | 1982 – 1991 | | | | |
| Arrowtooth flounder (*Atherestes stomias*) | | | | | | |
| Eastern Bering Sea – Aleutian Islands | 1.56 | 1976 – 2002 | NA | 135 | | |
| Arctic | 2.47 | 1961 – 2004 | | | | |
| Dover sole (*Microstomus pacificus*) | | | | | | |
| Gulf of Alaska | 0.85 | 1984 – 2004 | NA | 460 | | |
| Flathead sole (*Hippoglossoides elassodon*) | | | | | | |
| Bering Sea – Aleutian Islands | 0.73 | 1977 – 2005 | NA | NA | 5 | 17 |
| Gulf of Alaska | 0.86 | 1984 – 2006 | | | | |
| Fourspotted megrim (*Lepidorhombus boscii*) | | | | | | |
| ICES 8c9a | 0.50 | 1986 – 2010 | 4 | NA | | |
| Greenland halibut (*Reinhardtius hippoglossoides*) | | | | | | |
| NAFO Subarea 2 and Divisions 3 *KLMNO* | 4.34 | 1975 – 2010 | 3 | 150 | | |
| Eastern Bering Sea – Aleutian Islands | 3.17 | 1970 – 2011 | | | | |
| Northeast Arctic | 8.43 | 1964 – 2010 | | | | |
| Megrim (*Lepidorhombus whiffiagonis*) | | | | | | |
| ICES 8c9a | 0.45 | 1986 – 2010 | 4 | NA | | |
| Pacific halibut (*Hippoglossus stenolepis*) | | | | | | |
| North Pacific | 131.27 | 1996 – 2012 | 2 | 135 | | |
| Plaice (*Pleuronectes platessa*) | | | | | | |
| ICES IIIa | 2.46 | 1978 – 2004 | 2 | 60 | 10 | 25 |
| North Sea | 2.23 | 1957 – 2011 | | | | |
| Irish Sea | 1.58 | 1964 – 2008 | | | 31 | 19 |
| Celtic Sea | 1.98 | 1977 – 2009 | | | | |
| ICES VIId | 2.70 | 1980 – 2011 | | | | |
| ICES VIIe | 2.45 | 1980 – 2010 | | | | |
| Rex sole (*Glyptocephalus zachirus*) | | | | | | |
| Gulf of Alaska | 0.57 | 1982 – 2004 | 4 | 365 | | |
| Sole (*Solea solea*) | | | | | | |
| ICES IIIa | 1.20 | 1984 – 2011 | 4 | 45 | | |
| North Sea | 1.16 | 1957 – 2011 | | | | |
| Irish Sea | 0.98 | 1970 – 2011 | | | | |
| Celtic Sea | 1.31 | 1971 – 2011 | | | | |
| ICES VIId | 1.16 | 1982 – 2010 | | | | |
| ICES VIIe | 1.19 | 1969 – 2010 | | | | |
| ICES VIII | 1.91 | 1984 – 2010 | | | | |
| Summer flounder (*Paralychtis dendatus*) | | | | | | |
| North Atlantic | 3.48 | 1982 – 2007 | 1 | 50 | | |
| Winter flounder (*Pseudopleuronectes americanus*) | | | | | | |
| NAFO 5Z | 1.50 | 1982 – 2006 | 1 | 35 | | |
| Southern New England – Mid Atlantic Bight | 1.39 | 1981 – 2007 | | | 11 | |
| Witch flounder (*Glyptocephalus cynoglossus*) | | | | | | |
| NAFO 5Y | 1.10 | 1982 – 2007 | 4 | 240 | 14 | |
| Yellowfin sole (*Limanda aspera*) | | | | | | |
| Bering sea – Aleutian Islands | 0.91 | 1964 – 2003 | 2 | 45 | | |
| Yellowtail flounder (*Limanda ferruginea*) | | | | | | |
| Cape Cod – Gulf of Maine | 1.16 | 1985 – 2006 | 4 | 105 | | |
| Georges Banks | 1.44 | 1973 – 2007 | | | | |
| Southern New England – Mid Atlantic Bight | 1.28 | 1973 – 2006 | | | | |

### 2.2.4. A HBM to test for heteroscedasticity in flatfish recruitment process

A HBM was built to jointly analyze the 39 flatfish SR data sets (Table 2.2) and to assess the patterns of heteroscedasticity in the variance of the SR process. Based on the theoretical construction (1)-(2), the most parsimonious model in eq. (8) was considered, with a variance of the recruitment process $\sigma^2$ considered as a function of the stock size (see explanations below, in eq. (11)). Each SR data set, if considered alone, is suspected to provide insufficient information to estimate the variance as a parametric function of $S$ (Burrow *et al.*, 2013). Hence, a hierarchical approach was required to borrow strength between SR data sets.

*Data standardization*

To make the parameters comparable across stocks (Minto *et al.*, 2008), the SR data series were first standardized so all $S$ and $R$ are expressed in comparable units and ranges across the 39 stocks. To do so, the recruitment data were standardized into the same unit than the stock (*i.e.*, biomass of spawners). The standardization introduced by Myers (2001) was used. It consists in multiplying $R$ by $SPR_{F=0}$ which is the cumulative Spawning biomass Produced by a Recruit over its lifetime in the scenario of no fishing mortality (Gabriel *et al.*, 1989).

$$(9) \qquad SPR_{F=0} = \sum_{i_{rec}}^{i_{max}} e^{-[M_i(i-i_{rec})]} W_i Mat_i$$

where $i_{rec}$ is the age of recruitment, $i_{max}$ is the maximum age-class, $M_i$ is the natural mortality at age $i$, $W_i$ is mean weight at age $i$ and $Mat_i$ is the proportion mature at age $i$. Values of $SPR_{F=0}$ were estimated for each stock, using natural mortality, weights-at-age and maturity-at-age estimates from stock assessments reports.

All series of $S$ were then scaled with a maximum at 1, as in Minto et al. (2008), but recruitment series were standardized by the same factor than the stock, *i.e.*, the maximum $S$ for each stock. While the choice of standardization does not affect variance estimates, standardizing both $S$ and $R$ by the same constant (max($S$)) preserves the $R/S$ ratio in the original data, and thus allows for comparison of stock-recruit parameters such as the maximum $RPSB$ rate (or the maximum lifetime reproductive rate; Myers 2001). Henceforth, for clarity purposes, $S$, $R$ and $RPSB$ denote respectively the spawning biomass, recruitment, and $RPSB$ after standardization.

### Hierarchical Bayesian model

The Beverton-Holt (eq. 10a) and Ricker (eq. 10b) models were tested as two special cases of the generic model in eq. (8). Both models were reparameterized in terms of $\alpha$, the maximum $RPSB$ rate and $K$, the maximum recruitment ($K = \frac{\alpha}{\beta}$ and $K = \frac{\alpha}{\beta \cdot e^1}$ for the BH and Ricker forms, respectively):

(10) a $$\log(\mathrm{RPSB}) = \log(\alpha) + \log\left(\frac{1}{1+\frac{\alpha}{K}\cdot S}\right) + \varepsilon \sim N(0,\sigma^2)$$

(10) b $$\log(\mathrm{RPSB}) = \log(\alpha) - \frac{\alpha}{K\cdot e^1}\cdot \mathrm{S} + \varepsilon \sim N(0,\sigma^2)$$

This parameterization allows comparing parameters between the two particular forms. This is important for Bayesian models as it allows for the definition of common priors, which is a key issue for model selection (Lawrence *et al.*, 2013). The variance $\sigma^2$ in eqs. (10a) and (10b) was re-parameterized as a function of stock size $S$ (Minto *et al.*, 2008):

(11) $$\sigma^2(S) = \exp(\eta_0 + \eta_1 . S)$$

where $\eta_1$ scales the magnitude of heteroscedasticity. Fixing $\eta_1$ to 0 gives the classical widely used logNormal errors with constant variance.

Hierarchical structures were set on parameters $(\alpha, K, \eta_0, \eta_1)$. Parameters $(\alpha, K, \eta_0)$ were considered as stock-specific and exchangeable across stocks (all other models considering those parameters pooled by species or common to all stocks had very poor fit to the data). Parameter $\eta_1$ was considered either stock-specific or species-specific (17 species for 39 stocks; Table 2.2).

All parameters were given weakly informative prior distributions (Table 2.3) in the sense of Gelman (2009), *i.e.,* they let the data speak while being strong enough to exclude unrealistic values. Sensitivity to different priors on hyperparameters was also investigated, using flat normal instead of uniforms, with large bounds as in Table 2.3.

Table 2.3 - Model parameters and prior distributions in the configuration with all parameters $(\eta_1, \eta_1, \alpha, K)$ stock-specific.

| **Parameter** | **Description** | **Prior distribution** |
|---|---|---|
| *Hyperparameters* | | |
| $\mu_{\eta_1}$ | mean $\eta_1$ across stocks or species (according to model structure) | $N(0,20)$ |
| $\mu_{\eta_0}$ | mean $\eta_0$ across stocks | $N(0,20)$ |
| $\mu_{log\alpha}$ | mean log $\alpha$ across stocks | $N(0,10)$ |
| $\mu_{logK}$ | mean log $K$ across stocks | $N(0,10)$ |
| $\sigma_{\eta_1}$ | standard deviation of $\eta_1$ | $U(0.01,20)$ |
| $\sigma_{\eta_0}$ | standard deviation of $\eta_0$ | $U(0.01,20)$ |
| $\sigma_{log\alpha}$ | standard deviation of log $\alpha$ | $U(0.01,3)$ |
| $\sigma_{logK}$ | standard deviation of log $K$ | $U(0.01,3)$ |
| *Parameters at the stock level* | | |
| $\eta_1$ | heteroscedastic coefficient | $N(\mu_{\eta_1}, {\sigma_{\eta_1}}^2)$ |
| $\eta_0$ | density independent variance component | $N(\mu_{\eta_0}, {\sigma_{\eta_0}}^2)$ |
| $\alpha$ | slope at origin of S-R fits | $logN(\mu_{log\alpha}, \sigma_{log\alpha})$ |
| $K$ | asymptotic R value of S-R fits (carrying-capacity) | $logN(\mu_{logK}, \sigma_{logK})$ |

### Model selection and posterior checking

The different model formulations were compared using the Deviance Information Criterion (DIC, Spiegelhalter *et al.*, 2002). Internal model consistency was checked using Bayesian posterior checking (Gelman *et al.*, 2004, p. 175), with the procedure described by Michielsens and McAllister (2004). The realized (resp. predicted) discrepancy $\chi^2_{obs}$ (resp. $\chi^2_{pred}$) was computed for each stock as a measure of the discrepancy between the observed $\log(RPSB)$ (resp. predicted) and the expected $\log(RPSB)$ given the posterior parameters. If the model fits appropriately, replicated data should look similar to observations and $\chi^2_{pred}$ should not be too different from $\chi^2_{obs}$. The Bayesian *p-value* is the probability that $\chi^2_{pred} > \chi^2_{obs}$ estimated over the posterior sample of the parameters. Very high (*e.g.*, >0.95) or very low (<0.05) *p-values* provide serious warning (Gelman *et al.*, 2004) about lack of consistency between the model *a posteriori* and the data.

### Considering observation errors in $S$ and $R$

Recruitment and spawning biomass estimates used in our analysis are derived from stock assessment models, thus they are surrounded with errors due to the multiple sources of uncertainty in such models. A positive correlation between the errors on $S$ and $R$ could also be expected because of the cohort dynamics in age-structured stock assessment models. Estimates of SR parameters have been shown to be sensitive to observation errors in $S$ and $R$ (Walters and Ludwig, 1981; Walters and Martell, 2004). In particular, considering observation errors affect the balance between the different sources of variability and might in turn affect estimates of the variance of process errors. To assess how robust our results are to errors in $S$ and $R$, parameters estimation was also performed by considering that $S$ and $R$ were observed with logNormal errors with expected means centered on $S$ and $R$ values, in addition to the stochasticity in the recruitment process.

Several flatfish stock assessment reports provide measure of uncertainty in $S$ and $R$ that can be converted in coefficient of variation (CV) of logNormal distributions (Table 2.2). We rely on those values to fix the variance of observation errors to realistic values, and provide a sensitivity analysis of our results to CV ranging from 5% to 30%. Observation errors were included with or without covariance between observation errors on $S$ and $R$, with a maximum covariance defined as $\sqrt{Var(S).Var(R)}$.

**Computational details**

Bayesian posterior distributions were approximated via Monte Carlo Markov Chain (MCMC) methods using the JAGS software (http://mcmc-jags.sourceforge.net) through the Rjags (www.Rproject.org) package. Three MCMC-independent chains with dispersed initialization points were used. For each chain, the first 5000 iterations were discarded. Inferences were derived from a sample of 3*50,000 iterations. All the modeling results have undergone the Gelman-Rubin test (Brooks and Gelman, 1998) as implemented in the R Coda package to assess convergence of MCMC chains (R ratio < 1.05 for all variables).

### 2.2.5. Assessing the relationship between parameters estimates and life history traits

Relations between model estimates and different life history traits of flatfish species were investigated to test for the existence of patterns consistent with ecological theory. In particular, the following hypotheses were tested: (i) The density independent component of the variance of the recruitment process (as measured by $\eta_0$) is expected to be positively correlated with the duration of the pelagic stages (eggs and larvae), before benthic settlement (van der Veer *et al.*, 2000a); (ii) The intensity of density dependent regulation (as estimated by β and the heteroscedasticity coefficient $\eta 1$) is expected to be positively correlated with the level of dependence to restricted nursery areas (Iles and Beverton, 2000; MacKenzie *et al.*, 2003; Rooper *et al.*, 2004; Craig *et al.*, 2007; Juanes, 2007).

Life history traits (*i.e.*, the duration of the pelagic stage and the degree of concentration of juveniles in nurseries) were obtained from the literature (Gibson, 2004) for each species (Table 2.2) as they were not available at the stock level.

## 2.3. Results

### 2.3.1. Comparison of the recruitment variability across orders

Whatever the model form (Ricker or BH), Pleuronectiforms and Perciforms exhibited lower estimates of recruitment variability than other fish orders (Figure 2.1). For both BH and Ricker models, *p*-values of multiple Tukey pairwise comparison tests revealed significant differences between Clupeiforms and Perciforms or Pleuronectiforms, and between Gadiforms and Perciforms or Pleuronectiforms. But no significant differences exist between Clupeiforms and Gadiforms or between Perciforms and Pleuronectiforms. Within Pleuronectiforms, the few amount of stocks per species (only 1 stock for 9 out of 17 species) limits the analysis, so no interesting pattern could be found between the residual variance and the species.

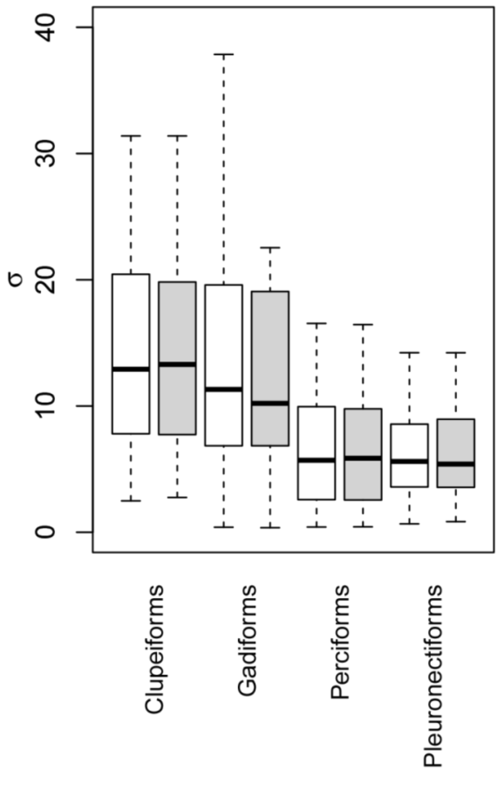

Figure 2.1 - Residual variability around SR models (a) among fish orders. Boxplots represent the between stocks variability of σ estimates (fit by least-square procedure), obtained under the Beverton-Holt (white) or Ricker models (grey).

### 2.3.2. HBM for flatfish species

**Model selection**

Model selection criteria were used to evaluate how well the data support the three nested different modeling assumptions, (i) the average form of the SR model (BH or Ricker), (ii) the existence of heteroscedasticity in the residual variance ($\eta_1 \neq 0$ in eq. (11)) and (iii) the level (species or stocks) at which the variability of $\eta_1$ is to be considered.

When $S$ and $R$ are considered known without observation errors, the greatest differences in DIC values were explained by the difference in deviance due to the form of the average SR model, the BH form being systematically selected, with differences in DIC values ≥ 15 in favor of the BH form (Table 2.4). Within a single form for the average SR model, difference in DIC between models without ($\eta_1 = 0$) or with ($\eta_1 \neq 0$) heteroscedasticity were low. However the most complex models including heteroscedasticity ($\eta_1 \neq 0$) had always smaller DIC values than the model with constant variance ($\eta_1 = 0$) (Table 2.4). For models including heteroscedasticity, models with $\eta_1$ considered variable between stocks (39 parameters) had smaller DIC values than when considering only between species variability (17 parameters), but evidence in favor of the most complex model were not so clear. Different types of weakly informative prior distribution affected neither model selection nor parameters estimates and results revealed robust to the existence of observation errors on $S$ and $R$ (Table 2.4).

To sum up, even if evidence in favor of a particular model was not very strong, results were in favor of a residual variance that depends upon the level of stock ($\eta_1 \neq 0$) for both BH and Ricker forms. Even in the presence of observation errors on $S$ and $R$, the BH model form with residual variance depending upon the level of stock, and with stock-specific $\eta_1$ parameters was the best supported by the data. For this model, posterior checking does not reveal any model failure to replicate data comparable to observations. As qualitative results concerning heteroscedasticity are not impacted by the model form (BH *vs* Ricker), only the results obtained in the BH model with stock specific parameter $\eta_1$ are detailed in the followings.

Table 2.4 - Differences between the DIC of the BH model with stock-specific $\eta_1$ (ref) and other model configurations. Differences are calculated independently for the model without or with observation errors on $S$ and $R$ (CV=15%).

| **WITHOUT OBSERVATION ERRORS** | **Beverton - Holt** | **Ricker** |
|---|---|---|
| **$\eta1 = 0$** ***(Constant variance model)*** | | |
| | +3 | +21 |
| **$\eta1 \neq 0$** ***(Heteroscedastic variance model)*** | | |
| Species specific $\eta1$ | +2 | +12 |
| Population specific $\eta1$ | **ref** | +18 |

| WITH OBSERVATION ERRORS | **Beverton - Holt** | **Ricker** |
|---|---|---|
| **$\eta1 = 0$** ***(Constant variance model)*** | | |
| | +5 | +25 |
| **$\eta1 \neq 0$** ***(Heteroscedastic variance model)*** | | |
| Species specific $\eta1$ | 0 | +24 |
| Population specific $\eta1$ | **ref** | +23 |

### Estimates of parameters

Most of the 39 flatfish stocks exhibit a clear decreasing $RPSB$ with increasing stock level (Figure 2.2). Parameters estimates, as revealed by their marginal posterior distribution in Figure 2.3, remain largely uncertain as commonly observed when fitting stock-recruit models, especially for the slope at origin $\alpha$. Some estimations of $\alpha$ are pretty low (*e.g.*, BSAI *R. hippoglossoides*), suggesting poor productivity for some flatfish stocks. Most of the β parameters (back calculated as $\beta = \alpha/K$) are clearly negative, which confirms the decrease of $RPSB$ with level of stock (Figure 2.2). However, the joint posterior distribution of $(\alpha, K)$ exhibits strong negative correlation and estimates of $\alpha$ are sensitive to the formulation of the residual variance (negative β induce lower α estimates).

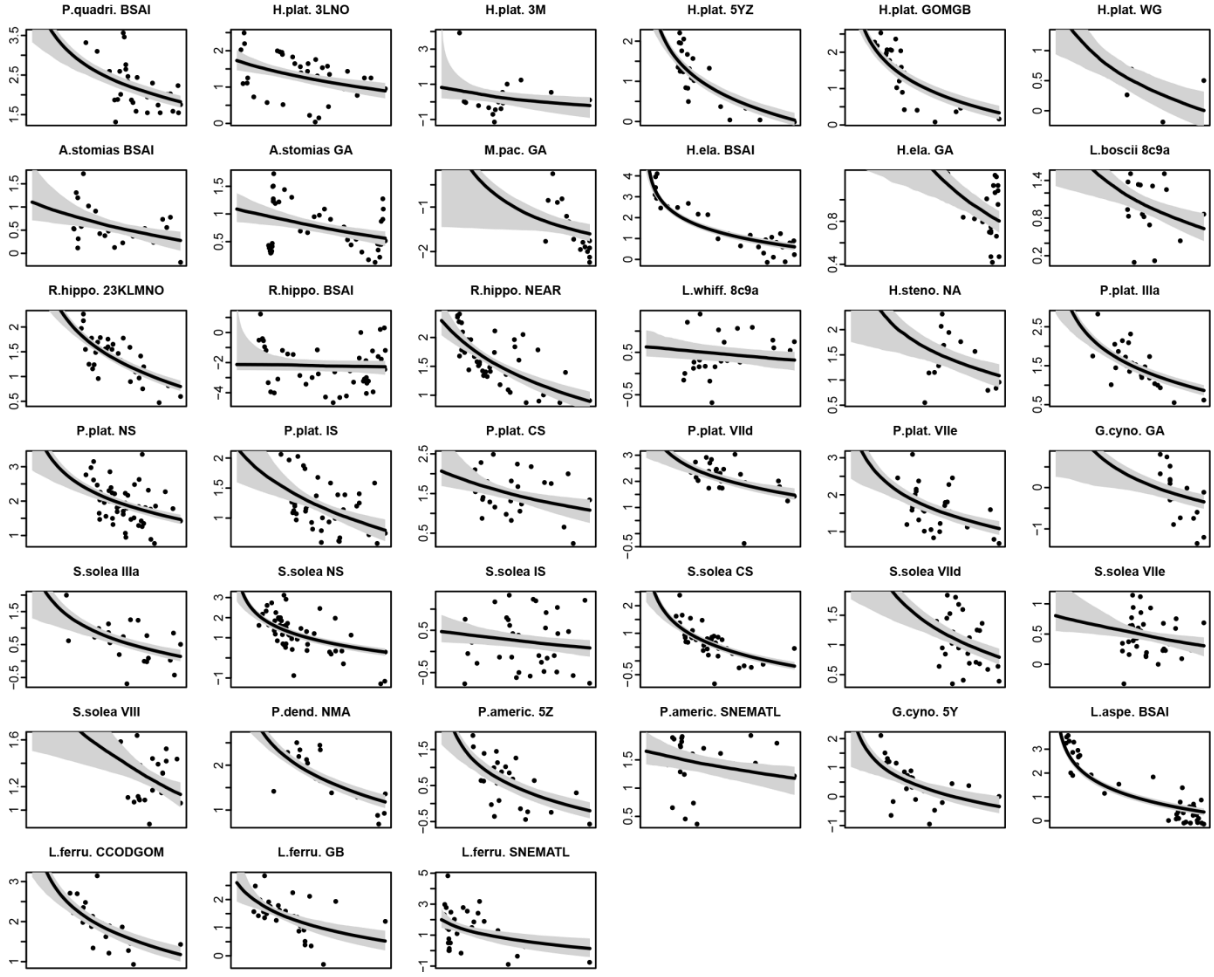

Figure 2.2 - Model fits with 95% Bayesian confidence interval. Model fit are drawn using posterior medians of parameters. Bayesian estimates are obtained under the Beverton-Holt model, with heteroscedasticity ($\eta_1 \neq 0$) and stock-specific $\eta_1$ parameters and no observation errors on S and R. x-axis : values of SSB standardized by max(SSB) (between 0 and 1); y-axis: log(RPSB).

There is no clear species pattern for both $\alpha$ and $K$ parameters (Figure 2.3), as the within-species variability is in the same order of magnitude than the across-species variability. This supports the retained exchangeable hierarchical structure on $(\alpha, K)$ across all stocks with no species effect on those parameters.

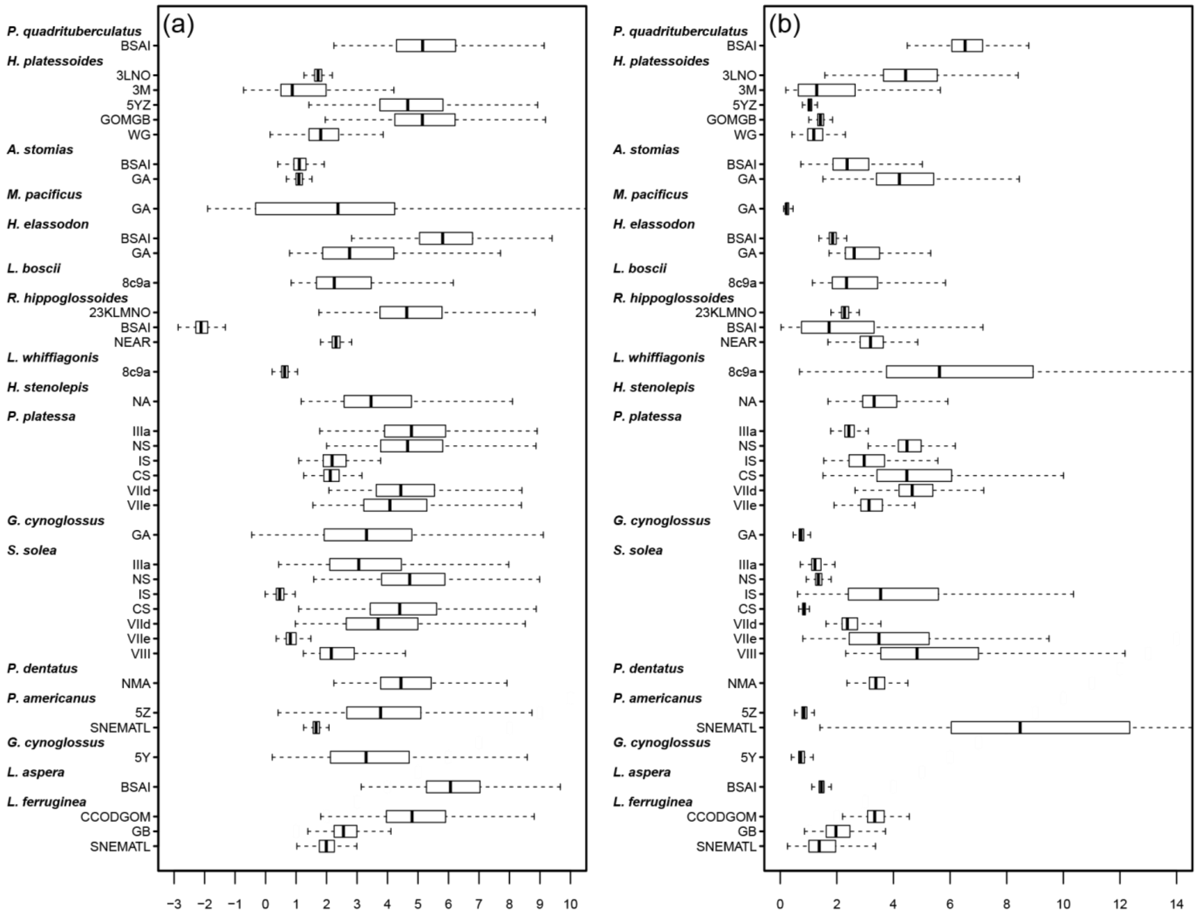

Figure 2.3 - Marginal posterior distributions of parameters α (a) and $K$ (b). Bayesian estimates are obtained under the Beverton-Holt model, with heteroscedasticity ($\eta_1 \neq 0$) and stock-specific $\eta_1$ parameters and no observation errors on S and R.

The residual variance is decreasing with stock level for almost all of the 39 stocks. Indeed, the marginal posterior distributions of parameters $\eta_1$ (Figure 2.4b) have a negative median for almost all stocks (37 out of 39), and have more than 75% of their mass in negative values for 29 out of the 39 stocks. The posterior distribution of $\mu_{\eta_1}$, *i.e.* the grand mean of $\eta_1$ across stocks, has its median at -0.40. Estimations of parameters $\eta_0$ do not show any particular pattern across species (Figure 2.4a). As expected because their sum codes for the total residual variance, estimates of parameters $\eta_0$ and $\eta_1$ for each stock were negatively correlated.

Overall, parameter estimates revealed robust to observation errors on $S$ and $R$. Increasing the variance of observation errors logically leads to higher uncertainty on parameters estimates. Estimates of $\alpha$ slightly decrease, while those of $K$ increase. As shown on Figure 2.5, estimates of $\eta_1$ remain robust for observation errors with coefficient of variations of 5% and 15% while they drop for most populations at 30 % CV. The introduction of covariance between $S$ and $R$ observation errors does not strongly affect parameters estimates.

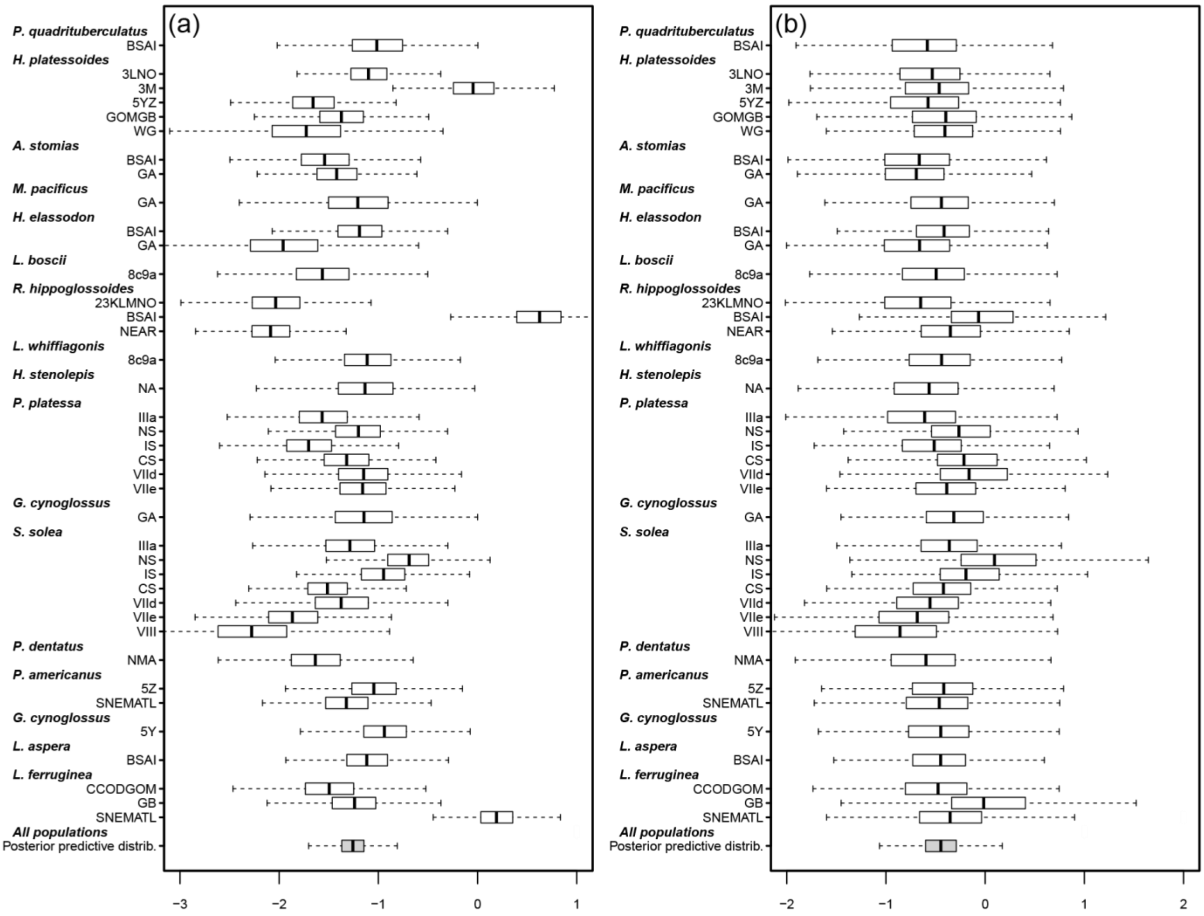

Figure 2.4 - Marginal posterior distributions of parameters $\eta_0$ (a) and $\eta_1$ (b) for all stocks. Bayesian estimates are obtained under the Beverton-Holt model, with heteroscedasticity ($\eta_1$≠0) and stock specific $\eta_1$ and no observation errors on S and R. The posterior predictive distributions (grey boxplots) show the grand mean of parameters estimated across the 39 stocks by the hierarchical model.

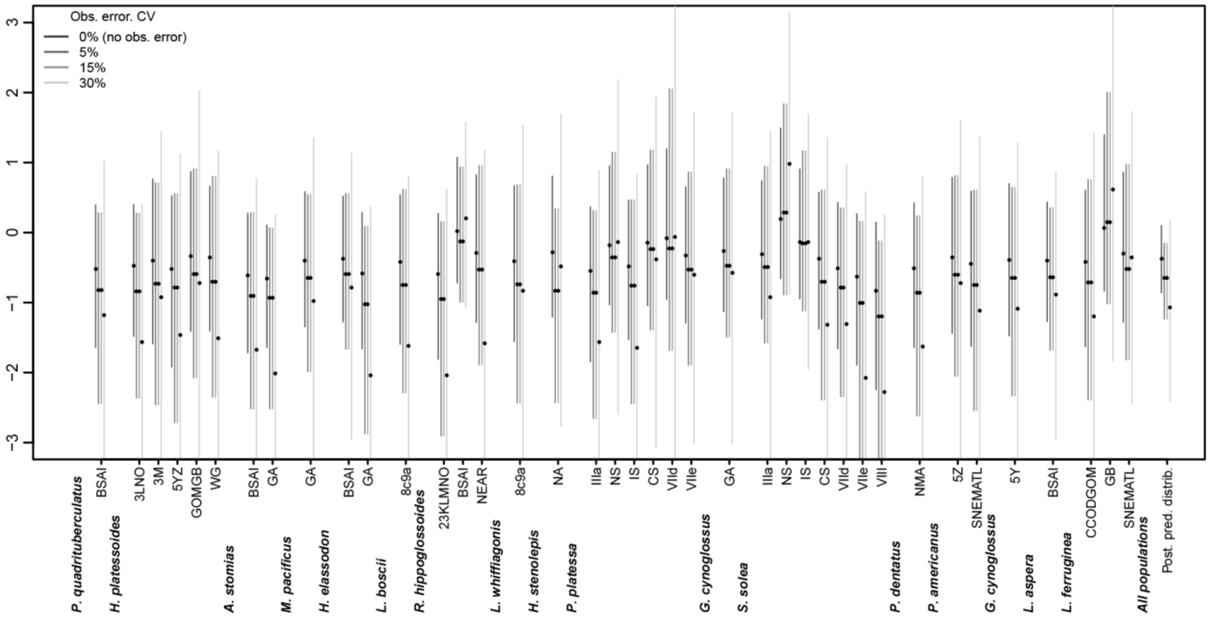

Figure 2.5 - Marginal posterior distributions of $\eta_1$ obtained with the BH model with stock-specific $\eta_1$ under increasing observation errors levels (CV obs. errors = 0, 5%, 15% and 30%; no covariance).

### Testing the expected relationships with life history traits

Data on life history traits could only be compiled for 10 out of the 17 species of Pleuronectiforms. For these 10 species, the variability among stocks in estimates of parameters $(\alpha, K, \eta_0, \eta_1)$ is high and in the same order as interspecific variability (Figure 2.3; Figure 2.4). No pattern can be identified between life history traits of species (pelagic stage duration, degree of concentration in nurseries) and parameter estimates (*e.g.* estimates of $\eta_0$) do not exhibit any link to larval stage duration (Figure 2.6), while a positive correlation was expected).

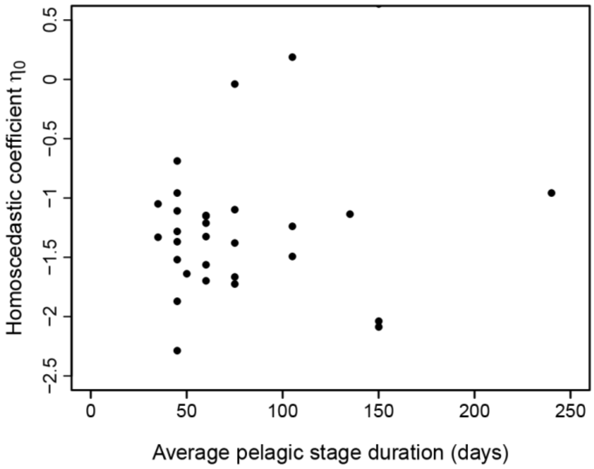

Figure 2.6 - Relation between average pelagic stage duration and posterior estimates (posterior medians) of $\eta_0$. Posterior Bayesian estimates are obtained under the Beverton-Holt model, with heteroscedasticity ($\eta_1 \neq 0$) and stock-specific $\eta_1$ parameters.

## 2.4. Discussion

This analysis offers a substantial contribution to the understanding of the variability of the recruitment process of marine fish, with a particular focus on flatfish species.

### 2.4.1. A hierarchical meta-analysis of recruitment variability with a focus on flatfish

#### A theoretical model describing recruitment variability

As a comprehensive model to analyze recruitment process including concentration at one life stage, we follow Minto et al. (2008) to propose a model where recruitment results from the combination of two sequential phases; a first egg/larval pelagic phase with mortality driven by stochastic density-independent processes combined with a second phase where both density-dependent mortality and environmental stochasticity occur. Such a theoretical model revealed a pertinent framework as it allows to formalize that (i) recruitment variability should be lower for species with density-dependence occurring at a later stage in the recruitment process; (ii) for a particular stock, if density dependence occurs at the latter stage, the recruitment variability should decrease with the level of stock, providing a test for the existence of density dependence even if noise dominates the signal.

#### Using stock assessments data to analyze recruitment variability

In his meta-analysis, Minto et al (2008) analyzed 147 exploited fish stocks, out of which only 7 were flatfish stocks. Iles (1994) explored stock-recruit data for 20 flatfish stocks. Our study used the most up to date stock recruitment data on exploited flatfish stocks. 39 flatfish stocks of 17 species were included, and longer time series were used, thus adding substantive material (+15% of stock*year lines) with regards to suitable flatfish data in RAM legacy database. As in Minto et al. (2008) and Iles (1994) previous works, all stock-recruits series included in our analysis were carefully selected. They were all derived from statistical catch-at-age models (*e.g.*, VPA, XSA, ADAPT) and constitute the best standardized information available. Of course, the quality of the data can be questioned. Stock-recruits estimates from those methods can provide poor estimates for the most recent years but they are more standardized than direct estimates from research vessels surveys that can exhibit unduly high variability due to high estimation error. Data standardization can also be the source of additional errors, due for instance to uncertainty in the maximum age that can have an impact on $SPR_{F=0}$ values used to standardize recruitment series. To account for the existence of errors in $S$ and $R$ data series, in addition to the recruitment stochasticity, our modeling approach explicitly considers errors caused by mismeasuring $S$ and $R$ with realistic observation error variance derived from stock-assessment reports. Our results revealed robust to observation errors, strengthening our conclusions.

### Testing for signal in recruitment variability

By combining approaches at different scales, including a comparison of the recruitment variability between different fish orders with an analysis of the changes in recruitment variability between low and high levels for 39 flatfish stocks, we provide a body of results consistent with the concentration hypothesis (Iles and Beverton, 2000) for nursery dependent flatfish species.

### Interorder patterns in recruitment variability

Pleuronectiforms exhibit significant lower recruitment variability than most other exploited marine fish species. Most flatfish species go through eggs and larval drift after spawning, inducing density independent mortality until settlement in suitable nursery habitats (Rochette *et al.*, 2012). As already stated (Bailey, 1994; van der Veer et al., 2000; Gibson, 2005), because flatfish egg and larval life stages do not differ from other teleost fishes (Gibson, 2004), the variability induced by these stages is likely to be comparable with other teleost fishes. The lower recruitment variability observed for flatfish species is then more likely to result from specific processes occurring at a later stage in the recruitment process. This is consistent with the concentration hypothesis (Iles and Beverton, 2000) which suggests that species with juveniles that concentrate in specific nursery habitats should display dampened variations in recruitment, caused by a limited carrying capacity of those nurseries (Le Pape *et al.*, 2003a). Pleuronectiforms are nursery dependent species (Van der Veer *et al.*, 2000; Gibson, 2005), whose life cycle relies on restricted nursery habitats, compared to a large proportion of pelagic (*e.g.* Clupeiforms) or bentho-demersal (*e.g.* Gadiforms) species with less restricted juvenile habitats and higher variations in recruitment. More significant differences between orders could even have been expected but a large amount of mechanisms influence survival (Hixon and Jones, 2005; Houde, 2008) leading to important recruitment variability, even for nursery dependent species as flatfish (van der Veer *et al.*, 2000a).

### Stock recruitment relation among flatfish

Stock recruitment models for the 39 flatfish stocks showed a general decreasing $RPSB$ rate when the level of stock increases. SR data generally exhibited highly stochastic recruitment around a rather constant average, even for a relatively wide range of stock levels (Iles, 1994). But when evaluating the $RPSB$ against stock values, this logically leads to a decreasing $RPSB$ with increasing stock level, interpreted as an evidence for a density dependent relationship between $S$ and $R$. This was consistent with flatfish literature. Iles (1994) previously explored stock-recruit data for flatfish using the Beverton-Holt, Ricker and Shepherd generalization forms (1982). He provided statistical evidence of underlying stock-recruit relationship for one third of those stocks, with model of constant recruitment retained in the two remaining thirds.

### Stock recruitment variability among flatfish

Results revealed that the variability of the $RPSB$ decreases when stock size increases, which is consistent with density dependent processes occurring at a later stage (after the settling phase) after a pelagic drift phase of larvae (Rijnsdorp *et al.*, 1995; van der Veer *et al.*, 2000a). The pattern of heteroscedasticity in the variance revealed consistent across almost all flatfish stocks.

Taken individually, each stock provides few information to estimate SR parameters, a fortiori parameters controlling how the variance depends upon the stock size. The HBM allowed to borrow strength among the 39 stocks (Rivot and Prévost, 2002; Michielsens and McAllister, 2004; Parent and Rivot, 2012; Pulkkinen and Mäntyniemi, 2013a) and provided estimates of parameters that could not be estimated from single SR data sets (Burrow *et al.*, 2013). Parameters $\eta_0$, $\eta_1$, and $\alpha$ are independent from the population size by construction, and transferring information between stocks for these parameters is fully justified. Sharing information on $K$ may appear more questionable. However, it is worth noting that because all recruitment data were standardized by the maximum stock size, all $K$ are also standardized by the population size and are in the same order of magnitude. Trials with all $K$ mutually independent between stocks provided similar results as setting a hierarchical structure on $K$.

Using model selection and validation tools, we were able to compare different model formulations. Results showed that evidence in favor of a model with a decreasing variance with increasing stock size did not depend upon the form of the average SR model (Ricker or BH). The model that best support the data was a Beverton-Holt form with all parameters specific to each stock (no generic inter-stocks species effect). As a difference with Minto et al. model (2008) in which the heteroscedastic parameter $\eta_1$ was estimated at the species level, our results were in favor of stock-specific parameters.

In addition to recruitment stochasticity, we explicitly consider error caused by mismeasuring $S$ and $R$ (measurement or observation error). Several approaches have been proposed to simultaneously account for process and observation errors in SR analysis. When considering inferences in the maximum likelihood framework, an additional constraint is needed to avoid problem with model identification, and several authors have proposed to fix the proportion of the total variation due to observation errors (Walters and Ludwig, 1981; Schnute, 1994; Schnute and Kronlund, 2002). Because of the influence of priors on all parameters, such constraints can be relaxed in the Bayesian context. Su and Peterman (2012) showed that both process and observation error variances can be estimated simultaneously in SR models considered in a Bayesian state-space framework. Considering the proportion of the total variation due to observation errors as known generally reduces the bias in SR parameters estimates, although the influence of arbitrarily fixing this proportion depends upon the productivity parameter (slope at the origin) and the contrast in the levels of stocks. However, fixing the proportion of the total variation due to observation errors was not an appropriate approach for our analysis. Indeed, this would mechanically lead to introduce heteroscedasticity not only in the natural variability but also in the observation errors, and no such a relationship was mentioned in any flatfish stock-assessment report. Following an approach similar to Rivot et al. (2001) who used capture-mark-recapture models to provide realistic estimates of observation errors in stock and recruitment, we rely on quantitative estimates of the observation error variance available from stock-assessment reports to fix the CV of observation errors to realistic values. We assess the sensitivity of our results to the value of the CV, with values ranging from CV=5% to CV=30%.

Considering observation errors in $S$ and $R$ does not impact the main conclusions. When the variance of observation errors increases, the proportion of the total variance explained by process errors decreases mechanistically, and then estimates of parameters $\eta_1$ decreases too. However, even with high level of observation errors, the process error variance significantly increases when the level of SSB decreases, indicating that our results are not an artifact due to observation errors in $S$ and $R$.

But still, our results could have been an artifact due to observation errors on $R$ with a decreasing variance as function of $S$. However, would the observation error on $R$ be dependent upon the level of $S$, the variance of observation errors on $R$ would rather be decreasing when $S$ decreases. Indeed flatfish stocks with lower $S$ are generally highly exploited stocks that in turn correspond to more informative catch data and to more precise recruitment estimates.

### 2.4.2. Habitat dependence at young stages and flatfish stocks management

Our results provide evidence for the existence of density dependent processes in relation to flatfish nursery habitat, pointing out the dependence of these species to the capacity of their nursery habitat (Rijnsdorp *et al.*, 1992; Rooper *et al.*, 2004). This flags that, for those kind of heavily exploited fish populations, measures aiming at improving or preserving the capacity of juvenile habitat could be especially effective to improve adults' biomass, and even much more effective than regulating fishing effort on the adults (Levin and Stunz, 2005; Wolfshaar *et al.*, 2011).

However, estimates of the slope at the origin of SR models, $\alpha$, appeared sensitive to variance formulation, pointing out the sensitivity of estimates of key population dynamic parameters to hypotheses made on the variance, in addition to those made on the average SR models (Burrow *et al.*, 2013; Pulkkinen and Mäntyniemi, 2013a). Moreover, it is worth noting that considering heteroscedasticity in the variance may complicate the computation of management reference points such as the MSY (Burrow *et al.*, 2013).

### 2.4.3. The recruitment variability is stock specific

One striking result of this study is the absence of species effect in estimates of parameters, as emphasized by the fully exchangeable hierarchical structure between the 39 flatfish stocks. Species effects could be identified in neither the model nor the variance parameters, the within-species variability of parameters being of the same order of magnitude than the between-species variability. As data on life history traits were only available at the species and not at the stock level, it is not surprising that no relationship between life history traits and parameters estimates could be found. Indeed, within the Pleuronectiforms order, there are moderate contrasts in life history so interspecific contrasts are limited in the present study. Moreover, intra specific patterns could be important amongst stocks belonging to the same species. For instance, larval life history for different stocks may strongly differ for a given species (Rochette *et al.*, 2012). Nursery habitat features may also play a role and the level of density dependence could vary amongst stocks for a given species (Le Pape *et al.*, 2003a, 2003c; Johnson, 2007), with consequences on recruitment variability (Le Pape *et al.*, 2003a). From an evolutionary perspective, life history traits for a given stock are the consequences of an adaptation to the local conditions encountered (Gibson, 2004; Galland *et al.*, 2013; McBride *et al.*, 2013) preventing the existence of a clear patterns at the species level. Thus, life history traits depend more on the environment (Félix *et al.*, 2011; Freitas *et al.*, 2012; Comerford *et al.*, 2013; Fincham *et al.*, 2013) than on contrasts amongst flatfish species. Finally, changes in environmental conditions affecting a given population during the time frame the data were collected are susceptible to occur, either hampering the underlying stock-recruits relationship (Clark and Hare, 2002) or the stability of life traits. As a perspective, it would be of major interest to compare parameters estimations to life history traits at the stock levels to account for observed differences between stocks, and to increase the contrast by extending the analysis to other orders of marine fishes.

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## Conclusion du chapitre

La méta-analyse conduite dans ce chapitre apporte des enseignements sur l'écologie des espèces nourriceries-dépendantes et permet de préciser certains éléments dans la perspective de la modélisation de leur cycle de vie.

Nous avons tout d'abord mis en évidence la faible variabilité des relations SR chez les pleuronectiformes par rapport aux autres ordres de poissons exploités. De plus, nous avons montré qu'il existait chez les poissons plats un signal consistant de diminution de la variance autour de la relation SR lorsque la biomase féconde augmente. L'analyse du comportement statistique d'un modèle de processus de recrutement structuré en deux phases successives montre qu'un tel signal est compatible avec l'hypothèse d'une première phase marquée par une mortalité densité-indépendante très stochastique suivie d'une phase de mortalité densité-dépendante (concentration). Par ailleurs, via une démarche de sélection de modèles, nous avons mis en avant l'absence d'« effet espèce » dans les paramètres de distribution de variance de la relation SR pour les poissons plats. Ces constats nous amènent à deux conclusions utiles pour l'intégration des connaissances dans un modèle de cycle de vie : (i) la modélisation du processus de recrutement en deux phases explicites a un sens et devrait permettre d'intégrer les facteurs principaux agissant sur chacune d'entres elles (i.e. hydroclimat puis habitat) ; (ii) en l'absence de signal lié à l'espèce, les paramètres issus de cette méta-analyse sont transférables comme information *a priori* sur la relation SR pour une population donnée de pleuronectiformes.

# 3. Quantifier l'impact de la connectivité aux differents stades du cycle de vie sur la perception du fonctionnement de la population de sole en Manche Est

## Introduction du chapitre

Nous avons souligné en introduction le caractère résolument spatial du fonctionnement des populations d'espèces nourriceries-dépendantes présentant des stades de vie successifs réalisés dans différents types d'habitats, chaque stade étant exposé à une source de pression spécifique (hydroclimat, habitat, pêche).

Dans ce chapitre, en nous appuyant sur la base du cas d'étude de la population de sole de Manche Est, nous proposons un modèle de cycle de vie représentant la composante spatiale aux différents stades (frayères/œufs/larves, juvéniles, adultes) et intégrant ces différentes pressions. Cette population nourriceries-dépendante présente plusieurs caractéristiques justifiant une approche spatiale : (i) l'occurrence de rétention larvaire au sein de différentes régions, avec une connectivité très limitée entre les zones de pontes et les nourriceries éloignées, (ii) une rétention forte des juvéniles au sein de nourriceries côtières et estuariennes et (iii) un faisceau d'indices convergents indiquant des mouvements limités des adultes.

Deux hypothèses de fonctionnement spatial sont comparées. Dans la première structure, nous nous appuyons sur les connaissances écologiques disponibles pour construire un modèle de fonctionnement de la population sous la forme de trois sous-composantes alimentées par trois groupes de nourriceries distincts et très faiblement connectées entres elles. Cette structure est comparée à une structure dans laquelle les différentes nourriceries alimentent une seule population adulte homogène (hypothèse standard utilisée par le groupe d’évaluation du CIEM). La démarche de modélisation s’appuie sur le cadre hiérarchique Bayesien intégrant les processus démographiques dans une approche statistique permettant d’assimiler les données disponibles aux différents stades ainsi que la connaissance sur certains paramètres du processus de recrutement sous la forme de distributions *a priori* informatives construites à partir des résultats du chapitre précédent.

# Adults mediated connectivity affects inferences on population dynamics and stock assessment of exploited marine populations

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## Abstract

We explore how spatial segregation at the successive life stages (i.e. eggs/larvae, juveniles, adults) along the life cycle may affect the functioning of an exploited flatfish population. The case study is the common sole population in the Eastern channel (ICES area VIId), that displays consistent eggs/larval retention patterns between spawning areas and adjacent nurseries combined to juvenile retention in coastal and estuarine nurseries and moderate adult movements. The high level of spatial segregation along the life cycle pushes to consider two alternative structures on the spatial functioning of the population: one single adult population supported by all nursery sectors contributing to a common pool of eggs (*i.e.*, the baseline stock assessment structure); and an alternative structure, with three subpopulations supported by their respective local nurseries, supplying local spawning grounds only. No exchange between the three subpopulations occurs during the juvenile stage (high segeregation on nurseries) and the sub-adult and adult stage, the connectivity between the three subpopulations being limited to the very low connectivity during the eggs and larval drift. Integrating relevant ecological processes and data at the successive stages through hierarchical Bayesian modeling of the whole life cycle, we were able to estimate indicators such as the spawning biomass (global and/or regional) or the contribution of each nursery sector to recruitment. We show how considering the full spatial structure of the population may provide additional insights on its state (e.g. local $SSBs$) and its functioning (e.g. local potential productivities; local reference points), while enabling the assessment of realistic (global or local) scenarios including spatial discrepancies in subpopulations trends. We also evaluate the level of knowledge and data required to test some critical hypotheses that remain impossible to weigh with the data at hand.

**Résumé**

Nous explorons comment la ségrégation spatiale entre individus tout au long du cycle de vie (i.e. œufs/larves, juvéniles, adultes) peut affecter le fonctionnement d'une population exploitée de poissons plats. La population étudiée, la sole commune de Manche Est (Zone ICES VIId), montre une rétention des œufs et des larves entre les zones de ponte et les aires de nourriceries adjacentes, associée à une rétention des stades juvéniles au sein des nourriceries et à des mouvements limités des adultes. Cette ségrégation aux stades successifs du cycle de vie nous amène à comparer deux structures alternatives de modèles. Dans la première, on considère que toutes les nourriceries alimentent une seule population adulte homogène qui contribue à un seul pool d'œufs, qui alimente en retour l'ensemble des nourriceries. Cette hypothèse correspond à celle faite par le groupe de travail du CIEM en charge de l'évaluation de cette ressource. Dans la deuxième structure, trois secteurs de nourriceries différents alimentent trois composantes d'une méta-population très peu connectées entre elles. Aucun échange d'individus n'intervient entre les trois sous-populations durant les stades juvéniles et (sub)adultes, la connectivité entre les trois composantes étant limitée à un échange très restreint durant les phases pélagiques (œufs/larves). Nous avons intégré les différents processus démographiques aux différents stades et les données disponibles dans un modèle hiérarchique Bayesien qui permet d'estimer des indicateurs tels que la biomasse féconde (globale et/ou régionale) ou la contribution des différentes nourriceries au recrutement. Nous montrons comment la perception de l'état de la population (e.g. biomasse féconde) et de son fonctionnement (e.g. productivité des nourriceries, points de références régionaux/globaux) dépend étroitement des hypothèses formulées sur la connectivité, mettant en exergue l'importance de considérer la connectivité à tous les stades du cycle de vie et pas seulement lors de la phase pélagique des jeunes stades. Cette approche permettra la simulation future de scenarios réalistes intégrant cette composante spatiale. Nous évaluons également le niveau de connaissances et de données nécessaire pour réaliser au mieux ce type d'approche.

## 3.1. Introduction

The understanding of marine population functioning is an ongoing challenge in fisheries science. In order to approach their full spatial dimension (Petitgas *et al.*, 2013), a definition of the different ecological processes and environmental or anthropic pressures associated with each life history stage is required (Carson *et al.*, 2011; Wolfshaar *et al.*, 2011; Ying *et al.*, 2011). While much research effort has been dedicated to this question (Ruiz *et al.*, 2009; Hinrichsen *et al.*, 2011; Rochette *et al.*, 2013), the current paradigm of population functioning for most exploited marine stocks assessments still considers a single adult population with no particular spatial structure. The underlying hypothesis is often that the population produces a single larval pool, which undergoes extensive dispersal and massive export (Warner and Cowen, 2002) covering the whole area of distribution of the population. When addressed, the question of connectivity and population structure is mostly focused on early life stages (Frisk *et al.*, 2013; Petitgas *et al.*, 2013), with a large body of studies evaluating the influence of physical and biological processes on their survival and dispersion (Huret *et al.*, 2010; Savina *et al.*, 2010; Peck and Hufnagl, 2012; Rochette *et al.*, 2012; Miller, 2007), that conditions the variability of recruitment in space and time (May, 1974; Chambers and Trippel, 1997; Levin and Stunz, 2005; Gallego *et al.*, 2012). Several studies have emphasized the occurrence of larval retention in marine populations (Cowen *et al.*, 2000; Warner and Cowen, 2002) and the need to assess its impacts, as populations which display strong retention may be locally more vulnerable to local recruitment overfishing or depletion due to catastrophic events (Strathmann *et al.*, 2002). Much less attention has been paid to the role of the spatial structure of populations at older life stages, although it is suspected to play a major role in population functioning and connectivity (Frisk *et al.*, 2013). Movements of adults could determine the structure and the dynamics of the population (Stelzenmuller *et al.*, 2011; Cianelli *et al.*, 2013; Frisk *et al.*, 2013; Huijbers *et al.*, 2013). It may even have a larger importance on (meta)population dynamics when larval and juvenile retention occurs (Grosberg and Levitan, 1992). There is therefore a strong need for population models which account for spatial structure and connectivity patterns at all successive stages (Petitgas *et al.*, 2013). These models shall provide outputs to help decision making in spatial management and conservation schemes. They should also prove useful in adapting fisheries management to local productivities (Carruthers *et al.*, 2011; Ying *et al.*, 2011; Guan *et al.*, 2013). Patterns of connectivity could also help at designing coherent marine protected areas (Lockwood *et al.*, 2002; Hilborn *et al.*, 2004; Botsford *et al.*, 2009; Kaplan, 2009; Gaines *et al.*, 2010; Grüss *et al.*, 2011a).

New challenges arise when building such models, as refined spatial data and knowledge of levels of connectivity between sub areas are scarce and uncertain: (i) Coupling of oceanographic circulation models and larval individual based models provides estimates of larval dispersal (Miller, 2007) but larval stages are rarely accessible to observations and the validation of the outputs remains an open question; (ii) Adult movements are difficult to track and largely ignored in most modeling approaches. Mark-recapture data (Drouineau *et al.*, 2010; Carruthers *et al.*, 2011), natural markers and genetic studies (Hellberg *et al.*, 2002) may provide insights on population structure, but they are costly and even structured population may display no genetic differentiation (Ward *et al.*, 1994; Smedbol *et al.*, 2002), especially with neutral markers (Exadactylos. *et al.*, 2003; Rolland *et al.*, 2007).

Data sources for spatialized population models are often heterogeneous and scarce, and linking the different ecological processes and stages along the life cycle (Hayes *et al.*, 2009) with the associated data also remains a methodological challenge. Hierarchical Bayesian modeling (HBM) framework constitutes an effective approach to embed complex demographic processes with different sources of noisy and incomplete data at different time and space scales (Thomas *et al.*, 2005; Buckland *et al.*, 2007; Parent and Rivot, 2012). They have proven their efficiency in numerous case studies of fish population dynamic models (Rivot *et al.*, 2004; Ruiz *et al.*, 2009; Swain *et al.*, 2009; Rochette *et al.*, 2013; Massiot-Granier *et al.*, 2014).

In this paper, using the common sole (*Solea solea*) population in the Eastern Channel as a case study, we investigate how considering alternative hypothese on the connectivity at the adult stage can affect population dynamics and stock assessment. This population displays consistent larval retention areas (Rochette *et al.*, 2012) coupled to post-settlement dependence of juveniles to specific coastal and estuarine nursery areas (Riou *et al.*, 2001; Rochette *et al.*, 2010) and moderate adult movements (Burt and Millner, 2008), and hence provides an ideal model to explore the impact of different hypotheses on adult spatial structure on population dynamics.

Rochette et al. (2013) have proposed an integrated life cycle model for the sole population in the Eastern Channel (EC) built in the HBM framework. The framework allows to embed (i) outputs of an individual-based model for larval drift that provided yearly estimates of the dispersion and mortality of eggs and larvae, from spawning grounds to settlement in several coastal nurseries; (*ii*) a habitat suitability model, based on juvenile trawl surveys to estimate the surface of each nursery sector and juvenile densities; (*iii*) a statistical catch-at-age model for the estimation of the numbers-at-age and the fishing mortality on subadults and adults. Rochette et al. (2013) considered that the different nurseries contribute to the recruitment of one single homogeneous population in the EC, this hypothesis being consistent with the stock-assessment model used by ICES (ICES, 2013). However, because of the strong larvae retention proved by the larval drift model, and ancillary data and expertize on (sub)adults movements, there is a strong assumption that only very low connectivity exists between three isolated subpopulations associated to different nurseries sectors.

In this paper, we elaborate on the framework proposed by Rochette et al. (2013) to explore how considering three isolated subpopulations instead of a single homogeneous one as supposed by ICES (2013) or Rochette et al. (2013) can affect inferences on population dynamics. In particular, we assess how considering alternative model structure can change evaluation of the productivity of each nursery area, and their respective contribution to the recruitment. We also show how different spatial structures of the adult population can affect the estimation of management reference points and the assessment of the stock status with regards to the spatial dynamics of the fishery.

## 3.2. Materials and methods

### 3.2.1. Case study

The common sole (*Solea solea*) is a coastal and estuarine nursery dependent flatfish species (Le Pape *et al.*, 2003b; Gibson, 2004). The population in the Eastern Channel (EC; ICES area VIId) is exploited with annual landings of about 4000t. The life cycle of EC sole is well described (Rochette *et al.*, 2013): adults reproduce in offshore spawning areas in early spring; pelagic eggs and larvae drift and will eventually die or settle as newly metamorphosed benthic individuals in late spring and early summer on restricted nursery grounds (Rochette *et al.*, 2012). The EC population renewal is supported by five separated nursery areas (Rochette *et al.*, 2010), along French (Veys, Seine and Somme nurseries) and UK coasts (UK West and Rye nurseries). Juveniles settle and grow in these shallow coastal and estuarine areas for about 2 years (Riou *et al.*, 2001). Afterwards, they migrate towards wider and deeper adult areas of distribution where their migrations remain limited (Burt and Millner, 2008), in spite of seasonal moderate movements to shallow waters in summer. The population faces multiple pressures, such as hydroclimatic conditions during the larval stages, nursery habitat degradation (Le Pape *et al.*, 2007; Rochette *et al.*, 2010), or fishing (ICES, 2013).

### 3.2.2. Hierarchical Bayesian life cycle model

We elaborate here on the life cycle modeling approach proposed by Rochette et al. (2013), who provided a flexible framework to model the functioning of the EC sole population. The model is based on the Bayesian state-space modeling framework, which integrates uncertainty in both process (i.e. process stochasticity) and data (i.e. observation errors). The model is stage-structured from eggs to settled larvae and then age-structured from juveniles to adults (Figure 3.1).

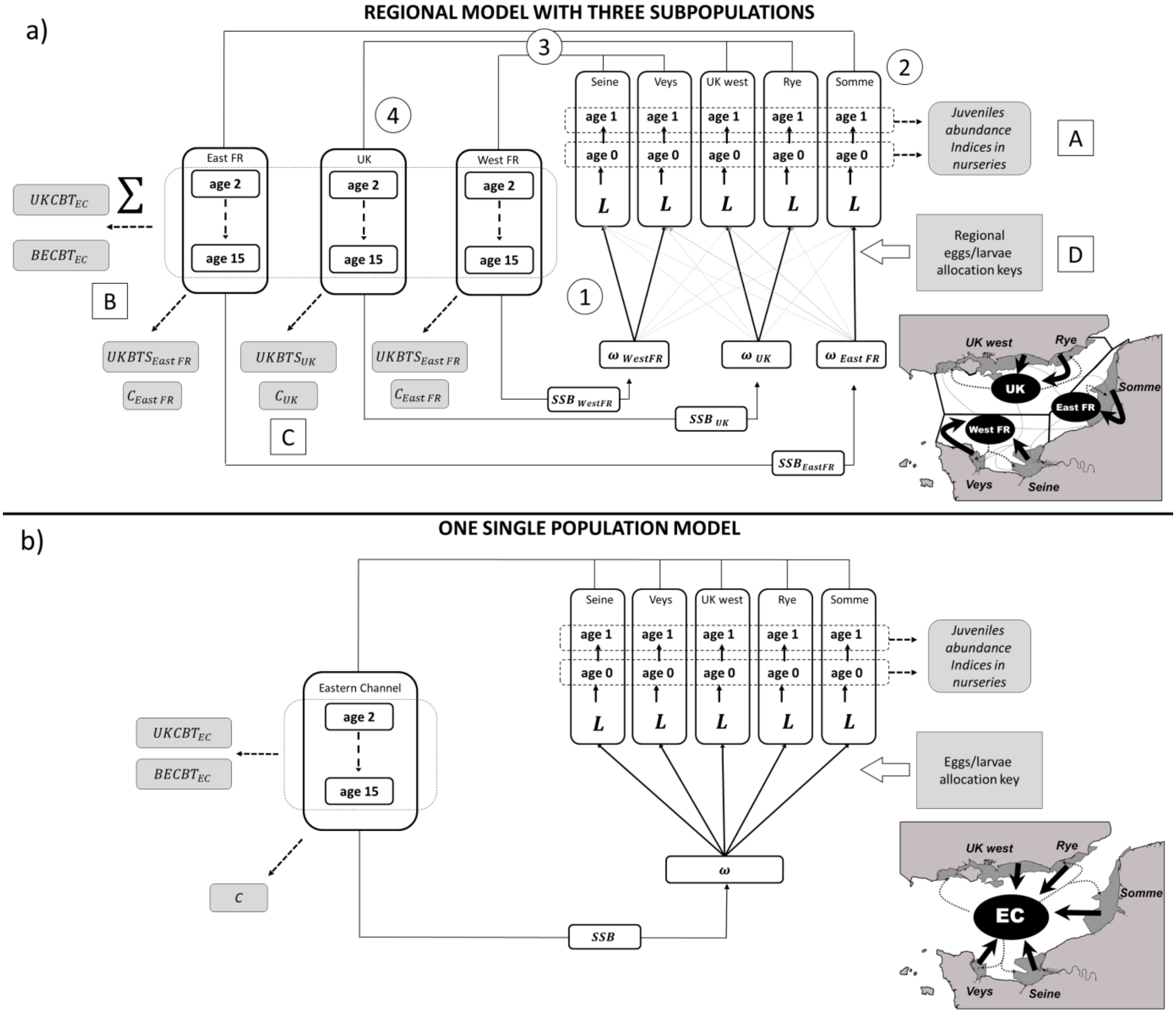

Figure 3.1- Structure of the HBM highlighting data integration and the two alternative hypotheses on the structure of the adults population a) with subpopulation structure of adults, b) without. Lettering and numbering refer to corresponding points in the *Material & Methods* section. White boxes: non observed state variables; Shaded boxes: data or model outputs considered as data. Dashed arrows indicate observation equations to link latent states variables to observations.

We first describe the model considering three (quasi)isolated subpopulations of sole in the EC. The second model considering only one homogeneous adult population is then presented as a simplification of the first one.

### Model considering three (quasi)isolated subpopulations

*Spatial structure*

Rochette et al. (2012) demonstrated the low dispersion of eggs of larval stages during the pelagic stages of the common sole. Indications of reduced movements of juveniles (Coggan and Dando, 1988; Anon., 1989), subadults and adults (Kotthaus, 1963; Anon., 1965) suggest that connectivity is limited after the juvenile stage in nursery grounds. Considering (i) this limited connectivity along the life cycle, (ii) the presence of natural barriers (e.g. rocky shores in the central southern coast and deep gravel grounds in the central part of the EC; Rochette et al., 2010), three different subpopulations (denoted r=1,2,3) associated with three spawning areas and attached nursery grounds were identified: the Western French subpopulation (West FR; Seine and Veys nursery sectors coupled to the southwestern spawning area), the UK subpopulation (Solent-Rye nursery sector coupled to the northern spawning areas) and the Eastern French subpopulation (East FR; Somme nursery sector coupled to the southeastern spawning area) (Figure 3.1a). The model is presented on Figure 3.1. Below we detail the demographic transitions with numbering matching Figure 3.1a. Equations and associated parameters are detailed in Suplementary Material.

*Eggs and larvae (1)*

Hatching of eggs is parametrized following the characteristics of the spawning season and spatial distribution of eggs (Rochette et al., 2012), the annual quantity of eggs in each spawning area being linked to the spawning biomass (see *section 4*). Eggs and larvae are transported from spawning areas and settle on the five identified nursery sectors (U.K West, Rye Bay, Somme, Seine and Veys) according to a drift/survival matrix estimated from a biophysical model (Rochette et al. (2012), updated by upgraded runs (Savina and Baulier, pers. comm.)). The annual number of settled larvae that are distributed among the nurseries was modelled as the product between the total number of eggs spawned by the population of each region and the drift survival rates derived from the larval transport model (Supp. Mat. (1)). Outputs from the larval-drift model pointed out a very low connectivity between the three spawning areas and distant nursery sectors over the times series, spawning areas feeding quite only the closest coastal and estuarine nursery grounds (Rochette *et al.*, 2012). Combined with the juveniles retention in nurseries, mixing of individuals between the three subpopulations occurs solely through the egg and larval drift (Figure 3.1) and therefore remains quasi inexistant.

The UK and in lesser proportions the East FR regions were also subject to larval inputs from the North Sea (NS) sole population (Savina, pers. comm.), which were integrated into the model.

*Juvenile from age 0 to age 2 (2)*

As in Rochette *et al.* (2013), settled larvae experience density-dependent post-settlement mortality (Iles and Beverton, 2000) over nursery sectors between settlement (late spring) and the end of summer, which corresponds to the growth period. The resulting expected number of age 0 juveniles is modeled through a Beverton-Holt relationship (Supp. Mat. (2a.i)) with logNormal process error (Supp. Mat. (2a.ii)). According to Rochette *et al.* (2013), these relations present biologically meaningful nursery-specific parameters: $\alpha_i$ the maximum survival rate and $K_i$ the carrying capacity per unit of surface. Because only poor information is available to estimate site specific parameters, exchangeable hierarchical structures (Gelman et al., 2004) were used to model the between-nursery variability of parameters $\alpha_i$ and $K_i$ (Table 3.3 in Supp. Mat.) allowing for "borrowing strength" between nursery sectors (Rivot and Prévost, 2002; McAllister et al., 2004). Available juvenile abundance indices on nursery sectors may contain enough information to estimate the carrying capacity parameters $K_i$. However, as observations at low levels of settling larvae are scarce, the maximum survival rates $\alpha_i$ (i.e. the slope at origin) could be difficult to estimate from data alone. An informative prior was set on the $\alpha_i's$ based on the meta-analysis of flatfish stock-recruitment relationships in Archambault et al. (2014) (Sup. Mat. 3.7.3 and Table 3.3 in Supp. Mat.).

Late age 0 juveniles (i.e. after the summer growth period = September) experiment a fixed natural mortality during 4 months until they reach age 1 in January (Supp. Mat. (2b)). These age 1 juveniles spend one year in nursery grounds where they suffer of a total mortality constituted by both natural and fishing mortalities (Supp. Mat. (2c)).

### *From nurseries to adult (3)*

Young fish are then assumed to leave nurseries at age 2 in January. At this stage, no quantitative data was directly available on the connectivity from nursery sectors (larvae to age 1) to deeper areas where older fish live (age a=2 to 15). Therefore, age 2 young fish emigrating from nurseries are supposed to contribute directly to the adjacent subpopulation part of the sub-systems described above according to their nursery of departure (Supp. Mat. (3)).

### *Sub adults and adults (4)*

Fish from age 2 to 15 are then structured in three different subpopulations with homogeneous biological and fishery related parameters. Within each subpopulation, cohort dynamics for ages 2-15 follow the standard dynamics accounting for both natural (fixed) and fishing (age/region/year specific) mortalities (Supp. Mat. (4a)). All remaining fish are assumed to die at age 15. Fishing mortality is a function of fishing effort (estimated) and age-specific gear selectivity (Fixed; Supp. Mat. (4b)).

Fish between age 3 and 15 take part in reproduction. The total amount of eggs for each year and each subpopulation was calculated from the spawning stock biomass by combining abundance at age with equations of female egg production used in Rochette et al. (2013).

### Simplifying the model to one single homogeneous adult population

The model considering three isolated subpopulations can easily be simplified into a single population model, which corresponds to the structure of Rochette et al. (2013) and to the stock-assessment (ICES, 2013). This single population model considers that the five nursery sectors contribute to one single population covering the whole Eastern Channel (Figure 3.1b). All other processes (e.g. juvenile dynamics) remain the same except the fishing mortality of adults that now occurs at the EC scale ($r = 1$). In the single-population model, eggs distribution in spawning area is assumed to exactly follow the repartition observed in 1991 (Rochette *et al.*, 2012).

### Data sources and observation model

*Model with three isolated populations*

The following data were available at the different stages (Synthesis and time series coverage in Table 3.1; model integration with matching lettering in Figure 3.1a):

[A] Egg and larval survival and allocation from spawning areas to the five nursery sectors over 1982-2007 were available as outputs from an upgraded run of Rochette et al. (2012) biophysical model (Savina and Baulier, pers. comm.). It ultimately provided the 3x5x26 probability key for eggs from each of the three subpopulation areas to reach each of the five different nursery sectors over 26 years of simulation (1982-2007); the last four years (2007-2011) were considered to be an average over the whole series.

[B] Juvenile abundance indices (age 0 and age 1) over the five nursery sectors were obtained from an upgrade of the habitat suitability model by Rochette et al. (2010), using up-to-date scientific trawl survey data. They were considered as observations of juveniles' abundance accounting for gear/age-specific catchability and observation error (Supp. Mat. (A1&A2)).

[C] Different abundance indices for adults were available and considered as observations of abundance accounting for gear/age-specific catchability and observation error (Supp. Mat. (B)). Abundance indices at the scale of the EC: the UK commercial fleet abundance (UKCBT) indices were updated from Rochette et al. (2013) and we also integrated the Belgium commercial fleet (BEBCT). Abundance indice at the scale of each subpopulation:

the scientific UK Bottom Trawl Survey (UKBTS) provides regional abundance indices at the adult stage for each subpopulation.

[D] Annual catch-at-ages per region ($C_{r,y}$) were reconstructed through the following procedure. Annual catches at ages $C_{a,y}$ ($a$ for age, $y$ for year) at EC scale and weights at age were available from stock assessment reports. The true spatial catch repartition in weight (originally per ICES statistical rectangle; aggregated at the scale of each of three subpopulations) was available solely from 2003. Before 2003, only catches in weight per country were reported.

- from 2003, catches-at-age for the three subpopulations r=1,2,3 were obtained by multiplying the catches with the true catch weight ratio per region $WKey_{y,r}$ (i.e. assuming identical age structure in catches amongst the three subpopulations) (See Eq.1a);
- between 1982 and 2003, the EC catches-at-age were multiplied by $CKey_{c,r}$, the constant key of catches (in weight) per subpopulation $r$ and country $c$ (See Eq. 1b), calculated on post-2003 data (i.e. assuming both identical age structures in catches and a constant spatial repartition of national fleets among subpopulation).

(1) $a)\ C_{a,y,r_{2003-2011}} = C_{a,y} * WKey_{y,r}$ b) $C_{a,y,r_{1982-2003}} = \sum_c C_{a,y} * CKey_{c,r}$

True catches-at-age (considered as a hidden state variable in the model) were calculated with the standard Baranov equation (Supp. Mat. (C1); Quinn and Deriso, 1999), and recorded catches were considered to be observed from true catches-at-age with sampling error (Supp. Mat. (C2)).

Table 3.1 - Synthesis of available data

| | | Time series coverage | Source |
|---|---|---|---|
| EGGS & LARVAE | Survival and allocation from spawning areas to the 5 nurseries sectors | 1982-2007 | Upgraded run of Rochette et al. (2012 ; Baulier and Savina, Pers. comm.) |
| JUVENILES | West UK | 1982-1999 | Rochette et al. (2010) |
| | Rye | 1982-2006 | Rochette et al. (2010) |
| | Somme | 1982-1983 ; 1987-2011 | Rochette et al. (2010) |
| | Seine | 1995-2002 ; 2006 ; 2008-2011 | Rochette et al. (2010) + GIP Seine Aval |
| | Veys | 2006 ;2010-2011 | Rochette et al. (2010) |
| ADULTS | Catches at age | 1982-2011 | ICES |
| | Spatial repartition of catches (total weights, no age structure) | 2003-2011 | Pers. comm. |
| | Spatial Scientific Abundance indice : UKBTS | 1990-2004 ; 2006-2011 | ICES |
| | UK commercial CPUE : UKCBT | 1986-2011 | ICES |
| | Belgium commercial CPUE : BECBT | 1982-2011 | ICES |

*Model with one single population*

In the single-population model (Figure 3.1b), the same sources of data are used but no spatial structure is considered for the catches (i.e. $r = 1$ in Supp. Mat. (D)) and only the non-spatial adult abundance indices are used (i.e. UKCBT and BECBT).

*Magnitude of observation errors*

A variance of observation errors is associated to each source of data. Due to both the nature of the data and local expertise, abundance indices from surveys were considered to be less reliable (i.e. a factor 2 on observation CV in the log scale) than aggregated catches reports (Table 3.3 in Supp. Mat.).

### 3.2.3. Estimating stock-assessment, productivity and management indicators

Site specific BH parameters and the annual contribution of each nursery sector to the overall adult population were estimated.

Indicators produced in stock assessments procedures, namely the spawning stock biomass ($SSB$), the recruitment ($R$), and the fishing mortality ($F$), were estimated at different scales (for each subpopulation and at the scale of the EC).

We also estimated the Maximum Sustainable Yield ($MSY$) and the associated fishing mortality ($F_{MSY}$) and spawning stock biomass ($SSB_{MSY}$) for each subpopulation. These were defined intrinsically i.e. not considering larval inputs from other subpopulation. Their calculation is not analytically straightforward, as the production of each subpopulation results from a combination of BH relationships fitted on each nursery sectors (2 in West Fr: Veys and Seine, 2 in UK: UK west and Rye, 1 in East Fr: Somme; Figure 3.1). The equilibrium curves were obtained by Monte Carlo simulations to integrate both process and parameters uncertainty (see Sup. Mat. for further details). Simulations were conducted for each subpopulation separately (i.e. by considering zero connectivity between the subpopulations). The population was simulated during 200 years to reach an equilibrium state. Drift and survival parameters for eggs and larvae were considered constant during the simulations and set to their average value (1982-2006). A range of $F$ large enough to cover all scenarios from no exploitation to heavy overexploitation (from 0 to 2 with a step of 0.05) was simulated.

### 3.2.4. Model configuration and computational details

All parameters except the slope of the BH relationships over nursery areas ($\alpha_i$, *cf.* 3.2.2.) were given weakly informative *a priori* distributions in the sense of Gelman (2004) i.e. they let the data speak while excluding unrealistic values. They are detailed in Table 3.3 (Supp. Mat) along with fixed parameters (e.g. variance of observation errors). Bayesian posterior distributions were approximated via Monte Carlo Markov Chain (MCMC) methods using the JAGS software (http://mcmc-jags.sourceforge.net) through the Rjags (www.Rproject.org) package. Three MCMC-independent chains with dispersed initialization points were used. For each chain, the first 5,000 iterations were discarded. Inferences were derived from a sample of 3*50,000 iterations with a thin of 10. All the modeling results have passed the Gelman-Rubin test (Brooks and Gelman, 1998) as implemented in the R Coda package to assess convergence of MCMC chains (R ratio < 1.05 for all variables).

## 3.3. Results

The model considering three subpopulations provides a spatial perspective to the population dynamics and to stock-assessment.

### 3.3.1. Weight of the different data sources

Before describing the results, we first provide an assessment of the contribution of each dataset towards final estimations as it may provide useful insights on limitations or further data needs. Four runs of the model with three subpopulations were conducted, successively adding the different sources of spatial data series (i.e. catches and abundance indices; Table 3.2).

Table 3.2 - Configuration of the different model runs to explore the respective contribution of data sources in the regional model.

| Run ID | Spatial catches | Spatial Abundance Indice (UKBTS) | Additional hypotheses |
|---|---|---|---|
| **a** | No | No | $F$ equals among regions |
| **b** | No | Yes | $F$ equals among regions |
| **c** | Yes | No | |
| **d** | Yes | Yes | |

The run (Figure 3.2a), with no spatial data and forced equal fishing mortality across subpopulations, displays highly uncertain estimates of $SSB$. The run (Figure 3.2b), with spatial abundance indice but equal fishing mortality across subpopulations, produces $SSB$ of close values which also follow a similar evolution with reduced variability. In the run (Figure 3.2c), with spatial fishing data but no spatial AI, there are more differences between $SSB$ than in Figure 3.2a and $SSB$ shifts could be identified between the East FR and the West FR regions at the end of the time series. Finally, with the run integrating all available data (Figure 3.2d), the "$SSB$ shift" still occurs but the $SSB$ variability across subpopulations shrinks, resulting in lower differences than in the first and third cases (Figure 3.2ac).

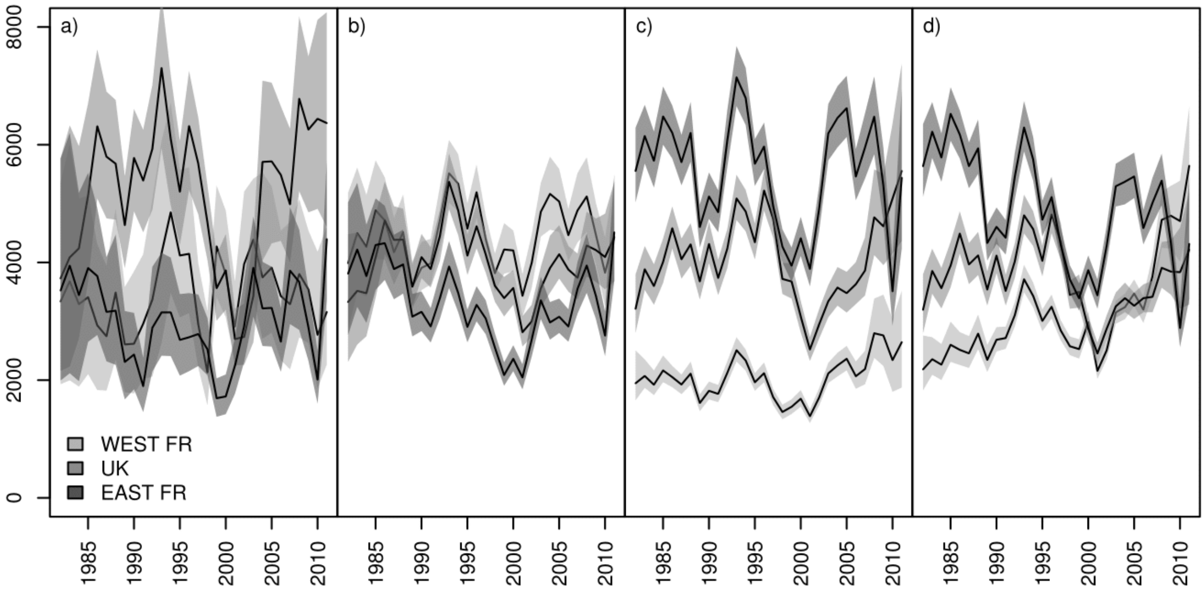

Figure 3.2 – Time series of $SB$ for the three subpopulations obtained with different data configurations: a) no spatial data; $F$ is equal among subpopulations $b$) spatial abundance indice (AI) data; $F$ is equal among subpopulations c) spatial catch data; no spatial AI data d) spatial catch data and spatial AI data. Plain lines: posterior medians. Shaded areas: 95% Bayesian credible intervals.

### 3.3.2. Abundance and fishing mortality in the Eastern Channel

The single-population model and the model considering three subpopulations provide similar results for variables and indicators considered at the stock scale. These were also consistent with ICES estimates (Figure 3.3abc), although displaying overall slightly higher $SSB$ and consequently lower $F$.

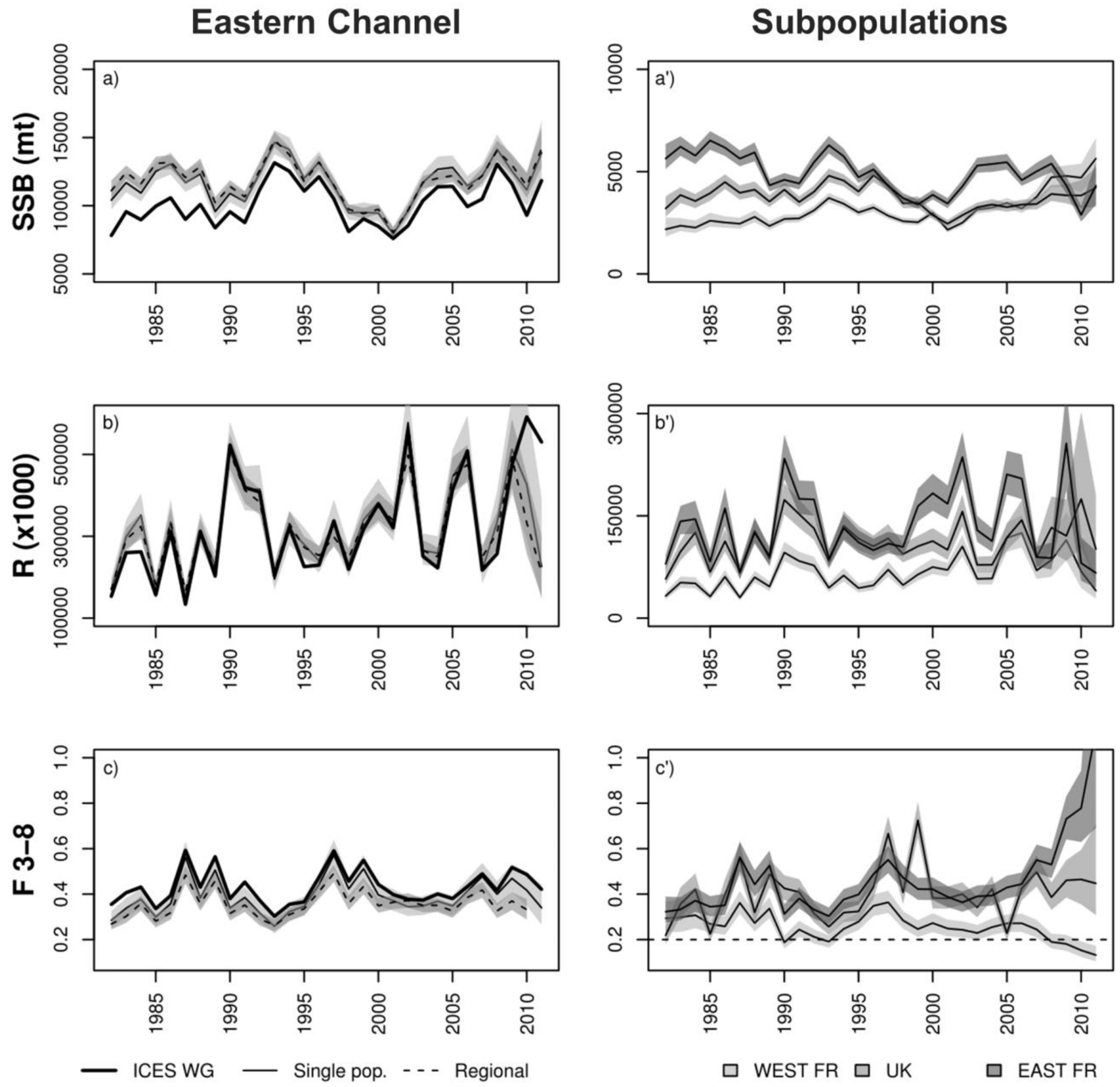

Figure 3.3 – Left column. Comparison of estimates of $SSB$, $R$ and $F_{3-8}$ at the Eastern channel scale obtained by the ICES WG (bold line), by the model considering one homogeneous adult population (plain line) and by the model considering three components of the adult population (dotted line). Right column. Comparison of estimates of $SSB$, $R$ and $F_{3-8}$ between subpopulations obtained by the model considering three components of the adult population. Plain lines: posterior medians. Shaded areas: 95% Bayesian credible intervals.

### 3.3.3. Impact of considering three isolated subpopulations

Considering a model with three isolated subpopulations changes inferences on population dynamics and assessment of stocks status.

**Reevaluation of the productivity of nurseries**

The contribution of each nursery sector to the recruitment at the EC scale strongly differed between the single-population and the three subpopulation structures (Figure 3.4). In the single-population structure, the Seine, Veys, Solent, Rye and Somme sectors contributed on average respectively 16, 20, 21, 21 and 23%. In the three subpopulation structures, these contributions were estimated at 13, 7, 18, 19 and 43% respectively. At the subpopulation level, this translates into a strong increase in the contribution from East FR subpopulation (from 23% to 43%) balanced by decreases in contributions from West FR (Seine+Veys: from 39% to 21%) and UK subpopulations (Solent+Rye: from 43% to 36%).

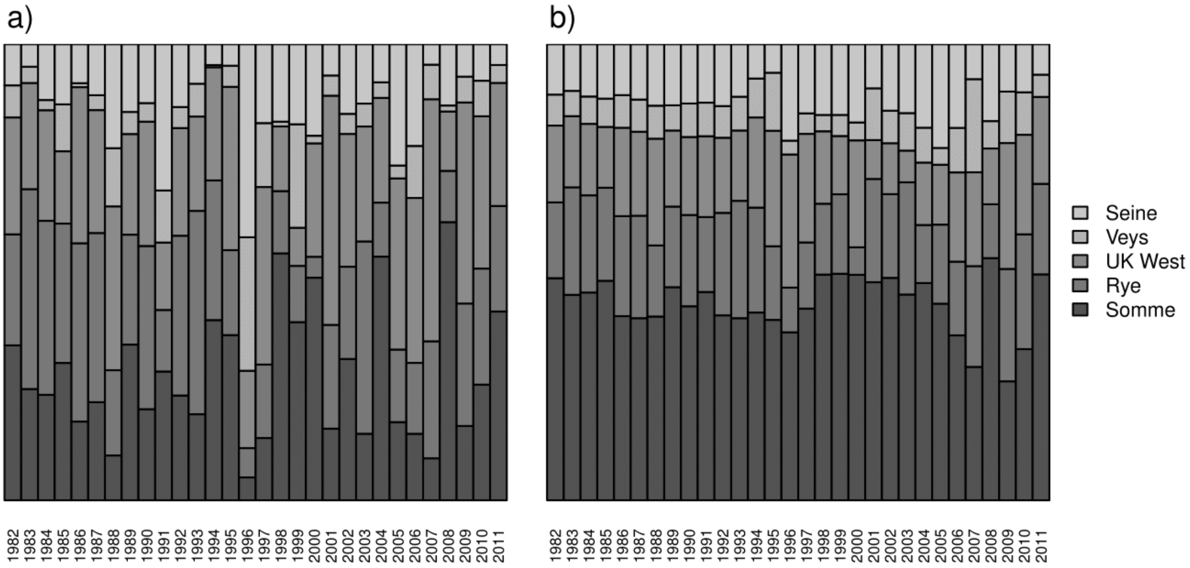

Figure 3.4 - Realized contributions of the nursery sectors a) in the model considering one single adult population and b) three subpopulations.

Similar patterns are logically found in the estimates of the BH relationship's carrying capacity per surface $K$ (Figure 3.5b), with $K$ of the Somme nursery sector being largely reevaluated, balanced by $K$ for UK West and Rye estimated to lower values when considering a model structure with three isolated subpopulations. $\alpha$ estimates did not display a particular trend (Figure 3.5a).

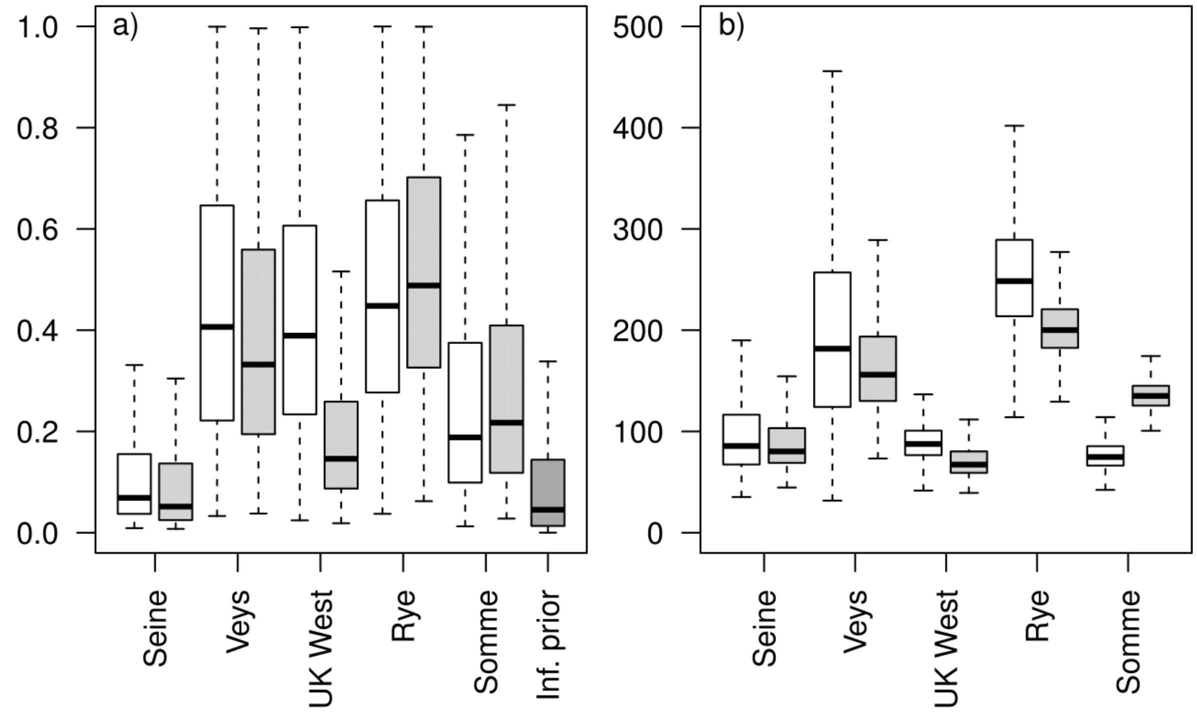

Figure 3.5 - Comparison of the posterior distributions of the nursery parameters $\alpha$ (a) and $K$ (b) obtained with the model considering one homogeneous adult population (white) and considering three components of the adult population (grey).

### Management reference points and stock assessment

The model with three isolated populations provides a spatial perspective to the population dynamics and to the impact of fishing pressure. Estimates of $SSB$ among the different subpopulations (Figure 3.3a') are contrasted with in increasing order of mean $SSB$ over the whole time series, the West FR subpopulation (average 3,240t), the UK subpopulation (average 3,680t) and the East FR subpopulation (average 4,940t). A shift in $SSB$ values occurs in the last years between the West FR and the East FR subpopulations: the East FR subpopulation displays a strong drop in $SSB$ over the past 4 years (50% decrease) while a significant increase (+100%) occurs in the West FR subpopulation. Concurrently, regional $F$ show opposite trends, with a small decrease in West FR subpopulation and a strong increase in East FR (+100%; Figure 3.3c'). The average $F$ over the past 4 years are estimated at 0.16, 0.44 and 0.8 respectively for the West FR, UK and East FR subpopulation.

The reference points $SSB_{MSY}, C_{MSY}, F_{MSY}$ (Figure 3.6) associated to each subpopulation were estimated respectively at 7,780 t, 970 t and 0.14 for the West FR subpopulation; 11,450 t, 1615 t and 0.16 for the UK subpopulation and 11,060 t, 1,900 t and 0.2 for the East FR subpopulation.

When considering one single population, $SSB_{MSY}$, $C_{MSY}$ and $F_{MSY}$ are estimated at 23,600 t, 3,900 t and 0.19 respectively, thus indicating that the sole population is globably underexploited.

However, at the current regional state of exploitation (see equilibrium points on Figure 3.6), it appears that the West FR subpopulation is at full exploitation while the UK and East FR subpopulations are overexploited, with $SSB/SSB_{MSY}$ dramatically lower than 1.

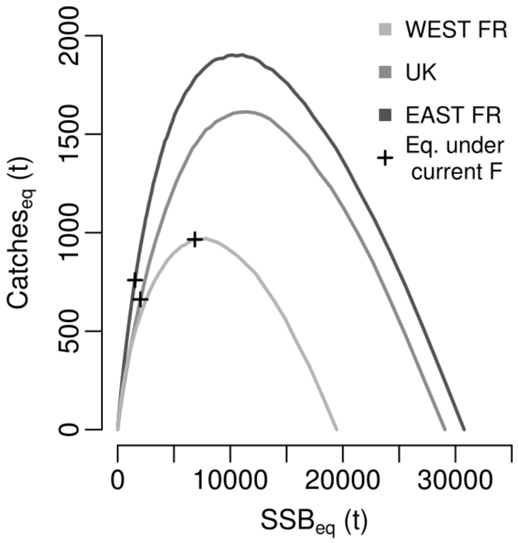

Figure 3.6 - Relation between the regional $SSB$ and catches at equilibrium obtained through the simulation approach in the model considering three components of the adult population Eq. under current F represent the situations at equilibrium with the current (average over 4 last years) fishing mortalities.

## 3.4. Discussion

### 3.4.1. Accounting for the adult mediated connectivity increases model complexity

The hierarchical Bayesian modeling framework proved to be a flexible tool for embedding prior knowledge on the ecological process and data from different sources (Parent and Rivot, 2012; Rochette *et al.*, 2013; Massiot-Granier *et al.*, 2014), and results provide significant contribution to the understanding of the population dynamics of the sole population in the Eastern Channel. While classic stock assessment methods are generally limited to consider simple homogeneous population with no spatial structure, our framework enables to explore the consequence of considering limited connectivity between three different subpopulations in the Eastern Channel. In the model considering one single population previously developped by Rochette et al. (2013), limited connectivity from spawning to nursery areas was accounted for (Rochette et al., 2012 and upgrade). Strong prior knowledge exists in favor of limited movements of juveniles (Coggan and Dando 1988, Anon. 1989) and of a low Adult

Mediated Population Connectivity (AMPC; Frisk et al. 2013) for the common sole in the Eastern Channel. Movements of adults are limited (Kotthaus, 1963; Anon., 1965; Burt and Millner, 2008) and physical rocky barriers exist between West and East FR subpopulations (Rochette *et al.*, 2010, 2012). This prior knowledge was used to design the regional spatial structure with the definition of the three subpopulations. This model structure differs strongly from the baseline structure used for stock assessment.

However, while a body of ecological knowledge and clues strongly justifies *a priori* the model structure, statistically assessing the relative likelihood of the two alternative spatial hypotheses is not straightforward. Usual Bayesian model performance indicators such as the Deviance Information Criterion (Spiegelhalter *et al.*, 2002) cannot be directly used to compare models which integrate different sources of data (e.g., spatial IA and fishing pressure), as in the present study. As expected, the component of the Deviance associated with the data shared by the two model structures (i.e. the spatialized abundance indices of juveniles in the five nursery sectors and the non-spatialized abundance indices of age 2-15) is slightly lower for the model with one single population than for the model with three isolated components. This is not surprising as considering three isolated components introduced rather strong structural constraints on the dynamics of latent variables in the model, and therefore slightly increases the discrepancy between the state variable and the observations. However, the difference is only light, indicating that the likelihood of the two models is quite comparable when considering the data shared by the two model structures.

We also compared egg distribution amongst the three spawning areas (i.e. function of the local $SSB$) to the spatial repartition of eggs given by the single available observations issued from the 1991 eggs survey (Rochette et al., 2012). Results indicate that the spatial distribution of eggs derived from the fit of the model with three isolated populations (West FR, 21%; UK, 39.5%; East FR, 39.5%) was highly consistent with the egg repartition observed in 1991 (25%, 34% and 41% respectively).

The model points out how taking into account the meta-population structure helps identifying current lacks and needs in knowledge, and may impact estimates of fisheries management indicators while paving the way for future scenario simulations.

### 3.4.2. Needs for spatial data

This study points out the need for reliable catches and abundances indices available in space and time. As spatial data availability has increased in recent years, our ability to conduct such studies should progress in the future.

### The predominant role of spatial catch data

The evaluation of the contribution of the different data sources highlighted the predominant contribution of catch data in the final assessment, while adult abundance indices only play a minor role. This is a common phenomenon in catch-at-ages models where catches are the main drivers (Hilborn and Walters, 1992). In the present case, the contrast and variability of abundance indices are weak compared to what we observe in catch data. Moreover, different uncertainty levels are used to integrate the different sources of data, catches being considered to be less uncertain (CV of observation error on lognormal distribution: 0.2) than abundance indices data (CV: 0.4) according to local expertise. This adds even more weight to catch data relatively to other sources.

The key role of the spatialized catch data in the final results would suggest to carefully assess the reliability of those data. Assumptions were made to produce time series of catches for the three subpopulations considered in the model over the whole time series (30 years). A constant spatial repartition of catch among regions per country was assumed before 2003, when spatialized catches were lacking. To weight the influence of these hypotheses on the results, we accepted a lower relevance of model outputs over periods where data were scarce. For instance other "$SSB$ shifts" similar to the one observed over the last years could have occurred earlier in the time series but remain undetected due to the lack of true spatial data at this time.

### Improving knowledge on adult mediated connectivity

Our approach considered two extreme and opposite connectivity scenarios (i.e. full adult connectivity versus full spatial segregation). Assumptions had to be made as data on juvenile-to-adult areas and adult migrations were lacking. While the integration of exchanges across the three subpopulations would be straightforward in the current modeling framework (i.e. modifying the adult connectivity matrix), there is a strong lack of data to support finer scenarios in this case study. This emphasizes the need to go further with data collection on movements and connectivity in marine populations (Frisk *et al.*, 2013). Knowing whether fish remain in the same location or move across habitats and zones is essential to understand the scale of their dependence upon different habitats (Saucerman and Deegan, 1991). Two main approaches could be used: natural markers studies or mark-recapture procedures. Natural markers include genetic markers, xenobiotics, stable isotopes, otolith microchemistry and parasites and their possible combination (Selkoe *et al.*, 2008; Fodrie and Herzka, 2013). The analysis of natural genetic neutral markers has proven its efficiency in inferring population structure on freshwater and anadromous fishes (Smedbol *et al.*, 2002), although the open nature of marine environment may not provide the level of isolation required for significant patterns to emerge (Waples, 1998; Exadactylos. *et al.*, 2003; Rolland *et al.*, 2007). However recent approaches using combined multi-marker approach (Cuveliers *et al.*, 2012) and adaptive markers (Diopere *et al.*, 2013) provide fruitful perspectives to understand the connectivity and segregation patterns among marine subpopulations with a finer spatial resolution. The estuarine origin of individuals has been successfully identified in similar populations through differences in otolith elemental composition (Cuveliers *et al.*, 2010) and could also provide information on connectivity. Mark-recapture techniques, including *de visu* or video observations and ultrasonic tagging (Benhamou, 2014) may be useful to estimate migration coefficients (Hilborn, 1990; Rijnsdorp and Pastoors, 1995; Darnaude and Hunter, 2008). Recent work focusing on old juvenile, sub-adult and adult flatfishes emphasized the interest of these approaches (Hurst and Duffy, 2005; Sackett *et al.*, 2008; Fairchild *et al.*, 2009; Furey *et al.*, 2013). However, these marking techniques also present drawbacks (i.e. the highly time-consuming and expensive nature of such experiments; Smedbol *et al.*, 2002) and possible bias due to fishing effort or sampling distribution resulting in overestimated recapture in fished areas (Bolle *et al.*, 2005). Overall, field studies aiming at characterizing the movements of individuals could provide great insights on population functioning (i.e. estimation of migration matrix between nurseries and adult areas and further adult movements). In the present state of knowledge, being unable to formally differentiate subpopulations should not prevent from considering a particular structure of the adult population, especially in a case study where both expert and not quantified knowledge point towards its existence.

### 3.4.3. Towards an understanding of meta-population dynamics

The present study provides significant insights towards the understanding of the life cycle of the EC sole population. Taking into account the moderate connectivity between the successive life stages, we were able to produce a diagnosis of the population which, while being consistent with ICES estimates at the scale of the EC, provided contrasted results at a more local scale. This approach enabled the reconstruction of local biomasses' evolution during the past three decades. This highlighted a potential "$SSB$ shift" which occurred between the two French subpopulations in the latest years, with a decrease in the East FR and an increase in the West FR. This observation revealed consistent with recent local drops in catches experienced by fishermen from the East FR (fishermen pers. comm.). Taking the spatialization into account also led to a substantial reevaluation of the productivity of the different nursery sectors, in accordance with the local biomasses estimated for the associated subcomponents. While these results are in part due to mechanistic constraints imposed by the population model (i.e. local $SSBs$ require certain levels of local juvenile production), they appear coherent from a life-cycle perspective. It is indeed likely that the actual contribution of nurseries to recruitment remains quite stable from year to year, as observed in the model with three subpopualtions, in accordance with the concentration hypothesis (Rijnsdorp *et al.*, 1992; Iles and Beverton, 2000; Rooper *et al.*, 2004). Such approaches may prove relevant in inferring nursery productivity in data-poor contexts where no sufficient data would be available to directly estimate the contributions of nurseries. One may be able to estimate the expected contribution of nursery sectors according to the dynamics of the subpopulation depending on these sectors.

More generally, the present study emphasizes the possible implications of spatial patterns on population functioning for other populations and species which display larval retention patterns and whose different life history stages are segregated among specific habitats (e.g. nursery-dependent species). Larval retention, demonstrated for the EC common sole (Savina *et al.*, 2010; Rochette *et al.*, 2012) is suspected to occur more than originally thought in marine populations (Cowen *et al.*, 2000; Warner and Cowen, 2002). As larval segregation is important at a local scale, i.e. scales smaller than population extent, the focus on connectivity is traditionally aimed at modeling the dispersal of first life stages (Frisk *et al.*, 2013). The approach has been extended here towards later stages. Frisk (2013) has recently pointed out the potential role of Adult Mediated Population Connectivity (AMPC) and therefore the need to assess more thoroughly the potential impact of adults on the spatial structure of marine fish populations. Regarding our case study, sole juveniles are known to remain in their nurseries once they are settled (Riou *et al.*, 2001; Rochette *et al.*, 2010) and the crucial stage for spatial dissemination should consequently be the adult stage.

### 3.4.4. Future implications for local management and room for scenarios

Our results raise concerns about both fishery and coastal habitat management.

EC sole, as most exploited marine fish stocks, is currently assessed as one single population. However, dynamics may strongly differ among different components of the meta-population, which could result in local over- (or under-) exploitation (Maury and Gascuel, 2001; Ying *et al.*, 2011). In this work, we were able to estimate regional references points and to identify local situations of overexploitation. These local patterns appear especially realistic when, as in the present study, the population is mostly exploited by regional fisheries with limited movement, without large scale tracking of fishes towards areas of higher abundance.

Essential coastal and estuarine habitats are subject to high but spatially contrasted anthropic pressures (Le Pape *et al.*, 2007; Rochette *et al.*, 2010). The reevaluation of nursery contributions, closely linked to regional dynamics, may provide insights into where to allocate particular efforts towards habitat preservation or restoration. Indeed, such measures may prove at least as important as fishing regulation in restoring EC sole population, and nursery-dependent species in general (Levin and Stunz, 2005; van de Wolfshaar *et al.*, 2011).,

Finally, the present approach should constitute a major step towards the simulation of various scenarios. Taking into account the impact of (the absence of) connectivity at each successive life stage is indeed a prerequisite to the evaluation of management measures in a spatial perspective. For instance, the present model may enable the impact assessment of one given nursery restoration/degradation at local/population scales, or of different spatial exploitation schemes.

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## 3.7. Supplementary material

In all equations below, indice $y$ denote the years in the time series, $i$ denote the nursery sector ($i$=1,…,5, with 1=Seine, 2=Veys, 3=Solent, 4=Rye, 5=Somme), and $r$ the component of the meta-population ($r$=1,2,3 with 1=West FR, associated with nursery grounds Seine and Weys; 2=UK, associated with nursery grounds Solent and Rye; 3=East FR, associated with nursery ground Somme).

### 3.7.1. Process equations

**1. Eggs and Larval drift**

$$L_{y,i} = \sum_{\boldsymbol{r=1}}^{\boldsymbol{r=3}} \omega_{y,r} \cdot D_{y,r,i} \tag{1}$$

where $L_{y,i}$ is the number of settling larvae (i.e. post-larvae) in nursery sector $i$ at year $y$, $\omega_{y,r}$ is the egg pool for the subpopulation $r$ at year $y$ and $D_{y,r,i}$ is the probability of success for an egg from the egg pool $r$ to reach the nursery sector $i$ at year $y$.

**2. From Post-larvae to subadults**

*a. Post-larvae to juvenile dynamics on nursery grounds, from settlement to Summer End*

$$E(N_{0_{y,i}}) = \frac{K_i \cdot L_{y,i}/Surf_i}{K_i/\alpha_i + L_{y,i}/Surf_i} \tag{2a.i}$$

where $E(N_{0_{y,i}})$ is the expected mean of age 0 individuals at year $y$ in nursery $i$, where $K_i$ is the nursery-specific carrying capacity per unit of surface and $\alpha_i$ the nursery-specific maximum survival rate.

The number of age 0 fish is logNormaly distributed:

$$\log(N_{0,\mathrm{y,i}}) \sim \mathrm{Normal}(\log(\mathrm{E}(N_{0_{y,i}}) - 0.5 \cdot \sigma_{BH}^2), \sigma_{BH}^2) \tag{2a.ii}$$

where $\sigma_{BH}^2$ is the BH process variance and is considered identical in the five nurseries.

*b. Age 0 mortality from summer end to December*

$$\boldsymbol{N_{1,y+1,i} = N_{0,y,i} \cdot e^{-1/3 \cdot M_0} \cdot e^{\varepsilon_{0,y,i}}} \tag{2b}$$

where $N_{0,\mathrm{y,i}}$ is the number of age 0 fish in each nursery $i$, $M_0$ is the fixed natural mortality at age 0 and $\varepsilon_{0,y,i}$ is a Normal environmental noise with variance $\sigma_p^2$.

*c. Age 1 mortality*

$$Z_{1,y,i} = M_1 + F_{1,y,r_i} \tag{2c.i}$$

$F_{1,y,r_i}$ is defined for each region $r$ which includes the nurseries $i$ (see (3) for details on nursery/region complexes),

$$N_{2,y+1,i} = N_{1,y,i}.\,\mathrm{e}^{-Z_{1,y,i}}.\,\mathrm{e}^{\varepsilon_{1,y,i}} \tag{2.c.ii}$$

where $N_{2,y,i}$ is the number of age 2 fish in each nursery $i$, $Z_{1,y,i}$ is the total mortality and $\varepsilon_{1,y,i}$ is a Normal environmental noise with variance $\sigma_p^2$.

#### 3. Emigration from nurseries to adult regions

$$\begin{cases} N_{2,y+1,r=1} = \sum_{\mathrm{i}=1}^{\mathrm{i}=2} N_{2,y,i} \\ N_{2,y+1,r=2} = \sum_{\mathrm{i}=3}^{\mathrm{i}=4} N_{2,y,i} \\ \quad N_{2,y+1,r=3} = N_{2,y,i=5} \end{cases} \tag{3}$$

$N_{2,\mathrm{y,r}}$ is the number of age 2 fish in each subpopulation after migration from included nursery sectors ($r$= from 1 to 3; with 1=West FR (Seine and Veys nurseries), 2=UK (Solent and Rye nurseries), 3=East FR (Somme nursery); see also Figure 3.1)

#### 4. Adults mortality

$$N_{a+1,y+1,r} = N_{a,y,r}.\,e^{-Z_{a,y,r}}.\,e^{\varepsilon_{a,y,r}} \tag{4a}$$

where $N_{a,y,r}$ is the number of individuals of age $a$ in region $r$ at year $y$, $Z_{a,y,r}$ is the total mortality rate at age $a$ in year $y$ and region $r$, defined as the sum of natural mortality $M_a$, considered constant across years and regions and fishing mortality $F_{a,y,r}$. $\varepsilon_{a,y,r}$ is a Normal environmental noise with variance $\sigma_p^2$. All remaining fish are assumed to die at age 15.

$$F_{a,y,r} = S_a \cdot E_{y,r} \tag{4b}$$

with $S_a$ an age-specific selectivity (logistic function with known parameters, Table 3.3 in Supp. Mat.), $E_{y,r}$ a year and region-specific fishing effort. Between-year variability of $F_{a,y,r}$ was captured through a random hierarchical structure for $F_{a,y,r}$ . Time variability of fishing effort $E_{y,r}$ was *a priori* modelled as a random walk (Table 3.3 in Supp. Mat.).

### 3.7.2. Observation equations

#### A. Juveniles abundance indices

$$\log(I_{0,y,i}) \sim \mathrm{Normal}\left(\log(q_0 \cdot N_{0,y,i}) - 0.5 \cdot \sigma_{I_{juv}}^2, \sigma_{I_{juv}}^2\right) \tag{A1}$$

$$\log(I_{1,y,i}) \sim \mathrm{Normal}\left(\log(q_1 \cdot N_{1,y,i}) - 0.5 \cdot \sigma_{I_{juv}}^2, \sigma_{I_{juv}}^2\right) \tag{A2}$$

with $q_0$ and $q_1$the age-specific catchability and $\sigma_{I_{juv}}^2$ the observation variance.

### B. Adults abundance indices

$$\log\left(I_{fleet_{a,y,(r)}}\right) \sim \text{Normal}\left(\log\left(q_{fleet} \cdot N_{a_{y,i,(r)}} . S_a\right) - 0.5 \cdot \sigma^2_{fleet}, \sigma^2_{fleet}\right) \quad \text{(B)}$$

where $I_{fleet_{a,y,(r)}}$ is the observed CPUE of age $a$ at year $y$ (in region $r$ for the UKBTS survey; in the whole EC for other indices), $q_{fleet}$ is the fleet-specific catchability and $S_a$ the age-specific selectivity .

### C. Catches

$$H_{a,y,r} = N_{a,y,r} \cdot \left(\frac{F_{a,y,r}}{F_{a,y,r}+M_a}\right) \cdot \left(1 - e^{-1(F_{a,y,r}+M_a)}\right) \quad \text{(C1)}$$

where $H_{a,y,r}$ are the true catches at age $a$ at year $a$ in region $r$

$$\log\left(C_{a,y,r}\right) \sim \text{Normal}\left(\log\left(H_{a,y,r}\right) - 0.5 \cdot \sigma_C^2, \sigma_C^2\right) \quad \text{(C2)}$$

where $C_{a,y,r}$ are the reported catches and $\sigma_C^2$ the sampling error variance.

### 3.7.3. Parameters and priors

Priors distributions or fixed values of parameters are described in Table 3.3

*Informative priors on the maximum survival rates* $\alpha_i$

Informative priors were set on the nursery-specific maximum survival rates $\alpha_i$. Taking away the EC sole dataset from the database used for the metaanalysis in Archambault et al. (2014), we reconstructed an informative prior for the present study based on the posterior predictive distribution of $\alpha$ from the meta-analysis. We took into account the characteristics of sole life history in EC (Archambault *et al.*, 2014); and Eq. 5, namely the eggs to post-larvae survival $S_{\omega-L}$, the average fecundity ($Fec$), the spawning biomass produced in the absence of fishing ($SPR_{F=0}$) and the natural mortality from observation in September to recruitment at age 1 in January ($M_0$). We also took into account the differences between the present model and ICES age 1 mortalities ($M_{1_{ICES}}$=0.1; $M_{1_{HBM}}$=2.6), as numbers at age 1 are back calculated from numbers at age 2 in ICES stock assessments (5).

$$(5) \qquad \alpha = \frac{\alpha_{meta}}{S_{\omega-L} * Fec * SPR_{F=0}} * e^{-M_0 * 4/12 *} e^{M_{1_{HBM}} - M_{1_{ICES}}}$$

The empirical distribution of $\alpha$ was approximated by lognormal distributions (Table 3.3).

Table 3.3 - HBM parameters and priors distributions

| **Parameters** | **Value / prior / structure** | **Description** |
|---|---|---|
| $\boldsymbol{M_a}$ | 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 $a$ ($y^{-1}$). |
| $\boldsymbol{\sigma_p^2}$ | $1E^{-3}$ | Variance of process error on dynamic equations |
| $\boldsymbol{E_{t,r}}$ | $\log\left(E_{t=1,r}\right) \sim Norm(E = 0, \sigma = \sqrt{10}\,)$<br>$\log(E_{t,r}) \sim Norm(E = \log\left(E_{t-1,r}\right), \sigma_E)$<br>$\sigma_E \sim Unif(0.01,0.5)$ | Priors on fishing effort $E_{y,r}$ with random walk |
| $\boldsymbol{S_a}$ | Age 0: 0.35 ; Age 1: 0.58 ; Age 3: 0.74 ; Age 4: 0.84 ; Age 5: 0.9 ; Age 6: 0.94 ; Age 7: 0.96 ; Age8: 0.99; Age 9-15: 1 | Age-specific gear selectivity (logistic with fixed parameters) |
| $\boldsymbol{\alpha_i}$ | $\log(\alpha_i) \sim Norm(E = \mu_{log\alpha}, \sigma = \sigma_{log\alpha})\vert[,0]$<br>$\mu_{log\alpha} \sim Norm(E = -3, \sigma = \sqrt{0.01})$<br>$\log(\sigma_{log\alpha}) \sim Norm(E = -1.273, \sigma = \sqrt{0.01})$ | Nursery-specific maximum survival rates. Hierarchical structure with informative priors based on Archambault *et al.* (2014) |
| $\boldsymbol{K_i}$ | $\log(K_i) \sim Norm(E = \mu_{logK}, \sigma = \sigma_{logK})$<br>$\mu_{logK} \sim Norm(E = 4, \sigma = 0.06)$<br>$\log(\sigma_{log\alpha}) \sim Norm(E = 0.2, \sigma = \sqrt{0.01})$ | Nursery-specitfic carrying capacity per surface. Hierarchical structure with uninformative (although realistic) priors. |
| $\boldsymbol{\sigma_{BH}^2}$ | $\log(\sigma^2{}_{BH}) \sim Unif(-10,10)$ | Variance of process error on the post-larvae to juvenile BH relationship |
| $\boldsymbol{\sigma_{I_{juv}}^2}$ | $\sigma_{I_{juv}}^2 = \log({CV_{I_{juv}}}^2 + 1)$<br>$CV_{I_{juv}} = 0.4$ | Variance of observation error on the juvenile survey |
| $\boldsymbol{\sigma_{fleet}^2}$ | $\sigma_{fleet}^2 = \log({CV_{fleet}}^2 + 1)$<br>$CV_{UKCBT} = 0.4$<br>$CV_{BECBT} = 0.4$<br>$CV_{UKBTS} = 0.4$ | Variance of observation error on adult abundance indices (UKCBT, BECBT, UKBTS) |
| $\boldsymbol{\sigma_C^2}$ | $\sigma_C^2 = \log({CV_C}^2 + 1)$<br>$CV_C = 0.2$ | Variance of observation error on catches |
| $\boldsymbol{q_0}$ | $\log(q_0) \sim Unif(-10,10)$ | Catchability of Age-0 |
| $\boldsymbol{q_1}$ | $\log(q_1) \sim Unif(-10,10)$ | Catchability of Age-1 |
| $\boldsymbol{q_{fleet_a}}$ | $q_{fleet_a} = q_{fleet_{a=15}}.S_a$<br>$\log\left(q_{fleet_{a=15}}\right) \sim Unif(-10,10)$ | Age-specific catchability of adult abundance indices (UKCBT, BECBT, UKBTS) |

### 3.7.4. Monte Carlo simulations to compute equilibrium curves

The population was simulated with constant $F$ in time and space during 200 years to reach an equilibrium state. Results obtained by varying $F$ in a wide range can be used to empirically construct the equilibrium curve relating $C$ (Catches) and $SSB$ at equilibrium, therefore enabling the estimation of management reference points such as $B_{MSY}$, $F_{MSY}$ and $C_{MSY}$.

Monte Carlo simulations were run to account for both process errors and parameters uncertainty. For a given value of $F$, the population dynamics was simulated over 200 years including process error. The ergodic state is considered reached after 100 years of simulation and the process error was integrated out by considering the distribution of the results between year 101 and 200. To integrate the parameter uncertainty, the procedure was repeated 1,500 times with 1,500 sets of parameters directly drawn in the joint posterior distribution of model parameters, ensuring that the statistical covariance structure between the parameters is fully accounted for.

## Conclusion du chapitre

Ce chapitre visait à intégrer le fonctionnement spatial au cours du cycle de vie d'une population exploitée d'une espèce nourricerie-dépendante, la sole de Manche Est. Nous avons comparé deux hypothèses contrastées sur la structure spatiale de la popualtion : (1) l'hypothèse standard utilisée par le groupe d'évaluation considérant une unique population adulte alimentée par l'ensemble des nourriceries côtières de la Manche Est, et (2) une hypothèse de structuration de la population en trois sous-composantes entretenant des échanges très limités, justifiée par la très faible connectivité entre ces sous-entités aux stades successifs du cycle de vie. Bien que la crédibilité relative de ces deux hypothèses ne puisse pas être testée faute de données disponibles, l'hypothèse d'une méta-population composée de trois composantes entretenant des échanges très limités semble la plus cohérente avec l'ensemble des connaissances disponibles.

Les résultats montrent que considérer trois sous-populations quasiment isolées conduit à une réévaluation des indicateurs de productivité des nourriceries. Par ailleurs, en terme de gestion, cela rend pertinent la réalisation d'un diagnostic d'évaluation des niveaux d'exploitation à l'échelle de chaque sous-composante, et renforce l'intérêt de mesures de gestion spatialisées. Cette structure de modèle ouvre la voie à la simulation de scenarios intégrant une gestion spatialisée des pressions anthropiques (e.g. pêche locale, restauration des nourriceries) qui fera l'objet du chapitre suivant.

# 4. Quantifier l'impact des pressions agissant au cours du cycle de vie de la sole en Manche Est

## Introduction du chapitre

Les populations d'espèces nourriceries-dépendantes sont soumises à différentes pressions au cours de leur cycle de vie. Celles-ci peuvent être d'origine environnementale (variation des conditions climatiques) ou anthropique (qualité des habitats de nourriceries, pêche). Chacune de ces pressions s'exerce plus particulièrement à un stade spécifique du cycle de vie : les conditions climatiques déterminent la survie des œufs et larves, la qualité et la disponibilité des habitats impactent le recrutement des juvéniles et la pêche cible principalement les (sub)adultes.

Le modèle développé au chapitre précédent a permis d'intégrer l'ensemble des données disponibles dans une approche couplant modélisation statistique et modèle de cycle de vie spatialisé. Dans ce chapitre, nous proposons de nous appuyer sur le modèle spatialisé développé et paramétré au chapitre précédent pour développer une approche de simulation visant à quantifier les impacts respectifs ou combinés de ces différentes pressions. Cette quantification de l'impact des pressions et le cadre de simulation de scénarios proposés doivent également permettre de poser les fondements d'une gestion spatialisée de la population de sole en Manche Est.

# Combining a life cycle approach with scenarios to assess the relative influence of multiple stressors on a flatfish population

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## Abstract

Exploited nursery-dependent species are subject to multiple stressors occurring (mainly) at specific stages of the life cycle: hydroclimatics determine the success of the first eggs/larvae stages, habitat characteristics condition nursery grounds productivity and fishing target mostly adults. We combine here a life cycle approach with scenarios to quantify the relative influence of multiple stressors on a coastal and estuarine nursery dependent flatfish population. The approach is applied to the Eastern channel common sole population, an abundant species sustaining important fisheries (>4,000 tons per year) in this area. The common sole has a complex life cycle: after the eggs have hatched, the larvae spend several weeks drifting in open water. Survivors go on to metamorphosis over nursery grounds into benthic fish. Juveniles spend their first two years of life in separate coastal and estuarine nurseries. At or close to maturation, they migrate to deeper areas, where different subpopulations supplied by different pools of nurseries reproduce and are exploited by fisheries. A spatialized age and stage-based hierarchical Bayesian life cycle model was built to integrate various pieces of ecological knowledge, data sources and expertize. The model represents the influence of multiple stressors, i.e.: hydroclimate, habitat quality and fishing on the life cycle, while accounting for the low connectivity between subpopulations. The model was used to develop scenarios, to assess and disentangle the effects of interacting stress factors on population renewal. Results emphasize the importance of nursery habitat availability and quality for these species, especially at the local scale. Realistic restoration scenarios of the Seine estuary lead up to a two-third increase in catch potential for the adjacent subpopulation, relative to the current *status quo* scenario. Fishing however remains the main source of population depletion when considering the whole Eastern Channel system. Indeed, adapting fishing mortality to local MSY levels leads to substantial increases in biomass (+100%) and catches (+33%) at the Eastern channel scale. We also show how hydroclimatic conditions are susceptible to interact with these two “manageable” pressures, e.g. overfishing increases the sensitivity to unfavorable hydroclimatic conditions. While our results are highly dependent to hypotheses on the spatial functioning of the (sub)population(s), they bring advances to the understanding of the dynamics of exploited nursery-dependent species while paving the way toward the assessment of spatial management schemes, in the context of marine spatial planning for sustainable management of fish resources.

*Keuwords*: life cycle model, nursery habitat degradation, fishing, Solea, multiple stressors, scenarios

## 4.1. Introduction

Fish populations are under the influence of a variety of environmental and anthropogenic pressures (Halpern *et al.*, 2007). Fisheries (Christensen *et al.*, 2003; Myers and Worm, 2003; Pauly, 2005) affect populations through their direct impact (i.e. fishing mortality) as well as indirect consequences, such as the reduction of genetic variability linked to selection pressure and the related demographic changes (Olsen *et al.*, 2004; Conover, 2007), the alteration of trophic networks (Pauly *et al.*, 1998) and the perturbations of habitat structure (Thrush *et al.*, 1998; Auster and Langton, 1999; Turner *et al.*, 1999; Kaiser *et al.*, 2006). In addition to fishing, other anthropogenic pressures affect fish populations. The increasing concentration of human activities along coastal waters has negative consequences on ecosystems and particularly affects the quality of coastal and estuarine ecosystems (Halpern *et al.*, 2008), subject to physical destruction and pollution impacting essential fish habitats (Beck *et al.*, 2001a; Peterson *et al.*, 2003). Hydroclimate impacts fish populations, which are exposed to climatic variability (Planque and Fredou, 1999; O'Brien *et al.*, 2000; Lehodey *et al.*, 2006), to climatic cycles (Francis *et al.*, 1998; Brander, 2007) but also to long term climate change (Perry *et al.*, 2005; Harley *et al.*, 2006; Petitgas *et al.*, 2013).

These different stressors (fishing, habitat degradation, hydroclimate) have their respective highest impact at different stages of the life cycle. At the time scale of the decade, long term process such as genetic adaptation or changes in geographical distribution can often be neglected and climate has most of its impact at the early stages (i.e. eggs/larvae). Indeed, hydroclimate controls the success of eggs/larval development (Pepin, 1991) and their chance of reaching favorable habitats (Bakun, 1996), both affecting recruitment success (May, 1974) and population connectivity (Cowen *et al.*, 2006; Gerber *et al.*, 2014). Habitat availability and quality mostly impacts the sensitive growth and development phase of juveniles, especially for nursery dependent species (Gibson, 1994; Beck *et al.*, 2001a). Fishing targets mostly (sub)adults (Hilborn, 2011).

Quantifying the respective impact of each of these stressors on population dynamics and renewal shall bring insights to the ecological understanding of population functioning and provide support to management schemes. There has been a considerable amount of studies addressing the impact of each of these stressors individually. A large panel of work has focused on climatic variability consequences on fish first stages (review in Houde, 2008). The impact of habitat suitability on juveniles was also well studied (Brown et al., 2000; Lindholm et al., 2001) especially at individual and local scales (Beck et al., 2001b; Stoner et al., 2001; Vasconcelos et al., 2014) for nursery dependent species. The assessment of direct fishing impact on populations has driven the development of fisheries models in the last century (Beverton and Holt, 1957; Hilborn and Walters, 1992) and their wide use for stock assessment (Hilborn, 2011). However, life cycle approaches integrating the successive impacts of these stressors along the life cycle and estimating their consequences on population dynamics are scarce despite being required to fully disentangle and quantify their respective effects. Also, less attention has been paid to the quantitative assessment of how the spatial structure of populations and patterns of connectivity interact with spatially structured stressors (Cianelli et al., 2013) such as non-homogenous fishing effort or local habitat degradation.

In this paper, we use the common sole population in the Eastern channel (EC, ICES area VIId) as an ideal case study to quantitatively assess the relative influence of various stressors on the population dynamics through a spatialized life cycle modelling approach. *Solea solea* is a nursery-dependent species (Gibson, 2004). In the EC, after pelagic larval stages (Rochette et al., 2010), juvenile sole settles on coastal and estuarine nursery grounds (Rochette *et al.*, 2012) before moving to deeper areas at (sub)adult stages and contributing to the reproduction (Horwood, 1993). During this life cycle, the common sole is facing several successive pressures such as: hydroclimate variability on first stages (Rochette et al., 2012), huge habitat loss and degradation of the quality of residual surfaces in coastal and estuarine nursery grounds, especially in the Seine estuary (Rochette et al., 2010), and high fishing mortality at (sub)adult stages (ICES, 2013). Rochette *et al.* (2013) then Archambault *et al.* (Submitted) have built an integrated spatialized life cycle model for the EC sole population in the Bayesian hierarchical modelling framework that proved successful in integrating ecological knowledge, heterogeneous sources of data and expert information (Rivot *et al.*, 2004; Parent and Rivot, 2012; Massiot-Granier *et al.*, 2014). Archambault *et al.* (Submitted) suggest a metapopulation structure due to the segregation of three regional subpopulations (Figure 4.1). This metapopulation structure results from the persistence of very low connectivity along the successive stages of the life cycle: (i) eggs/larval retention within regions (Rochette *et al.*, 2012) (ii) spatial segregation of juvenile inside separated coastal and estuarine nurseries (Coggan and Dando, 1988; Anon., 1989; Riou et al., 2001) and (iii) limited individual movement at the (sub)adult stages (Kotthaus, 1963; Anon., 1965).

Here, we rely on the model structure and parameterization proposed by Archambault *et al.* (Submitted) to run simulations based on scenarios designed to assess the relative influence of different stressors along the life cycle : (i) hydroclimatic variability affecting the success (i.e. chance of settlement on nursery grounds) of eggs and larvae (ii) quantity/quality of coastal and estuarine nursery grounds (iii) exploitation of (sub)adults by fisheries. This study aims at evaluating the respective impact of each stressor on the realization of the life cycle but also explores the possible interactions between different stressors (e.g. hydroclimate and fishing). Because the magnitude of adult mediated connectivity remains uncertain, we also use the model to qualitatively assess how the patterns of connectivity between the three subpopulations may interact with the quantitative influence of the different stressors.

## 4.2. Materials and methods

### 4.2.1. Operating model for the population dynamics

Relying on previous analyses (Rochette *et al.*, 2013; Archambault *et al.*, Submitted), five nursery grounds (indices $i$ from 1 to 5 in the followings) located on French (Veys, Seine and Somme sectors) and UK (UK West and Rye sectors) are considered (Figure 4.1). Each of these five nursery sectors is associated with one of the three subpopulations (indice $r$ from 1 to 3 in the followings): the West FR region (including Veys and Seine nurseries), the UK region (West and Rye nurseries) and the East FR region (Somme nursery).

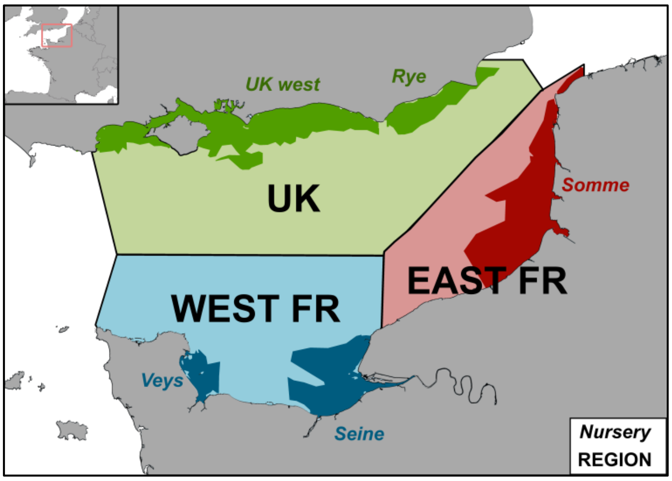

Figure 4.1 - Study area with the three components of the Eastern Channel sole population (in bold) and the five coastal and estuarine nursery sectors (in italic).

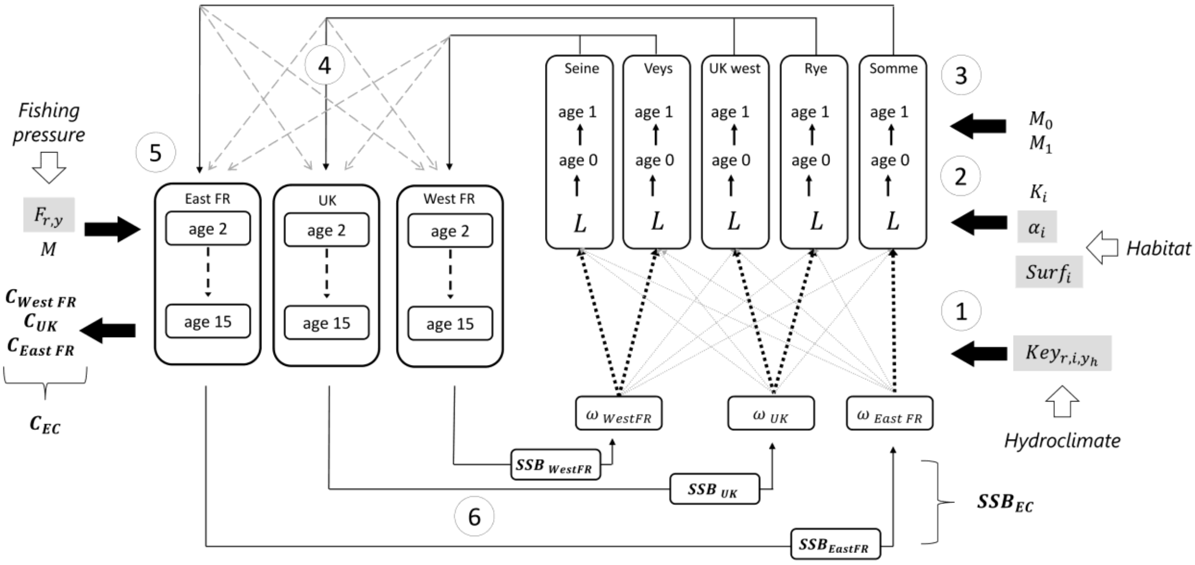

Figure 4.2 - Structure and main parameters of the simulation model. Parameters in grey squares are modified according to the simulated scenarios on stressors. Light grey arrows from eggs pools to nursery sectors (step 1) traduce very low connectivity. Step 4 is altered with additional links (dotted light grey arrows) when considering the structural hypothesis $S_1$ including adult-mediated connectivity across subpopulations (see text).

The main processes and key parameters of the life cycle are given in the followings (see model structure in Figure 4.2 with matching numbering):

(1) Eggs and larvae are transported from each of the three spawning areas and eventually die or settle in one of the 5 identified nursery sectors. The probability for an egg from an egg pool $\omega_r$ in year $y$ to reach a nursery $i$, given hydroclimatic conditions based on historical year $y_h$ (fixed within a simulation; from 1982 to 2007) is given by an allocation and survival

matrix $D_{r,i,y_h}$ (Rochette *et al.*, 2012; upgrade by Savina , pers. comm.; see Archambault *et al.*, Submitted). The number of larvae reaching a given nursery sector $i$ at year of simulation $y$ ($L_{y,n}$) is calculated from Eq. 1:

Eq. 1 $L_{y,i} = \sum_r \omega_{r,y} * D_{r,i,y_h}$

It is worth noting that given the values of the drift and survival rates $D_{r,i,y_h}$ considered here, eggs and larvae mediated connectivity between the three regions is extremely low (Rochette *et al.*, 2012; Figure 4.2).

(2) Settled larvae experience compensatory density-dependent post-settlement mortality (Archambault *et al.*, Submitted; Iles and Beverton, 2000) over nursery sectors between settlement (late spring) and the end of age 0 juveniles growth period (early September). The expected number of juveniles in nursery $i$ in September of year $y$ is modelled by a Berverton-Holt relationship (Eq. 2).

Eq. 2 $E(N_{y,\mathrm{a}=0,i}) = \frac{K_i * L_{y,i}}{K_i/\alpha_i + \frac{L_{y,i}}{Surf_i}}$

where $K_i$ and $\alpha_i$ are respectively the nursery-specific carrying capacity per surface and maximum survival rate, $Surf_i$ the nursery sector surface. Interannual variability of the survival is represented through a logNormal process error with a ${\sigma_p}^2$ process error variance.

(3) Age 0 juveniles in nursery sectors are then assumed to suffer from a fixed natural mortality $M_0$ during 4 months from September until they reach age 1 in January. Age 1 juveniles suffer from a natural mortality $M_1$ until age 2.

Age 2 (subadult) fish are assumed to leave nurseries at the beginning of year $y + 2$. Two structural model hypotheses $S_0/S_1$ were considered here: in the baseline structural hypothesis $S_0$ (Figure 4.1, Figure 4.2 step 4; Table 4.1), there is no (sub)adult mediated connectivity between the three subpopulations. As a consequence, the number of age 2 fish in the subpopulation $r$ at the beginning of year $y + 2$ only results from the age 1 fish of year $y + 1$ from the nurseries associated with subpopulation $r$ (West FR=Veys+Seine, UK=UK West+Rye, East FR= Somme).

In the alternative structural hypothesis $S_1$, a connectivity induced by the mixture of age 2 fish between the three subpopulations is introduced (Table 4.1). Age 1 fish in nursery $i$ contribute mostly (80%) to their associated subpopulations $r$, the remaining (20%) contribute equally to the two other subpopulations (10% / 10%). Those values were set arbitrarily in order to qualitatively assess the impact of considering adult-mediated migration.

In both structural hypotheses, no exchange between the three subpopulations is considered after age 2.

(4) The adult population consists of 14 age classes between age 2 and age 15, which suffer from both natural ($M$, fixed) and regional fishing mortalities $F$ (Eq. 3). All remaining fish are assumed to die at age 15.

$$\text{Eq. 3} \qquad N_{y+1,a+1,r} = N_{y,a,r} * e^{-(M_a+F_{y,a,r})}$$

(5) Mature fish in each region $r$ contribute to the local eggs pools $\omega_r$, accounting for weights-at-age, female proportion, fecundity and maturity.

Although quantitatively very limited under the structural hypothesis $S_0$ (because they only results from the low eggs and larvae drift-mediated connectivity between the three subpopulations), exchanges between the three subpopulations cannot be neglected. As a consequence, the population dynamics of each of the three subpopulations cannot be considered as independent under both structural hypotheses.

Table 4.1 - Connectivity matrix from nursery to subpopulations under the structural hypothesis $S_0$ (no subadult migration case) and under $S_1$ (including subadult mediated connectivity)

| | **$S_0$ - No subadult migration** | | | **$S_1$ - With subadult migrations** | | |
|---|---|---|---|---|---|---|
| | *West FR* | *UK* | *East FR* | *West FR* | *UK* | *East FR* |
| *Seine* | 1 | 0 | 0 | 0.8 | 0.1 | 0.1 |
| *Veys* | 1 | 0 | 0 | 0.8 | 0.1 | 0.1 |
| *UK West* | 0 | 1 | 0 | 0.1 | 0.8 | 0.1 |
| *Rye* | 0 | 1 | 0 | 0.1 | 0.8 | 0.1 |
| *Somme* | 0 | 0 | 1 | 0.1 | 0.1 | 0.8 |

### 4.2.2. Simulations and parameterization

For each scenario (described later), Monte Carlo simulations were run to account for both process errors and parameters uncertainty. For a given set of parameters, the population dynamics was simulated over 200 years including process error (larvae to age 0 survival; Eq. 2). In all scenarios, the ergodic state is considered reached after 100 years of simulation and the process error was integrated out by considering the distribution of the results between year 101 and 200. To integrate the parameter uncertainty, the procedure was repeated 1,500 times with 1,500 sets of parameters directly drawn in the joint posterior distribution of model parameters provided by Archambault *et al.* (Submitted), ensuring that the statistical covariance structure between the parameters is fully accounted for.

### 4.2.3. Scenarios on environmental and anthropogenic pressures

We explored realistic scenarios on the main stressors (Table 4.2) to analyse separate and combined effects of stressors on the population for the two structural model hypotheses concerning spatial structures of adults ($S_0$ and $S_1$; Table 4.1).

### Hydroclimatic conditions

To our best knowledge, no model exists to relate climate change scenarios to future hydroclimatic conditions in the Eastern Channel and the knowledge on future circulation in this area is presently too spurious to propose realistic scenarios. Therefore, the analysis focused on the influence of climate variability only, without any prospective trend. The influence of the between year variability of hydroclimatic conditions on eggs and larvae drift and survival was assessed through scenarios based on historical time series estimated in previous studies (Rochette *et al.*, 2012; Savina Comm. pers.). This survival and allocation matrix $D_{r,i,y_h}$ (26 years $y_h$ from 1982 to 2007) was used as a reference of possible hydroclimatic conditions for future scenarios. 26 hydroclimatic scenarios were built by running the population during 200 years with the survival and allocation matrix considered constant over the simulation time and fixed to each of the 26 possible matrices $D_{r,i,y_h}$.

### Juvenile habitat

Scenarios of juvenile habitat restoration only concern the Seine estuary. Indeed, other nursery sectors have not gone through equivalent degradation, including dramatic reduction in both surface and quality of residual areas (Le Pape *et al.*, 2007; Rochette *et al.*, 2010).

The Seine estuary has undergone notable morphological changes in the past century through channel dredging, constructions of dikes and harbours (Rochette *et al.*, 2010). This led to a strong reduction of sole essential nursery habitat, and especially shallow muddy areas (Lesueur, 1999). Rochette et al. (2010) evaluated the habitat loss (i.e. surface only) to be responsible for a 42 % decrease of nursery capacity since the early 19th century. Based on this previous work, we considered a first habitat restoration scenario where the Seine estuary is restored to its early 19th century surface, modelled by increasing $Surf_i$ for the Seine estuary (Eq. 2) by a factor of 1.724.

In addition to surface loss, the Seine estuary is subject to strong chemical contamination that further declines habitat quality (Gilliers et al., 2006; Courrat *et al.*, 2009). In accordance, results of Archambault *et al.* (Submitted) show that the density independent component of the larvae-to-age 0 survival ($\alpha$ parameter of the Beverton-Holt equation in Eq. 2) was the lowest for the Seine estuary (83% lower than the median of the four other sectors). To evaluate a potential restoration of habitat quality and its impact on the critical settlement phase, we simulated an increase of the parameter $\alpha$ for the Seine estuary by setting $\alpha$ to the median of the four other sectors (i.e. increase of density independent survival rate $\alpha$ by a factor of 5.9).

We are only interested in the state of the system after equilibrium is reached, not in the kinetics of the restoration. We therefore considered (unrealistic) immediate complete restoration of the surface and the density independent survival rate (i.e.quality).

#### Fishing pressure

The effect of fishing pressure was assessed by exploring a wide range of $F$ (Table 4.2) balanced or not between the three different subpopulations to explore alternative spatial fishing scenarios. For all configuration of $F$, the population was simulated with constant $F$ in time and space during 200 years to reach an equilibrium state. Results obtained by varying $F$ in a wide range can be used to empirically construct the equilibrium curve relating $C$ (Catches) and $SSB$ at equilibrium, therefore enabling the estimation of management reference points such as $B_{MSY}$, $F_{MSY}$ and $C_{MSY}$ (Hilborn and Walters, 1992).

Because the population dynamics of each of the three subpopulations are interconnected for both model configurations, reference equilibrium points for each subpopulation $r$, denoted $B_{MSY,r}$, $F_{MSY,r}$ and $C_{MSY,r}$ , were conditional and estimated by fixing the fishing pressure for the two others subpopulations at their reference value (Archambault et al., Submitted; Table 4.2). Equilibrium point at the scale of the whole Eastern Channel (i.e. global $MSY$) was estimated by exploring all possible combinations of $F_{WestFR}$,$F_{UK}$, $F_{EastFR}$ within the explored range.

### 4.2.4. Simulation plan and indicators

To isolate the intrinsic impact of each stressor (hydroclimate, habitat, fishing), we successively modified the modality of one stressor (Table 4.2) while the two remaining stressors were set at a reference value. Reference values are defined from the "*status quo*" scenario $Sce_{ref}$, which considers average hydroclimatic conditions (i.e. average survival and allocation matrix of eggs/larvae), no modification of nursery habitat (i.e. constant Seine $Surf$ and $\alpha$) and local fishing pressure $F_r$ set at their average estimated values in the last 4 years (2007-2011; $F_{WestFR}=0.16$, $F_{UK}=0.44$, $F_{EastFR}=0.8$; Archambault *et al.* (Submitted)).

The simulation plan consists in 794 scenarios combining different modalities for each stressor (Table 4.2).

For each simulation we monitored the stock spawning biomass ($SSB$) and catches ($C$) at equilibrium (100 last years of simulation) to establish equilibrium curves ($C_{eq}$ versus $SSB_{eq}$), from which estimates of $C_{MSY}$ and $B_{MSY}$ can be derived.

For each indicator, we calculated the relative percentage of gain/loss between the explored scenario $Sce$ and $Sce_{ref}$ (Eq. 4)

Eq. 4
$$\%_{gain/loss_{Sce}} = 100 * \left(1 - \frac{indicator_{Sce}}{indicator_{Sce_{ref}}}\right)$$

Last we identified the scenario maximizing $C_{MSY}$ within all simulated scenarios (i.e. the "best" scenario $Sce_{best}$, Table 4.2) and compared it to $Sce_{ref}$ following a similar procedure.

Table 4.2 - Scenarios and associated modalities of stressors.

| **Investigated Effects** | **Stressors** | | |
|---|---|---|---|
| | Hydroclimatic $Key$ | Habitat | Fishing |
| Reference scenario $\boldsymbol{Sce_{ref}}$ | Average | Unrestored Seine sector | $F_{WestFR} = 0.16$<br>$F_{UK} = 0.44$<br>$F_{EastFR} = 0.8$ |
| Climate x fishing | Historical series $y_h$ from 1982 to 2007 | Reference | $F_r's$: 0 to 1.5 (step of 0.01) |
| Climate x habitat | Historical series $y_h$ from 1982 to 2007 | Unrestored Seine sector<br>Restored surface<br>Restored quality<br>Combined restoration | Reference |
| Habitat x fishing | Reference | Unrestored Seine sector<br>Restored surface<br>Restored quality<br>Combined restoration | $F_r's$: 0; from 0.15 to 0.30 (step of 0.01); 0.5; 0.8; 2 |
| "Best" scenario $\boldsymbol{Sce_{best}}$ | Hydroclimatic conditions year $y_h$ = 1993 | Combined restoration | $F_r's$ at $F_{MSY}$(0.2 for all subpopulations) |

## 4.3. Results

For clarity purposes, all results are firstly provided through mean estimates on indicators obtained under the baseline structural hypothesis $S_0$ (i.e. no subadult exchanges between subpopulations; Table 4.1). We then explore the impact of considering the alternative structural hypothesis $S_1$ (i.e. with subadults-mediated connectivity between subpopulations; Table 4.1).

### 4.3.1. Baseline model configuration $S_0$

#### Reference scenario

The reference scenario $Sce_{ref}$ leads to mean local $SSB$ at equilibrium (denoted $SSB_{eq}$) of 7,565, 4,060 and 2,305 t for respectively the West FR, UK and the East FR subpopulations (Figure 4.3), and of 13,930 t at the Eastern Channel scale. Catches at equilibrium for each subpopulation ($C_{eq,r}$) are respectively at 1,065, 1,330 and 1,140 t (West FR, UK, and East FR, respectively), and 3,535 t at the EC scale. If not mentioned otherwise, all indicators in the present section are compared to this reference "status-quo" scenario.

Uncertainty in indicators, estimated from the combination of both process error and parameters uncertainty, is quite high (Figure 4.3). Because process errors and parameters uncertainty is the same for all scenarios, uncertainty remains identical and does not affect ranking of scenarios. Thus, for clarity purposes, scenarios were further compared using only the expected mean of all indicators.

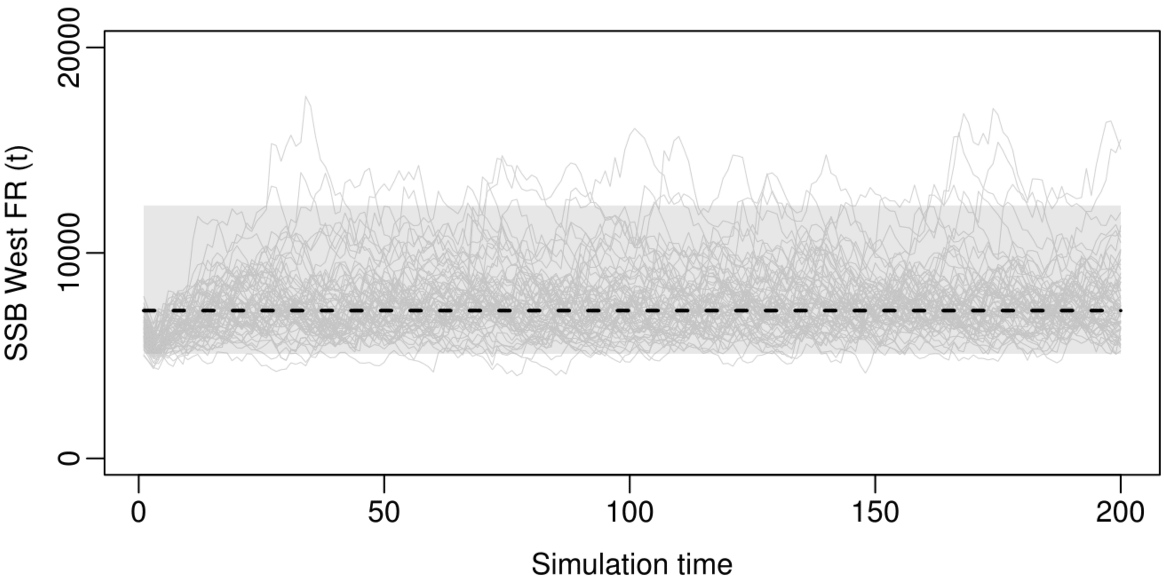

Figure 4.3 - Evolution of $SSB$ in the West FR subpopulations under the reference scenario. Uncertainty results from both process error (within chain) and parameters (between chains). Only 60 chains out of the 1,500 are displayed here for clarity purposes. Grey area indicates 95% confidence interval, dashed line the median.

### Marginal impacts of stressors

#### *Hydroclimate*

Within this 26 years' time series, a range of high/low survival and allocation patterns for the five nurseries are represented, but inter-regional exchanges always remain very low, as discrepancies among interannual regional variations. Years with low survival of eggs and larvae at the scale of the Eastern Channel are also years of low survival for each particular subpopulation.

The variability of the hydroclimatic conditions during the 26 years between 1982 and 2007 and the related fluctuations in larval settlement success on nursery grounds, ($Key_{r,i,y_h}$), induced a maximum variation of 42% of the productivity (max. loss = 34%; max. gain = 8%).

Conditions encountered for some years in the 1982-2007 period led to substantially reduced production at the scale of the Eastern Channel, as illustrated by year 1991 (Table 4.3) when the worst conditions of larval survival were observed for the EC but also for both UK and East FR (Table 4.3) subpopulations and the second worst for the West FR subpopulation.

Table 4.3 - Intrinsic and cumulative impacts of stressors on selected indicators, expressed as %loss / gain with regard to the reference scenario

| **Details** | **Indicators** | **EC** | **West FR** | **UK** | **East FR** |
|---|---|---|---|---|---|
| *Hydroclimate* | | | | | |
| Worst/best hydroclimatic conditions versus $Sce_{ref}$ | $SSB_{eq}$ | -34 / +8 | -12 / +7 | -60 / +11 | -31 / +7 |
| | $C_{eq}$ | -26 / +6.5 | -12 / +7 | -60 / +11 | -31 / +7 |
| | Worst/best years | 1991 / 1993 | 2001 / 1982 | 1991 / 1993 | 1991 /1992 |
| *Habitat* | | | | | |
| Carrying capacity restoration scenario of Seine estuary versus $Sce_{ref}$ | $SSB_{eq}$ | +22 | +42 | _ | _ |
| | $C_{eq}$ | +12 | +42 | _ | _ |
| Quality restoration scenario of Seine estuary versus $Sce_{ref}$ | $SSB_{eq}$ | +7 | +13 | _ | _ |
| | $C_{eq}$ | +4 | +13 | _ | _ |
| Surface and quality restoration scenario of Seine estuary versus $Sce_{ref}$ | $SSB_{eq}$ | +36 | +66 | _ | _ |
| | $C_{eq}$ | +20 | +66 | _ | _ |
| *Fishing* | | | | | |
| Exploitation at MSY versus $Sce_{ref}$ | $SSB_{MSY}$ | +96 | 0 | +146 | +362 |
| | $C_{MSY}$ | +32 | 0 | +29 | +68 |
| Absence of exploitation versus $Sce_{ref}$ | $SSB_{pristine}$ | +470 | +158 | +616 | +1235 |
| Absence of exploitation versus at MSY | $SSB_{pristine}$ | +191 | +157 | +190 | +188 |
| *Cumulative* | | | | | |
| Best hydroclimatic conditions + Surface and quality restoration + $F_{MSY}$versus $Sce_{ref}$ | $SSB_{MSY}$ | +131 | +42 | +155 | +384 |
| | $C_{MSY}$ | +59 | +73 | +34 | +68 |

### *Habitat restoration*

Restoration of nursery habitat on the Seine estuary has a substantial impact on the productivity on the West FR subpopulation (Figure 4.4). On the contrary, under the baseline structural hypothesis $S_0$, the impact is only local without exchanges between the subpopulations and SSB and C in the East FR and UK subpopulations are not affected by habitat restoration in the Seine estuary (Table 4.3).

Restoring the surface (capacity) and the quality of nursery habitat has a scale effect on the population abundance at equilibrium in the West FR subpopulation, with identic variations of $SSB_{eq}$ and $C_{eq}$ (42% increase in the scenario of capacity restoration, 13% increase in the quality restoration scenario and 66% increase with combined restoration; (Table 4.3 and Figure 4.4).

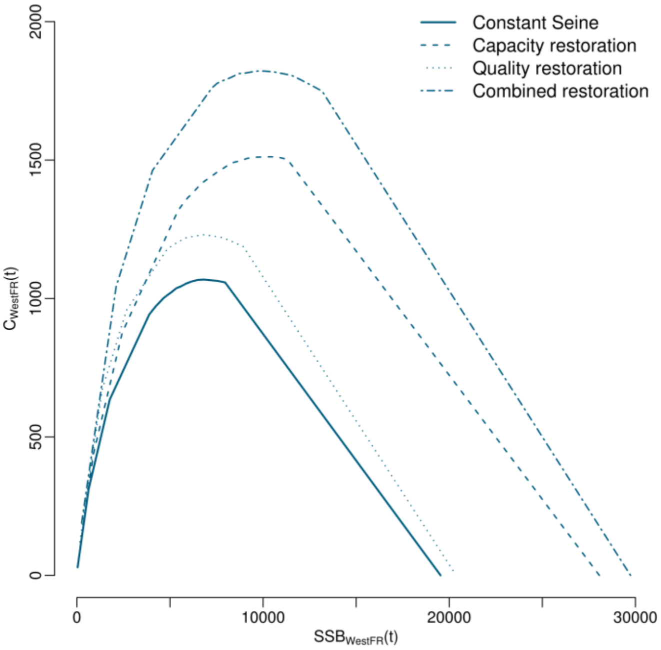

Figure 4.4 - Regional Catch/SSB at equilibrium curves with relation to habitat scenarios on Seine estuary on West FR subpopulation production in the baseline structural hypothesis $S_0$.

At the scale of the whole EC population, these scenarios translate into smaller increases as the two remaining subpopulations do not benefit from habitat restoration (Table 4.3).

### *Fishing pressure*

For each subpopulation $r$, when considering the fishing pressure of other subpopulations fixed at their reference values, the conditional $MSY$ is estimated at $\mathrm{F_r} = 0.2$. Because the exchanges between the different subpopulations are very low, the global $MSY$ (obtained by testing all possible combination of $F_r$) is also found at $F_r = 0.2$ . Adjusting regional fishing mortalities to 0.2 for all subpopulations leads to $C_{MSY}$ of 4,700 t and $SSB_{MSY}$ of 24,300 t at the scale of the whole EC, corresponding respectively to increases of 33% in catches (Table 4.2) and 100% in SSB with regards to the reference situations (i.e. estimated $F$ over the past 4 years). Additionally, $SSB_{MSY}$ is estimated at about a third of $SSB_{pristine}$ (SSB with no fishing), while $SSB_{eq}$ at current levels of fishing (i.e. reference) is at about a sixth (Table 4.2).

Results at the scale of the EC mask strong differences between the subpopulations (Table 4.3). The West FR indicators are not affected because the fishing pressure at $MSY$ is close to the reference level for this region. By contrast, the gain of biomass and catches at equilibrium would be high for the UK (+146%) and the East FR (+362%) subpopulations if exploited at local $F_{MSY}$, as those two subpopulations are already overexploited in the reference scenario.

### Combined impacts

The "best" scenario with optimum hydroclimatics (i.e. repetition of 1997 conditions), habitat (i.e. restored carrying capacity and habitat quality in Seine estuary) and fishing levels (i.e. regional $F$'s set at local $F_{MSY}$'s) leads to a 63% increase in catches at equilibrium ($C_{MSY}$) and a 140% increase in SSB et equilibrium ($SSB_{MSY}$) compared to $Sce_{ref}$. But evidence exists for interactions between stressors effects.

#### *Hydroclimate X Fishing*

Increasing the fishing pressure simultaneously on all subpopulations drastically increases influence of the between year variability of the hydroclimatic conditions (Figure 4.5). Indeed, at sustainable levels of fishing, the impact of hydroclimate variability on $SSB_{eq}$ (and catches) at equilibrium is limited, but the impact (mostly negative as the reference scenario (average hydroclimatics) is close to the optimum) of hydroclimate dramatically increases with increasing levels of $F$ (Figure 4.5). In other words, the unfavourable hydroclimatic conditions have a wider negative effect under overfishing conditions.

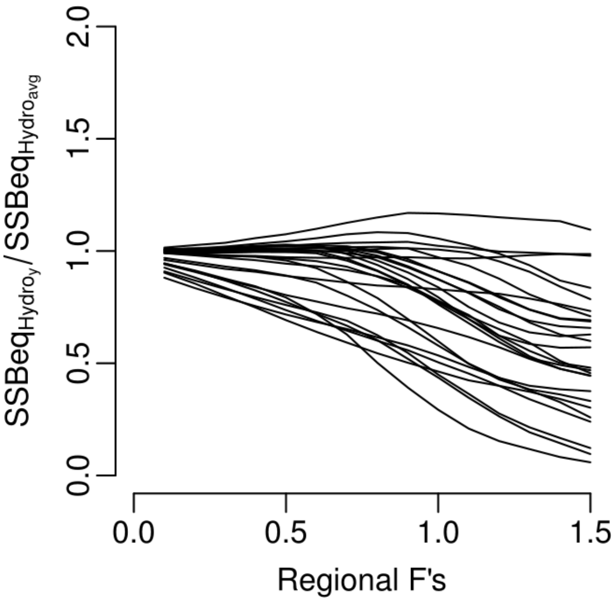

Figure 4.5 - Combined effect of hydroclimate and different exploitation levels on the ratio between the $SSB_{eq}$ obtained under each of the different hydroclimate scenarios (26 years; 1982-2007) and the $SSB_{eq}$ obtained under the average hydroclimate scenario. Model configuration $S_0$.

*Habitat X Hydroclimate*

No combined effect of habitat and climate was identified as the relative range of annual hydroclimatic conditions impact on SSB and C was not affected by the different habitat scenarios (Table 4.3). Hydroclimate and habitat capacity appear as independent factors of pressure.

*Fishing X Habitat (i.e. manageable anthropogenic pressures)*

When the habitat restoration only concerns the carrying capacity (surface) of the nursery habitat, increasing the fishing pressure has roughly no impact on the gain in the catches at equilibrium with regards to the habitat reference scenario. The absolute gain in SSB depends on SSB/F but the relative gain of larger nursery grounds remains stable at about 42% (Table 4.3 ; Figure 4.6).

By contrast, when the maximum survival rate of early juveniles is enhanced, the resilience of the nursery to fishing pressure (i.e. decreased larval inputs) is increased and the relative gain in the catches at equilibrium with regards to the habitat reference scenario increases when the fishing pressure increases (Figure 4.6).

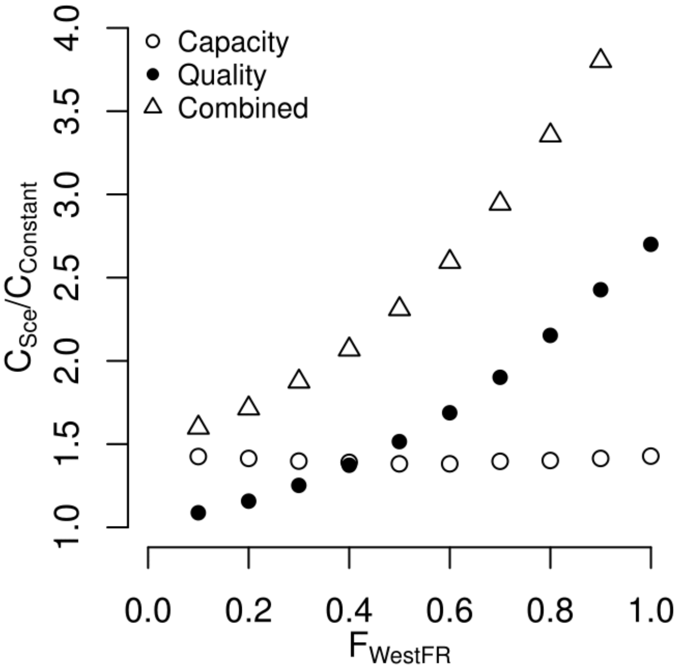

Figure 4.6 - Combined effect of habitat restoration scenarios and different exploitation levels in the West FR region on the gain in catches relative to the reference scenario, under structural hypothesis $S_0$.

### 4.3.2. Impact of considering subadults mediated connectivity between the three subpopulations (structural hypothesis $S_1$)

Introducing exchanges between subpopulations logically affects the dynamics of the whole EC system. It results in a more complex meta-population system characterized by multiple spatial interactions. Overall, the effects of stressors with a direct local impact (habitat restoration, fishing pressure) are locally dampened and spread to the whole Eastern Channel. We present the results obtained with the reference scenario and highlight some striking results on the effects of stressors.

When considering all stressors set at their baseline reference levels, because of the difference in the population size at equilibrium between the different subpopulations, introducing homogeneous emigration/immigration rates between the subpopulations does not lead to homogeneous emigration/immigration rates in terms of fish numbers.

The subpopulation with the lowest $SSB_{eq}$ in the baseline model configuration ($S_0$) benefits from the immigration of fish from the other subpopulations, while subpopulations with higher equilibrium population size loose individuals. Introducing exchanges leads to a + 9% variation of $SSB_{eq}$ in the West FR, -1.5% in the UK and -4.5% in the East FR. Overall, this results into a +3.5% variation at the EC scale, linked to the supply of adult fish toward the less fished area, with a better survival at adult stage.

Restoring the habitat in Seine estuary (combined effects of increasing the carrying capacity and the maximum survival rates of juveniles) under hypothesis $S_0$ increases local $C_{MSY,West\ FR}$ by 66%, without impact on other subpopulations (Figure 4.7a). In the model with migrations of sub-adults ($S_1$), the gain of restoring habitat in the Seine estuary is slightly lower for the West FR (+50), but is shared with all other subpopulations (+13% for UK and +5% for East FR; Figure 4.7b).

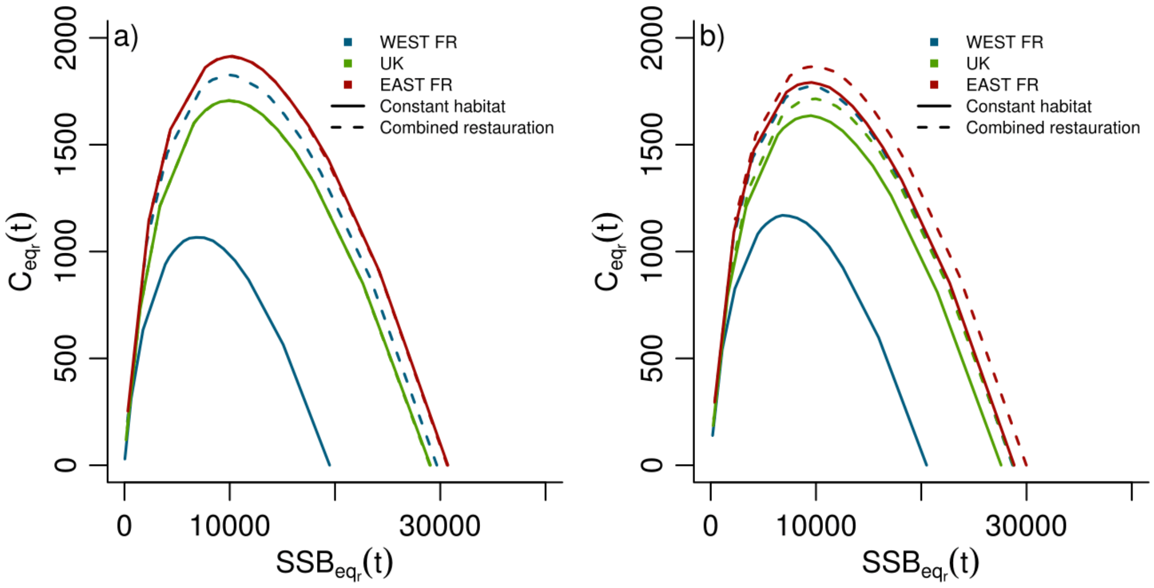

Figure 4.7 - Impact of habitat restoration on $C$ versus $SSB$ at equilibrium for the three subpopulations, under the $S_0$ structural hypothesis (a; no subadult migration) and the $S_1$ structural hypothesis (b; subadult migration). The equilibrium curves for each subpopulation are established by varying $F$ and considering the $F$ values for the other subpopulations fixed at the reference levels.

In the model configuration with subadult migrations ($S_1$), the local fishing pressure on one particular subpopulation also impacts the other subpopulations. As illustrated on Figure 4.8, when considering the fishing pressure $F_{West\ FR}$ and $F_{UK}$ fixed to their reference level, increasing $F$ in the East FR decreases the abundance and the level of catches in UK and East FR.

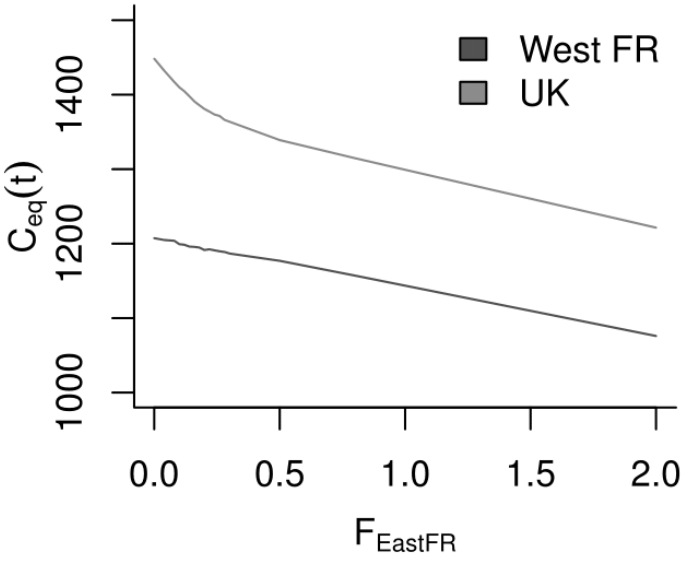

Figure 4.8 - Impact of increasing the fishing pressure on the East FR subpopulations ($F_{East\ FR}$) on the catches in the two other subpopulations (considering $F_{West\ FR}$ and $F_{UK}$ fixed to their reference values).

The global $MSY$ under $S_1$, estimated by simulating all combinations of $F_{WestFR}$, $F_{UK}$, $F_{EastFR}$, is estimated at the same level than $MSY$ under $S_0$ (4,700t, all $F_r$ at 0.2), although subpopulations contribute differently to this total under each hypothesis ($S_0$: 22.5%, 36.5%, 41% for West FR, UK and East FR; $S_1$ respectively 26%, 35.5% and 38.5% )

The lack of regional contrast between hydroclimatic years (i.e. similar patterns of larval survival and absence of consequences on local population dynamics among subpopulations, see 4.3.1) prevents differences in outputs of scenarios $S_0$ and $S_1$ due to varying hydroclimatics.

## 4.4. Discussion

Our approach combined ecological knowledge and parameterization derived from a Bayesian inference procedure (through the use of Bayesian posteriors as input parameters) and simulation procedures based on realistic scenarios. Uncertainty was integrated in coherence with the estimation approach, including process error on recruitment and parameters uncertainty. This simulation approach enables the assessment of the impacts of the main stressors affecting the different life stages of an exploited flatfish population, while providing more general insights on spatial management considerations for exploited nursery dependent species.

### 4.4.1. Caveats of the simulation approach and challenge of building realistic scenarios

The model parameters were previously estimated through a Hierarchical Bayesian life-cycle modelling approach (Archambault *et al.*, Submitted) with a similar structure. The scope of modelled stressors and scenarios is limited by this structure, but the integration of their effects and the simulations are based on a coherent framework integrating credible ecological processes and available data. As with any simulation approach, a body of assumptions had to be formulated. Many parameters were considered constant, namely biological parameters (e.g. juvenile to adult natural mortality, fecundity, weight at ages) and exploitation parameters (e.g. fisheries selectivity). The consequences of these preliminary choices were analysed during the development of the model and are discussed in Rochette *et al.* (2013) and Archambault *et al.* (Submitted).

The challenge for using this model in a simulation-scenario approach was the formulation of a reference scenario and realistic future ones. Strong hypotheses were made to define these scenarios (e.g. hydroclimatics conditions or regional exploitation levels considered constant within one simulation). Also, we did not pay much interest to the transient dynamics during the first 100 years of each simulation, but rather focused on the equilibrium state.

In the present study, a wide range of fishing mortalities was simulated to build equilibrium curves. Of course, the assessment of pristine states (no fishing) and the explored extreme levels of fishing (very low or very high) do not constitute credible near-future scenarios. However, simulating a large range of hypothetical fishing pressures enabled the investigation of various states of the system, including the present situation, and the estimation of sustainable target reference points (e.g. $MSY$ and the related biomasses and fishing mortality; Hilborn, 2011).

On the contrary, habitat restoration scenarios were less hypothetical. They were based on the reversion of known historical degradation of the Seine estuary, which allowed for estimating the consequences of both historical successive losses of estuarine habitats and low quality of remaining nursery grounds (Le Pape *et al.*, 2007; Rochette *et al.*, 2010).

Finally, future hydroclimatic scenarios were not available and the 27-years time series of hydroclimatic conditions derived from Rochette *et al.* (2012) and Savina-Rolland (pers.comm.) was used as a credible range of future variability. It would however be of great interest to investigate the link between hydroclimatic indicators, for which expected trends will be available in the future, and observed patterns in larval settlement success variability. This would pave the way toward the simulation of realistic hydroclimatic scenarios in accordance for example with Intergovernmental Panel on Climate Change (IPCC) projections.

In addition to the marginal impact of each of these three stressors, the life cycle approach offers the possibility to assess the influence of their interactions and their consequences along the life cycle. To our knowledge, the present approach is the very first assessing together the consequences of hydroclimate variability, nursery habitat degradation and fishing pressure on an exploited marine fish population.

Another challenge consisted in building structural hypotheses to approach the uncertainty in the spatial structure of the (sub)adult fraction of the population. Indeed, while the no-migration scenario is based on ecological clues (Archambault *et al.*, Submitted), it is unlikely that zero migration truly occurs. The introduction of migrations results in a complex meta-population system characterized by multiple spatial interactions. Migrations dramatically increase the complexity of the system, the associated uncertainty and data requirements. While not investigated here, the dynamics of this system are obviously highly sensitive to the magnitude and the directions of these migrations. Moreover, these migrations could also happen at any time of the adult stage and not necessary only at the sub-adult stage as introduced here. In order to fully assess the spatial impact of management measures, the estimation of realistic migrations coefficients appears mandatory. Two types of approaches could be used in this purpose: (i) mark-recapture experiments, (ii) information from natural markers. Mark-recapture techniques, despite being costly (Smedbol *et al.*, 2002), and potentially subject to sampling biases (Bolle *et al.*, 2005), may be useful to estimate migrations coefficients (Hilborn, 1990; Rijnsdorp and Pastoors, 1995; Darnaude and Hunter, 2008). In the present case, with a focus on estimating average nursery to region migration matrixes, natural markers such as otoliths elemental compositions could also be used to identify nursery provenance (Cuveliers *et al.*, 2010). Ideally, such data or knowledge should be directly integrated at the estimation stage of the process (Goethel *et al.*, 2014).

### 4.4.2. Assessing the relative impact of different stressors along the life cycle

As for most exploited marine fish populations, fishing is identified as the main source of depletion (Jackson *et al.*, 2001; Myers and Worm, 2003). The current levels of fishing mortality for two subpopulations (i.e. the reference scenario) are higher than $F_{MSY}$, and the population's level at $MSY$ would still be highly depleted (by a factor of 3) compared to the pristine population. This is common in most marine fish populations which can sustain relatively high level of exploitation due to the nature of marine fish reproductive strategies (Adams, 1980).

In addition to fishing pressure, juvenile habitat quantity and quality were identified as being of major importance. The common sole is a nursery-dependent species (Gibson, 2004) and the success of the life cycle realization is highly dependent to restricted coastal and estuarine nurseries. The restoration of the Seine sector results in a production increase (+22%) at the scale of the whole EC population with a large gain at the local scale (Western French coasts), especially at higher fishing levels. This echoes the idea that, for some populations (or subpopulations if connectivity is low), measures aiming at improving or preserving the capacity of juvenile habitat could be especially effective to improve adults' biomass, and even more effective than regulating fishing effort on the adults (Levin and Stunz, 2005; van de Wolfshaar *et al.*, 2011).

Considering the current level of exploitation, the variability of hydroclimatic conditions, as estimated in the historical time series 1982-2007, results in a moderate variability of the biological production. This is a consequence of density-dependence due to the concentration of juveniles within nurseries with limited carrying capacities, that dampens larval input variability (Iles and Beverton, 2000; Archambault *et al.*, 2014; Le Pape and Bonhommeau, in press) and reduces the effect of the between years variability in larval inputs. However, our results show that when the population size is heavily depleted under high fishing pressure, arrivals of larvae become limitant (Perry *et al.*, 2010; Planque et al, 2010), increasing the influence of the variability in the hydroclimatic conditions.

In the present approach, we associated each life stage with a particular pressure considered as the most important. This is obviously a strong simplification, as some of the stressors may impact more than one stage. For instance, hydroclimatic conditions may affect juveniles and adults survival, fecundity and spawning success (Portner, 2012). Habitat quality may influence the survival or the fitness of adult in their deeper living grounds; either from direct perturbation of habitat structure (e.g. impact of aggregates extraction; Marchal *et al.*, Accepted), or through delayed effects of the exposition to xenobiotics during growth and development stages in nursery grounds, which can decrease fish condition and reproduction potential (Adams *et al.*, 1992; Johnson *et al.*, 1998).

### 4.4.3. Towards integrated spatial management of nursery dependent exploited species

This approach provides useful insights on spatial management measures. We showed how the interaction of adjusted fishing levels and habitat restoration measures could synergize to improve local population production. The different scenarios on habitat are limited in the present case study but such approach could support decision making in the context of multiple spatial management options (e.g. restoration of different nursery areas combined to fishing management measures). Such tool shall help decision making in spatial management and conservation schemes, to prioritize protections of essential fish habitats (Le Pape *et al.*, 2014) and design coherent marine protected areas (Lockwood *et al.*, 2002; Hilborn *et al.*, 2004; Botsford *et al.*, 2009; Gaines *et al.*, 2010).

Our study also highlights how accounting for the spatial functioning of the population may influence management of fishing pressure with a spatial perspective. For instance, migrations could increase the resilience of the whole population as they induce a dampening of local effects which spread to other components of the metapopulation. Especially, according to our results, the target $MSY$ should account for the spatial functioning of the population. Our analyses show that the current levels of $F$ for each subpopulation do not fit to the local $F_{MSY}$ that must be set.

While being based on a specific case study, our qualitative conclusions are most likely extendable to other exploited flatfish populations, and more generally to exploited species that concentrate in limited habitats during the juveniles stages: the “nursery-dependent” species. Nursery dependence concerns not only flatfish (Archambault *et al.*, 2014) but a large amount of fish and other marine species (Vasconcelos *et al.*, 2014). For instance, 44% of all ICES advice species rely on coastal habitats, and these stocks contributed 77% of the commercial landings of these species (Seitz *et al.*, 2014). Coastal waters are subject to a large amount of anthropogenic pressures (Halpern *et al.*, 2008; Barbier *et al.*, 2011); and these pressures are expected to grow as world population increases (Brown, 2006). This global decrease in estuarine and coastal ecosystems affect critical ecosystem services (Worm *et al.*, 2006) among which the provision of nursery habitats, facing a 69% decline worldwide (Barbier *et al.*, 2011). As fishing pressure is high on exploited flatfish (Archambault *et al.*, 2014) and other nursery dependent species (Seitz *et al.*, 2014), the challenge faced by the present case study can be widely generalized and the same approach provide a useful tool to be applied to a large extent of fishing resources.

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## Conclusion du chapitre

Ce chapitre a permis, via une approche de simulation reposant sur les estimations issues du modèle développé au chapitre précédent, de quantifier les impacts respectifs et combinés des principales sources de pressions agissant au cours du cycle de vie de la sole commune en Manche Est.

Les résultats rappellent l'impact majeur de la pêche sur les populations marines exploitées, mais mettent également en avant l'importance de la conservation/restauration des habitats de nourriceries pour les espèces nourriceries-dépendantes. En revanche, la variabilité issue des conditions hydroclimatiques apparait de moindre ampleur. L'impact de la variabilité des conditions hydroclimatiques et de modifications de l'habitat est d'autant plus fort que le niveau d'exploitation de la population augmente.

En écho au chapitre précédent, ces conclusions sont fortement dépendantes des hypothèses concernant le fonctionnement spatial de la population, et renforcent la nécessité d'acquérir de la donnée spatialisée afin de progresser dans la compréhension du fonctionnement spatial des populations marines exploitées dans une perspective de gestion spatialisée de la ressource.

# 5. Discussion générale

Après un rappel des acquis de ce travail (5.1), cette discussion tirera un bilan sur l'apport des outils de modélisation Bayesienne hiérarchique (5.2) avant de discuter du modèle de cycle de vie de la sole de Manche Est (5.3) et enfin de synthétiser la contribution de ces travaux à la compréhension de l'écologie des poissons plats (5.4) et les perspectives de gestion qu'ils soulèvent (5.5).

## 5.1. Synthèse des acquis

Les travaux engagés au cours de cette thèse visaient à intégrer les différentes pressions auxquelles sont exposées les populations marines exploitées au cours de leur cycle de vie au sein de modèles de dynamique, afin d'estimer et de déconvoluer leurs impacts mais également de fournir des outils d'aide à la décision dans un contexte de gestion durable des ressources. Le travail a porté sur les espèces nourriceries-dépendantes, avec un focus sur les poissons plats (deuxième chapitre), et plus particulièrement la population de sole de Manche Est (troisième et quatrième chapitres). Ce choix de modèle d'étude était justifié par l'exposition de ces espèces à différents facteurs de pression agissant à des stades spécifiques de leur cycle de vie.

Une part importante de la problématique de recherche est guidée par la prise en compte des processus démographiques associés aux premiers stades dans le cycle de vie, marqués par une mortalité très élevée. Chez les poissons plats, les tout premiers stades sont marqués par une phase de dérive des œufs et des larves avec les courants marins vers les zones de nourriceries côtières. Puis, les post-larves s'installent dans les nourriceries côtières à leur métamorphose et donnent des juvéniles. Ces processus démographiques sont fondamentaux car ils conditionnement plusieurs aspects du fonctionnement des populations. Ils contrôlent la dynamique du recrutement, mais aussi la structure spatiale des populations (Planque *et al.*, 2011; Petitgas *et al.*, 2013). Ils sont aussi associés à deux facteurs de pression clés pour le fonctionnement des populations, l'influence des conditions environnementales pendant la phase de dérive larvaire pélagique, et l'influence des activités anthropiques sur la qualité et la quantité des habitats de nourriceries côtières.

De par leur complexité et aussi de par la difficulté d'observation de ces jeunes stades, ces différentes phases du cycle sont rarement prises en compte dans les modèles de dynamique de population. Dans cette thèse, nous nous sommes appuyés sur une stratégie de modélisation associant une modélisation parfois mécaniste (e.g. dérive larvaire) des processus démographiques avec une démarche statistique pour explorer l'importance et l'intérêt d'intégrer ces tout premiers stades dans des modèles de dynamique de populations d'espèces nourriceries-dépendantes.

### *Chapitre 2*

Le Chapitre 2 de la thèse s'est concentré sur l'analyse du processus de recrutement, central dans la modélisation du cycle de vie. Les résultats apportent une contribution substantielle à la compréhension des processus de recrutement des populations de poissons marins nourriceries-dépendantes et en particulier des poissons plats (pleuronectiformes).

Un modèle théorique décrivant le processus de recrutement des espèces nourriceries-dépendantes est proposé et confronté aux données. Le modèle considère explicitement le recrutement comme la combinaison de deux phases séquentielles : une première phase pélagique marquée par une mortalité contrôlée par des phénomènes stochastiques densité-indépendants, combinée à une seconde phase au sein des nourriceries où la mortalité est marquée à la fois par une régulation densité-dépendante (compétition entre juvéniles pour l'espace et les ressources) et des phénomènes aléatoires.

L'analyse du comportement de ce modèle permet de formaliser deux hypothèses qu'il est possible de tester : (i) la variabilité du recrutement devrait être plus faible pour les espèces dont le processus de recrutement est marqué par l'existence d'une phase de contrôle densité-dépendant de la mortalité ; (ii) au sein d'un stock particulier, si le processus de recrutement correspond effectivement au modèle séquentiel proposé, la variabilité du taux de recrutement par unité de stock devrait être plus faible pour des niveaux de stock élevés. La mise en évidence de ce patron de variabilité décroissante dans les données offre une manière originale de tester l'existence de densité-dépendance même lorsque le caractère aléatoire semble dominer le signal contenu dans le jeu de données.

Ces hypothèses ont été confrontées à une base de données stock-recrutement pour des poissons de différents ordres, comprenant notamment les données stock-recrutement les plus à jour pour 39 stocks de 17 espèces différentes de poissons plats.

En combinant des approches à plusieurs échelles, allant de la comparaison de la variabilité du recrutement entre différents ordres de poissons à l'analyse de la variabilité intra-stock, notre analyse a permis de produire un ensemble de résultats qui renforcent l'hypothèse de concentration pour les espèces nourriceries-dépendantes (Iles and Beverton, 2000).

Considéré indépendamment, chaque stock apporte peu d'information pour estimer les paramètres de modèles stock-recrutement. L'analyse des 39 stocks de poissons plats simultanément au sein du même modèle hiérarchique Bayesien a permis de transférer de l'information entre stocks (Rivot and Prévost, 2002; Michielsens and McAllister, 2004; Parent and Rivot, 2012; Burrow *et al.*, 2013; Pulkkinen and Mäntyniemi, 2013) de façon à extraire des signaux qui n'auraient pas pu être mis en évidence à partir d'une analyse séparée des données stock-recrutement de chaque stock.

L'analyse a mis en évidence que les poissons plats montrent une plus faible variabilité du recrutement que les autres ordres de poissons marins exploités. Ce résultat est attribué à des processus de concentration spécifiques au cycle de vie des poissons plats, les juvéniles se concentrant dans des secteurs de nourriceries à la capacité d'accueil limitée (Iles and

Beverton, 2000; Le Pape *et al.*, 2003a), processus entrainant une atténuation de la variabilité des apports de larves à l'issue de la phase de dérive pélagique en écrêtant les valeurs élevées (Le Pape et Bonhommeau, *in press*).

En combinant les données stock-recrutement pour les 39 stocks de poissons plats au travers d'une méta-analyse, les résultats ont aussi montré que la variabilité du recrutement par unité de biomasse féconde était plus faible pour les niveaux de stock élevés. La mise en évidence de ce patron moyen est cohérente avec l'hypothèse d'un processus de mortalité densité-dépendant de type compensatoire intervenant pendant la phase de concentration sur les nourriceries (Rijnsdorp *et al.*, 1995; van der Veer *et al.*, 2000a).

*Chapitre 3*

L'approche de modélisation du cycle de vie développée au Chapitre 3 permet de parvenir à une représentation intégrée à partir de séries de données hétérogènes. Elle apporte une contribution à la compréhension du fonctionnement spatial de la population de sole de Manche Est et des facteurs de forçage associés à différents stades du cycle de vie.

Les travaux précédents réalisés sur cette population ont été valorisés pour alimenter la modélisation des processus démographiques des jeunes stades (œufs → juvéniles installés sur les nourriceries). Les acquis du Chapitre 2 ont permis de préciser les hypothèses sur les processus de recrutement et la façon de les formuler pour alimenter le modèle de cycle de vie développé au Chapitre 3. Ainsi, le processus de recrutement est explicitement considéré dans le modèle de cycle de vie comme la séquence de deux phases : (1) une phase pélagique marquée par une forte mortalité densité indépendante (issue du modèle de dérive larvaire) ; suivie (2) du passage du stade de post-larve pélagique au stade de juvénile benthique marqué par une mortalité densité-dépendante, représentée sous la forme d'un modèle compensatoire de type Berverton-Holt paramétré par la survie maximale (obtenue pour des densités très faibles) et la capacité d'accueil dont dépend le recrutement maximum. Le modèle biophysique développé par Rochette *et al.* (2012) a été repris et mis à jour pour réaliser des simulations de la dérive larvaire sur un plus grand nombre d'années. Le modèle initialement développé par Rochette *et al.* (2010) permettant d'analyser les données de campagne scientifiques (traits de chalut à perche) sur les nourricerie pour estimer la variabilité spatio-temporelle des densités de juvéniles 0+ et 1+ de sole à l'automne a également été mis à jour.

Mais surtout, l'essentiel des développements a consisté à proposer une structure spatiale pour la fraction adulte de la population, en se basant sur le modèle intégré proposé par Rochette *et al.* (2013). Un faisceau d'éléments permet d'appuyer l'hypothèse d'un fonctionnement de type méta-population où trois sous-composantes de la population de

Manche Est fonctionneraient dans un isolement démographique assez marqué (Figure 5.1). Ainsi, un modèle intégré de la dynamique de cette méta-population est construit sous l'hypothèse d'une connectivité entre les trois sous-composantes limitée aux seuls échanges de larves entre les trois zones dues à la dispersion pendant la phase de dérive larvaire (Figure 5.2).

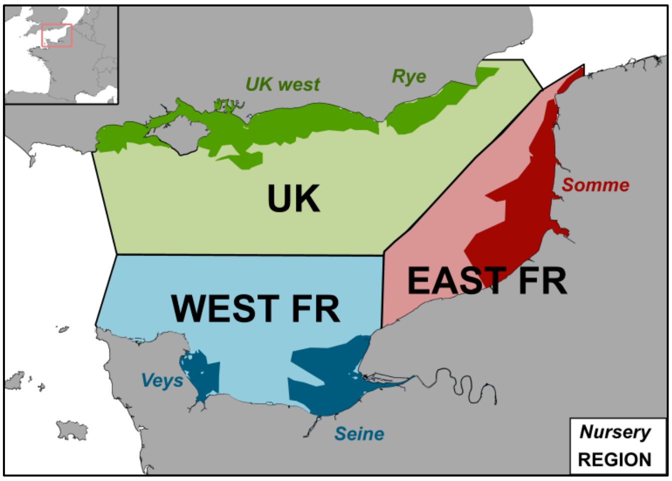

Figure 5.1. Structure régionale de la population de soles de Manche Est

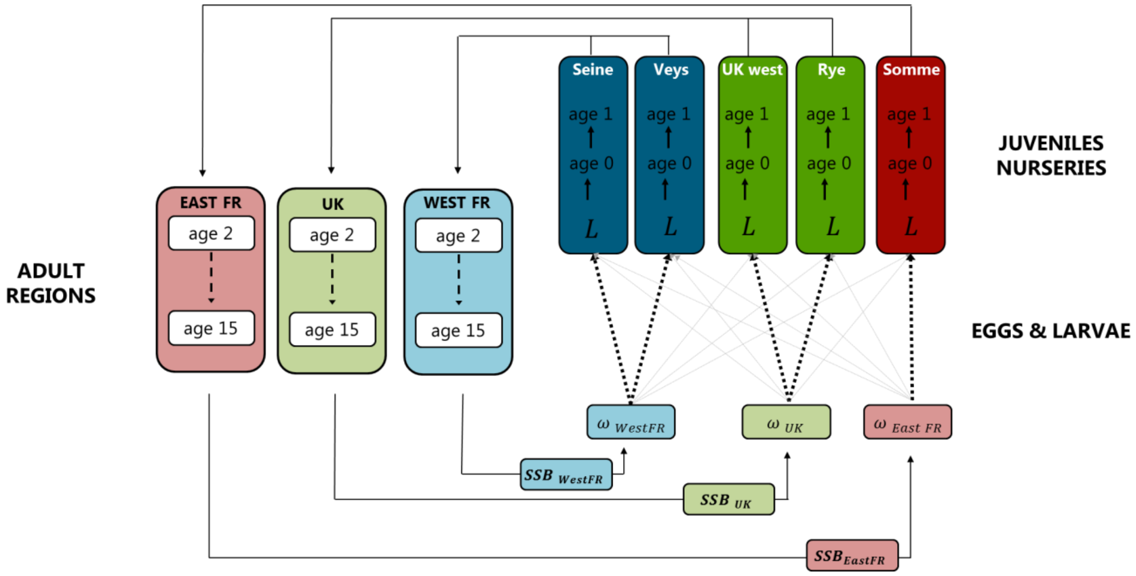

Figure 5.2. Modèle de cycle de vie pour la population de la sole en Manche Est sous l'hypothèse d'absence de connectivité induite par les faibles déplacements des sub-adultes et adultes entre les trois composantes

Ce modèle de cycle de vie apporte plusieurs contributions par rapport aux travaux existants. Le modèle d'évaluation actuel de la sole de Manche Est (ICES, 2013) n'intègre pas de relation stock-recrutement, le recrutement (âge 1) étant défini comme une moyenne géométrique des recrutements passés (e.g. moyenne sur 1982-2010 pour la cohorte de 2012 dans l'évaluation de 2013 ; ICES, 2013). Celui-ci est ensuite mis à jour les années suivantes. L'approche proposée permet des estimations du recrutement en « temps réel » car intégrant directement les observations des âges 0 et des âges 1 dans les nourriceries. Un autre intérêt de l'introduction d'une relation stock-recrutement sous-jacente (résultante de la dérive larvaire + relation post-larves → Age 0 des cinq nourriceries) est la possibilité d'estimer les points de référence $B_{RMD}$ et $C_{RMD}$ dont la connaissance est recommandée dans le cadre de l'approche écosystémique des pêches.

La comparaison avec un modèle dans lequel la fraction adulte de la population est représentée par un seul pool homogène alimenté par les cinq secteurs de nourricerie montre que considérer une connectivité très limitée entre les trois sous-composantes de la population modifie drastiquement les inférences sur la dynamique de population et sur l'influence des différents facteurs de forçage sur cette population. Les paramètres des différents secteurs de nourriceries sont estimés différemment, conduisant à une réévaluation du rôle fonctionnel des nourriceries au regard de leur contribution au recrutement total (augmentation de la contribution des secteurs de la Baie de Somme et diminution des contributions des secteurs de nourricerie des Baies de Seine et de Veys et des secteurs des côtes anglaises). Aussi, des indicateurs de l'état des stocks et de leur niveau d'exploitation par rapport au RMD ont pu être estimés pour chacune des trois composantes. Il apparait ainsi que le constat global de « surexploitation modérée » (ICES, 2013) pourrait masquer des disparités régionales, avec une sous-population exploitée au RMD sur l'ouest des côtes françaises de Manche Est et deux autres surexploitées, dont une très fortement (Est des côtes françaises).

*Chapitre 4*

Le modèle de cycle de vie intégré développé au Chapitre 3 a permis d'ouvrir la voie à une démarche de simulation de scénarios (Chapitre 4). Dans cette dernière partie, nous nous sommes attachés à quantifier l'effet des différentes pressions s'exerçant aux différents stades du cycle de vie de la sole de Manche Est, en s'appuyant sur les acquis des chapitres précédents. Les estimations des paramètres du cycle de vie ont ainsi été utilisées au sein d'une approche de simulation de scénarios visant à quantifier l'influence des différents facteurs de pression et à identifier les potentiels d'amélioration de production en lien avec la gestion de ces pressions. Il apparait ainsi que la restauration de l'estuaire de Seine serait susceptible d'entrainer une augmentation considérable (+66% de captures) de la production du sous-stock associé (partie ouest des côtes françaises), se traduisant par une augmentation plus mesurée à l'échelle de la Manche Est. Cependant, à l'échelle de l'ensemble de la Manche Est, la gestion (régionalisée) de la mortalité par pêche demeure le principal levier d'action pour restaurer la population et ainsi augmenter sa production. L'analyse des scénarios montre aussi que l'hypothèse d'une connectivité entre les trois sous-composantes de la population, même limitée, engendrée par une migration des adultes entre les trois régions, modifie largement les conséquences des différents scenarios testés. La prise en compte d'un degré même limité de connectivité entre les sous-entités fait que des scénarios de gestion spatialisés (e.g. régulation de la pression de pêche dans une des trois sous-composantes ou restauration d'un secteur de nourricerie), voient leurs effets locaux se diluer et se répercuter sur l'ensemble de la Manche Est. Cela met l'accent sur la nécessité d'améliorer la connaissance sur les patrons de connectivité pour pouvoir proposer des mesures de gestion efficaces.

## 5.2. Entre approche mécaniste et statistique : doit-on toujours adapter la complexité d'un modèle à la richesse des données disponibles ?

L'approche privilégiée au cours de cette thèse diffère conceptuellement de celle qui sous-tend les modèles classiques de dynamique de population structurés en âge utilisés pour l'évaluation des stocks.

Les modèles classiques sont entièrement structurés autour des séries de données disponibles, c'est-à-dire la plupart du temps les séries de captures aux âges et une ou plusieurs séries d'indices d'abondance issues de CPUE scientifiques ou commerciales. Ainsi la complexité des processus démographiques représentés est souvent nivelée par le bas (par rapport aux connaissances biologiques et écologiques disponibles) pour s'adapter à la richesse des séries de données disponibles. Notamment, la phase de dérive larvaire n'étant pas accessible à l'observation, les modèles classiques n'intègrent pas explicitement les tout premiers stades du cycle de vie, le recrutement étant rétro-calculé à partir de la dynamique des cohortes reconstruite sur la base des données de captures aux âges.

L'approche de modélisation intégrée du cycle de vie développée dans la thèse (notamment dans le Chapitre 3) diffère de par sa philosophie. Elle consiste à articuler des connaissances de différentes natures (données mais aussi informations provenant de différentes sources) et des hypothèses écologiques pour proposer une structure *a priori* pour le fonctionnement démographique et la paramétrisation associée, puis à confronter ces hypothèses sur les processus démographiques aux observations par une méthode d'inférence.

Cette démarche s'est largement appuyée sur le cadre des modèles hiérarchiques Bayesiens. Ils ont l'avantage de séparer explicitement la modélisation des processus (hypothèses *a priori*) de l'assimilation des données dans le modèle, et se rapprochent en ce sens des méthodes d'assimilation de données qui donnent une place prépondérante à la modélisation des processus avant de les confronter aux observations (Hobbs and Ogle, 2011; Peng *et al.*, 2011).

Ainsi ils permettent de représenter les hypothèses *a priori* sur le fonctionnement du système au travers d'une modélisation des processus démographiques ($\mathrm{p}(Z|\theta)$) et de l'intégration de distribution *a priori* sur les paramètres ($\mathrm{p}(\theta)$). Dans la mesure où les variables d'état du système ($Z$), les paramètres ($\theta$) et les relations démographiques ($\mathrm{p}(Z|\theta)$) sont explicitement séparés des données ($y_{obs}$), la structure peut être développée indépendamment des données disponibles. Le modèle d'observation $\mathrm{p}(y_{obs}|Z,\theta)$ permet alors d'intégrer des sources de données multiples et variées (e.g. sources, nature et échelles différentes) pour mettre à jour la connaissance sur l'état du système.

Dans cette vision de la modélisation, les contraintes de structure et de paramétrisation imposées dans la distribution *a priori* jointe des paramètres et des états du système $\mathrm{p}(\theta,Z)$ peuvent prendre une part prépondérante dans l'analyse. Dans ce sens, on peut dire que les MHB permettent une certaine réconciliation entre des approches de modélisation mécaniste et statistique (Clark, 2005; Cressie *et al.*, 2009; Waller, 2010; Parent and Rivot, 2012; Rivot, 2013).

Dans notre cas d'étude, des hypothèses fortes ont étés formulées concernant les processus démographiques (notamment dans le Chapitre 3). La phase de dérive larvaire est représentée en utilisant des sorties d'un modèle biophysique mécaniste de couplage de circulation océanique avec des hypothèses individus-centrées de dérive et de comportement des œufs et larves de sole (Rochette *et al.* 2012 ; Savina, com. pers.). Dans l'état des données disponibles actuellement, ce modèle biophysique ne peut pas être validé et est considéré comme une hypothèse *a priori*. Des hypothèses fortes ont aussi été formulées sur les capacités de déplacement des subadultes et adultes une fois sortis des zones côtières de nourriceries.

Enfin, la possibilité de transférer de l'information entre différents cas d'étude ou entre différentes strates des modèles au travers des distributions *a priori* sur les paramètres a été exploitée à plusieurs niveaux. Dans le Chapitre 2, les propriétés des modèles hiérarchiques pour cumuler l'information d'un grand nombre de jeux de données (Rivot and Prévost, 2002; Jiao *et al.*, 2011; Punt *et al.*, 2011) ont été valorisées dans une méta-analyse des processus stock-recrutement chez les poissons benthiques (et en particulier chez les plats) pour extraire des patrons communs inaccessibles par l'analyse des jeux de données individuels par population. Les paramètres de survie densité-dépendante des juvéniles au sein des nourriceries étant difficiles à estimer, des lois *a priori* informatives issues de la méta-analyse du Chapitre 2 ont été introduites dans le modèle de cycle de vie du Chapitre 3.

Ainsi au cours de cette thèse, nous nous sommes directement confrontés à la question de savoir si la complexité d'un modèle doit toujours être adaptée à la richesse des données disponibles (Adkison, 2009; Lavine, 2010; Lele, 2010).

Si l'approche et les résultats montrent l'intérêt de dépasser les seules données disponibles pour articuler les connaissances et explorer des hypothèses sur les processus démographiques complexes, les limites de cette approche apparaissent aussi clairement. Ces limites concernent notamment notre capacité (ou incapacité !) à tester et à valider ces hypothèses, pour l'essentiel liée à la disponibilité en données.

Ainsi par exemple, en l'absence de données sur l'intensité et la portée des déplacements des (sub)adultes au-delà du voisinages des nourriceries côtières, des hypothèses fortes ont dû être faites sur les patrons de connectivité entre trois grandes régions définies par les patrons de rétention larvaire. L'approche montre la possibilité et l'intérêt de considérer ces différentes hypothèses, les résultats de l'analyse dépendant fortement des patrons de connectivité entre différentes sous-composantes de la méta-population (par exemple en termes d'évaluation du niveau de prélèvement par la pêche par rapport au RMD). Mais les hypothèses testées restent difficiles à départager au sens statistique.

Cependant, l'approche garde le mérite de proposer une articulation des connaissances, des hypothèses et des données dans une cadre cohérent pour mettre en lumière l'importance de certains processus démographiques clés (ici la connectivité). Elle stimule des voies de recherche et permet de prioriser l'effort de récolte de données supplémentaires (ici par exemple des données de marquage sur les adultes) en vue de pouvoir réfuter ou valider les hypothèses alternatives sur ces processus clés.

## 5.3. Limites et perspectives d'amélioration du modèle de cycle de vie

### 5.3.1. Des modèles d'évaluation des stocks Bayesiens en routine ?

Malgré l'existence de logiciels dédiés tels que OpenBUGS, JAGS ou encore ADMB (Bolker *et al.*, 2013), capables de mettre en œuvre les simulations MCMC nécessaires à l'estimation des distributions Bayesiennes *a posteriori*, la manipulation de ce type de modèle de cycle de vie dans un cadre Bayesien peut rester délicate et coûteuse en temps de calcul. Les résultats peuvent être sensibles au choix des distributions *a priori*, et les simulations MCMC peuvent être coûteuses en temps de calcul pour atteindre la convergence (Craigmile *et al.*, 2009; Bolker *et al.*, 2013). Même si des avancées méthodologiques sont constamment réalisées et permettent d'envisager des progrès considérables à court terme, ces difficultés peuvent expliquer la difficulté de transfert des méthodes Bayesiennes depuis la recherche vers l'utilisation en routine par les groupes d'évaluation, où des solutions éprouvées tendent logiquement à être privilégiées (Maunder and Piner, 2014). Toutefois l'approche présente des avantages indéniables pour l'écologie halieutique (Rivot, 2013) et pour l'évaluation de stock : l'intégration de l'incertitude, un cadre adapté à l'analyse du risque et sa capacité à rassembler des scientifiques ou gestionnaires autour de la construction du modèle (FAO, 2001).

### 5.3.2. Influence forte des données de captures aux âges dans l'ajustement

L'influence des équations d'observation des captures aux âges est très importante dans le processus d'ajustement et les données de captures aux âges sont la source d'information dominante dans le résultat de l'inférence statistique. Il est possible de diminuer le poids de ces données dans le modèle, par exemple en augmentant la variance de l'erreur d'observation associée aux données de capture (fixée par dire d'expert à CV=20% dans le modèle). Il est aussi possible d'augmenter l'influence des autres sources de données, par exemple les indices d'abondance des juvéniles sur les nourriceries, en diminuant les variances des erreurs d'observation associées à ces données. Il n'en reste pas moins que les erreurs d'observation utilisées dans le modèle correspondent aux estimations (indices d'abondance) et à l'expertise (captures) disponibles.

### 5.3.3. Améliorer la modélisation du processus de mortalité sur les nourriceries

Le processus de mortalité entre le stade post-larve (larve arrivée sur un secteur de nourricerie et prête à se métamorphoser) et le stade âge 0 sur les aires de nourriceries est décrit dans le modèle selon une simple loi de Berverton-Holt, paramétrée avec une mortalité densité-dépendante de type compensatoire dépendante de la densité des post-larves par unité de surface des nourriceries. L'importance de cette phase, mise en évidence dans la méta-analyse stock-recrutement, justifierait une modélisation plus aboutie. Il serait possible d'affiner cette relation par une révision de la manière dont sont intégrées les données disponibles, conduisant à une représentation plus réaliste des phénomènes de densité-dépendance.

La nourricerie est ainsi considérée au sein du modèle comme un secteur homogène, alors que ses caractéristiques physiques sont variables dans le temps et dans l'espace. L'hétérogénéité spatiale des nourriceries est prise en compte plus en amont lors de la construction des indices d'abondance de juvéniles sur ces nourriceries (Rochette *et al.*, 2010) qui sont introduits sous la forme d'observations dans le modèle. Il serait envisageable de considérer des indices d'abondance de juvéniles stratifiés en fonction des différentes classes d'habitat représentées dans le modèle de Rochette *et al.* (2010) afin de prendre en compte les erreurs d'échantillonnage non homogènes entre les strates (certaines strates étant plus riches en données que d'autres) (Ancelet *et al.*, 2009). Pour aller plus loin, le modèle d'observation des indices d'abondance de juvéniles n'est pas explicitement représenté au sein du modèle Bayesien intégré. On pourrait imaginer une représentation explicite du processus d'observation *local* de la densité de juvéniles par les traits de chalut au sein des nourriceries, et coupler directement ce processus d'observation au modèle de cycle de vie afin de mieux caractériser l'hétérogénéité spatiale (par type d'habitat, par secteur) et temporelle (par année) des erreurs d'échantillonnage. Ce raffinement spatial ouvrirait la voie à une représentation des processus de densité-dépendance à une échelle plus fine au sein de chaque secteur de nourricerie afin de rendre compte de la répartition non homogène des juvéniles en fonction des caractéristiques de l'habitat (Rochette *et al.*, 2010; Trimoreau *et al.*, 2013).

Il serait également envisageable de définir les paramètres de survie des juvéniles dans les nourriceries. Du fait de la limitation nutritive subie par les juvéniles (Le Pape and Bonhommeau, *in press*), un indice d'abondance de proies ou un indicateur de productivité annuelle (e.g. lié au débit des fleuves et à l'enrichissement terrigène en estuaire ; Le Pape et al., 2003a, Kostecki et al., 2010) pourraient s'avérer informatifs.

L'hypothèse d'une mortalité densité-dépendante de type compensatoire pourrait aussi être remise en cause. A défaut de pouvoir être testée faute de données disponibles dans les très faibles niveaux de stocks, l'hypothèse d'une densité-dépendance de type *dépensatoire* (aussi appelé effet *Allee* ; Clark, 1974; Liermann and Hilborn, 1997, 2001) mériterait d'être explorée dans la réalisation des simulations (Chapitre 4). En effet, les hypothèses actuelles du modèle induisent que la population est toujours capable de se restaurer même après une très forte déplétion (notamment par la pêche). Or, il existe de nombreux exemples où des stocks très fortement impactés par la pêche n'ont pas pu retrouver leur niveaux de biomasse historiques malgré un arrêt complet de l'exploitation (Hutchings, 2000; Hutchings and Reynolds, 2004; Petitgas *et al.*, 2010).

### 5.3.4. Intégrer d'autres sources de mortalité

La pêche n'est pas l'unique pression subie par les adultes. L'habitat des adultes est également soumis à d'autres perturbations d'origine anthropique. La contamination du sédiment est susceptible d'affecter aussi les adultes, bien moins concentrés toutefois dans les zones côtières et estuariennes les plus contaminées (Dorel *et al.*, 1991). Les perturbations physiques du milieu telles les extractions de granulats marins peuvent également avoir un impact, d'autant plus que les zones d'extraction recoupent les secteurs de vie des adultes en Manche Est (Marchal *et al.*, Accepted). Cet impact peut être direct dans le secteur concerné par l'extraction mais également indirect via une altération qualitative et quantitative de la couverture benthique et donc de la composition spécifique des proies des poissons. Ces conséquences semblent toutefois limitées dans le cas de la sole (Marchal *et al.*, Accepted). Le modèle développé dans le cadre de ce travail est spatialement implicite et ne permet pas de tester ces effets avec une finesse spatiale suffisante.

Par ailleurs, la mortalité naturelle des adultes actuellement considérée fixe et homogène est susceptible de varier selon la densité de prédateurs. Ainsi, les pêcheurs opérant dans le secteur oriental des côtes françaises, sous-composante de la population pour laquelle nos résultats indiquent une décroissance de l'abondance ces dernières années, mettent en avant l'augmentation de la population de phoques communs (*Phoca vitulina*) pour expliquer cette diminution[1]. Il serait intéressant d'étudier cet impact potentiel via une approche trophique pour ensuite corréler la mortalité naturelle à la densité de prédateurs si cet impact apparait comme significatif.

### 5.3.5. Réponses de la population à long terme

Au-delà de leur intérêt pour étudier les états d'équilibre, la simulation de scénarios à long terme pose la question de la réponse et de l'adaptation des populations exploitées aux changements globaux. L'augmentation de la température des océans impacte la biologie et la distribution des espèces, et est plus globalement de nature à modifier la structure des écosystèmes (Perry *et al.*, 2005). La pêche engendre également des adaptations génétiques des populations (Conover and Munch, 2002; Jorgensen *et al.*, 2007), notamment une maturité plus précoce et une croissance moindre (e.g. sole de mer du Nord Mollet et al, 2007). Ces effets à long terme ne sont pas pris en compte dans les scénarios actuels.

### 5.3.6. Mieux intégrer les différentes échelles de connectivité entre adultes

A l'échelle de la Manche Est, si les patrons de dispersion des premiers stades sont déduits de modèles développés par ailleurs (œufs et larves ; modèle biophysique) ou considérés comme connus (juvéniles ; rétention), ceux des adultes reposent sur des hypothèses. Dans le second chapitre, nous avons confronté deux hypothèses extrêmes sur la connectivité entre adultes en Manche Est : absence de mouvement conduisant à trois composantes démographiquement

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[1] « Baie de Somme : les pêcheurs déclarent la guerre aux phoques », *Le Parisien* (http://www.leparisien.fr/environnement/baie-de-somme-les-pecheurs-declarent-la-guerre-aux-phoques-06-10-2013-3200505.php)

isolées versus un unique *pool* d'adultes. Dans le modèle de simulation (Chapitre 4), l'hypothèse de ségrégation spatiale complète est relaxée et nous explorons l'impact des migrations depuis les nourriceries vers les zones adultes « éloignées » sur l'estimation des effets des pressions. Ces approches permettent d'explorer le fonctionnement du système et soulèvent des aspects importants en termes de gestion spatiale. Elles demeurent toutefois insatisfaisantes dans une optique d'aide à la décision en contexte réel. Sous réserve de données ou de connaissances expertes pertinentes, il serait possible d'inclure dans le modèle de cycle de vie développé au chapitre 3 une estimation des échanges entre les sous-populations. Par exemple, si des données de marquage-recapture étaient disponibles, ceci pourrait être réalisé via l'intégration d'un module de marquage (Drouineau *et al.*, 2010; Hulson *et al.*, 2011; Goethel *et al.*, 2014) où les individus marqués suivent des processus identiques et sont observés de manière similaire aux individus non-marqués (i.e. observation des captures d'individus marqués) afin d'intégrer dans le modèle l'estimation des taux d'échange entre sous-populations. Dans un cas *data poor*, le cadre Bayesien pourrait être valorisé pour intégrer de l'expertise sur des taux d'échanges moyens réalistes.

Par ailleurs, si les apports de larves depuis la Mer du Nord sont faibles à l'échelle du *pool* de larves total de Manche Est, ils peuvent être importants à l'échelle locale de certaines nourriceries (e.g. jusqu'à 80 % des larves arrivant sur le secteur de la baie de Rye proviennent de la Mer du Nord). Ces apports ont été ajoutés *a posteriori* au modèle de cycle de vie i.e. sommés avec les arrivées de larves issues de Manche Est prédites par le modèle. Il serait possible de construire un modèle couplant les deux populations (Manche Est et Mer du Nord) basé sur des données et processus similaires pour chaque population, et ainsi d'intégrer les échanges entre les deux composantes de la Manche Est et de la mer du Nord.

### 5.3.7. Des perspectives bridées par la disponibilité en données spatialisées

La complexité des processus et échelles représentés entraine des besoins élevés en données et/ou en hypothèses. Par exemple, la spatialisation du modèle de cycle de vie requiert des captures et des indices d'abondances spatialisés. Les séries disponibles à cette échelle spatiale plus fine ne couvrent pas l'ensemble de la série temporelle de simulation (1982-2011). Nous avons donc eu recours à des hypothèses, (e.g. homogénéité des paramètres biologiques et des diagrammes d'exploitation entre les trois composantes ; répartition spatiale des captures homogène par pays), ou avons accepté de moins bonnes performances du modèle pour les années non couvertes (e.g. indices d'abondance spatialisés). Ces hypothèses, sans être sciemment irréalistes, vont toutefois à l'encontre de la vision de trois sous-populations quasi-autonomes. Dans l'idéal, pour pallier ces manques ou renforcer/préciser les hypothèses formulées, il faudrait orienter la collecte de données vers la prise en compte de la composante spatiale de la population (e.g. marquage/recapture) ou analyser plus finement les données existantes à une échelle désagrégée (e.g. poids aux âges dans les ports de débarquement de chaque zone). Si ces données existent *pro parte*, l'absence de séries standardisées disponibles sur une partie significative de la série temporelle prise en compte pour le développement du modèle (1982-2011) n'a pas permis de les intégrer à ce stade.

De manière similaire, si l'intégration de nouvelles pressions (e.g. trophiques) ou scénarios ne pose pas de défi technique majeur, le problème demeure la production de variables de forçage reflétant ces pressions (i.e. données) et le lien de causalité entre pression et cycle de vie (i.e. processus et paramètres). D'autres approches portant sur la modélisation de l'ensemble de l'écosystème en Manche Est, et intégrant ces différentes pressions, sont en cours de développement dans le cadre du projet VECTORS (http://www.marine-vectors.eu/). Ces modèles spatialement explicites et au pas de temps plus fin permettent une meilleure interaction spatio-temporelle des processus. Ceci se fait au prix d'hypothèses supplémentaires et le caractère résolument mécaniste de ces approches diffère de l'approche d'intégration de données conduite dans le cadre de ce travail.

## 5.4. Contributions à l'écologie des espèces nourriceries-dépendantes et en particulier des poissons plats

Les travaux menés dans le cadre de cette thèse contribuent à la compréhension du fonctionnement des espèces nourriceries-dépendantes. Nous rappelons ici les apports principaux de ce travail en terme de dynamique de population et de réponse aux pressions anthropiques, à savoir (i) la confirmation de l'hypothèse de concentration de Iles et Berverton (2000) et de son impact sur le déterminisme du recrutement chez les espèces nourriceries-dépendantes, (ii) la structuration spatiale des populations de ces espèces et ses conséquences en terme de dynamique spatialisée et de réponse aux pressions s'exerçant à différentes échelles spatiales au cours du cycle de vie.

### 5.4.1. Le stade juvénile, la « *critical period* » des espèces nourriceries-dépendantes

La méta-analyse des relations stock-recrutement réalisée au Chapitre 2 a mis en évidence (i) la pertinence d'une approche du processus de recrutement en deux phases, (ii) la spécificité des pleuronectiformes par rapport à d'autres ordres sujets à une moindre concentration durant le stade juvénile et (iii) la manifestation de processus densité-dépendance lors du recrutement des pleuronectiformes. La méta-analyse appuie l'hypothèse de concentration (Iles and Beverton, 2000) selon laquelle les espèces dont les juvéniles sont concentrés dans des habitats restreints (e.g. nourriceries) ont un recrutement moins variable que les autres, et ceci en raison de la capacité d'accueil limitée de ces nourriceries.

Le concept de *critical period*, introduit par Hjort (1914) et popularisé par May (1974) désigne les tout premiers stades (i.e. larvaires) comme étant critiques dans la détermination du succès du recrutement (Houde, 2008). Leur mode de vie planctonique, l'influence de la circulation hydrodynamique (Cushing, 1995), à même de conduire les futurs alevins dans des zones défavorables à leur développement, leur dépendance aux conditions trophiques à petite échelle et leur résistance très limitée au manque de disponibilité en nourriture (May, 1974) engendrent chez ces premiers stades une mortalité forte (Le Pape et Bonhommeau, *in press*) et très variable (Houde, 2008). Les travaux conduits durant cette thèse indiquent que ce concept, développé initialement sur le hareng, ne semble pas adapté à l'histoire de vie des espèces nourriceries-dépendantes et notamment des pleuronectiformes. La variabilité du recrutement de ces espèces est limitée sous l'influence de la densité-dépendance sur les nourriceries. En conséquence, les apports des larves vers les zones de nourriceries deviennent limitants à partir d'un seuil très bas de production d'œufs et de survie larvaire, seuil inférieur aux niveaux généralement observés. Cette notion de seuil non atteint est déterminante, car même si la mortalité élevée et variable (Hjort, 1914; Chambers and Leggett, 1992; Gibson, 2004; Levin and Stunz, 2005) des tout premiers stades (œufs et larves) est susceptible d'engendrer une forte variabilité des apports de larves, celle-ci aura une influence limitée au-delà de ce seuil. Pour les espèces nourriceries-dépendantes, la *critical period* se situe donc plutôt aux stades suivant la vie larvaire, et en particulier pour les poissons plats après la métamorphose, au stade juvénile (Le Pape and Bonhommeau, *in press*). Les processus densité-dépendants intervenant durant ce stade apparaissent donc particulièrement déterminants (Archambault *et al.*, 2014).

### 5.4.2. Une structuration spatiale des populations en interaction avec les différentes pressions

Du fait des processus de concentration sur les nourriceries, la variabilité des apports larvaires a un impact vraisemblablement limité sur le recrutement des espèces nourriceries-dépendantes. Toutefois, les tout premiers stades conservent une importance majeure car ils sont susceptibles de contribuer à la structuration spatiale des populations (Scheltema, 1986; Cowen and Sponaugle, 2009). Ceci est particulièrement vrai pour les poissons plats, dont les stades juvéniles sont cantonnés à des habitats restreints et localisés (Gibson, 2004) et donc définis spatialement (i.e. pas d'échanges et de déplacements entre ces habitats au-delà d'une échelle très limitée lors de la phase juvénile). Par exemple, dans le cas d'étude de la sole de Manche Est, les phénomènes de rétention larvaire (Rochette *et al.*, 2012) couplés au cantonnement des juvéniles dans les nourriceries (Le Pape and Bonhommeau, *in press*; Le Pape *et al.*, 2003b) et aux mouvements limités des adultes (Kotthaus, 1963; Anon., 1965) a conduit à revisiter le fonctionnement de la population, en mettant en évidence l'isolement de sous-entités spatiales très faiblement connectées. Il est probable que ce cas de figure particulier se retrouve chez d'autres populations aux caractéristiques similaires (Warner and Cowen, 2002).

Si le stade juvénile semble déterminant pour la variabilité de la survie, les patrons de connectivité des stades larvaires et adultes structurent le fonctionnement spatial de la population et interagissent avec les différents facteurs de pression.

Les conditions climatiques rencontrées par les tout premiers stades (œufs, larves) vont conditionner leur survie et leur chance d'atteindre une zone de nourricerie. Toutefois, dans le cas particulier de la population de sole de Manche Est, les simulations ont montré que les fluctuations interannuelles de survie larvaire impactent simultanément les apports de larves au niveau de chaque secteur de nourricerie. Cet exemple suggère que la survie de ces premiers stades est *in fine* gouvernée par des processus opérant à large échelle (e.g. influence océanique). Les pressions sur les habitats de nourricerie interagissent également avec la structure spatiale de la population, en termes de contribution respective des habitats à des sous-populations locales ou à un pool commun d'adultes, et donc en termes de lien entre la dégradation/restauration de nourriceries et d'impact localisé ou à large échelle. De plus, l'alimentation locale en larves dépend de la répartition spatiale des œufs et donc des adultes durant la reproduction. Cette dépendance à la structure spatiale de la population adulte est fortement liée à l'impact de la pêche, qui a un effet de déplétion local dans le cas de sous-populations isolées, plus complexe et plus général dans le cas de sous-populations en interactions ou d'une population homogène. Il apparait ainsi que l'évaluation des effets des pressions est indissociable de leurs interactions avec le fonctionnement spatial de la population.

## 5.5. Un outil d'aide à la décision généralisable aux autres espèces nourriceries-dépendantes

Le modèle de cycle de vie développé dans les chapitres 3 et 4 et appliqué à la sole de Manche Est est généralisable à d'autres populations d'espèces nourriceries-dépendantes. Les données nécessaires sont souvent disponibles pour les populations exploitées : les modèles biophysiques de dérive larvaire sont de plus en plus développés, les campagnes de pêche scientifique dans les nourriceries sont courantes et la fraction adulte intègre des données similaires aux évaluations de stock. De plus, le cadre proposé est suffisamment flexible pour introduire d'autre types de données ou complexifier/simplifier les processus, afin de s'adapter au niveau de données et connaissances de la population concernée.

### 5.5.1. Un socle de simulation de scénarios de pressions

Les avancées réalisées sur le modèle d'estimation (3ème Chapitre) et le modèle de simulation basé sur la même structure (4ème Chapitre) permettent la simulation de scénarios portant sur l'évolution de la quantité et de la qualité d'habitat de nourricerie et de la mortalité par pêche en tenant compte de la variabilité climatique. Dans le cadre ce travail, nous nous sommes cantonnés à une appréciation des effets respectifs de ces différents facteurs de pression, mais un travail approfondi devrait permettre la projection de scénarios de gestion plus réalistes et applicables (e.g. impact de la création d'une zone de fermeture de la pêche ; Pastoors *et al.*, 2000).

### 5.5.2. Vers une gestion spatialisée multi-pressions

Les travaux menés au cours de cette thèse mettent en lumière plusieurs composantes essentielles pour une bonne gestion des populations d'espèces nourriceries-dépendantes. Les résultats montrent l'importance d'une bonne évaluation du fonctionnement spatial de la population pour l'établissement de mesures de gestion adaptées. Par exemple, le chapitre 3 montre que l'hypothèse (fortement probable) selon laquelle la population de sole de Manche Est fonctionnerait sous la forme de trois sous-composantes presque isolées démographiquement modifie drastiquement l'évaluation du niveau d'exploitation par la pêche par rapport au RMD. D'une manière générale, plusieurs auteurs ont déjà montré que l'ignorance de la structure spatiale des populations peut conduire à des situations de surexploitation (ou sous-exploitation) locale, lorsque la répartition spatiale de la pression de pêche n'est pas en accord avec les potentiels de production locale (Cooper and Mangel, 1999; Ying *et al.*, 2011).

La gestion de ces populations doit également prendre en compte les pressions multiples auxquelles elles sont soumises. L'importance de la disponibilité et de la qualité des habitats a été mise en exergue via l'approche de simulation. Si une exploitation à des niveaux de pêche autorisant le bon renouvellement des populations est primordiale, la préservation ou la restauration des habitats essentiels à ce renouvellement est également bénéfique, en raison du caractère limitant de la phase juvénile (van de Wolfshaar *et al.*, 2011) souligné au cours de ce travail de thèse.

La modélisation du cycle de vie permet d'alimenter les outils d'aide à la décision pour l'évaluation de mesures de gestion spatialisées en intégrant l'influence de plusieurs facteurs de pressions agissant à différents stades du cycle de vie et à différentes échelles spatiales.

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# Annexes

## Exemple de code JAGS pour la méta-analyse stock-recrutement

```
#Model with observation errors, n0 and n1 at stock scale, CVs given in data
#Hyperparameters
mu_n1 ~ dnorm(0,0.05)
sd_n1 ~ dunif(0.01, 20)
tau_n1 <- 1 / (sd_n1 * sd_n1)
mu_n0 ~ dnorm(0,0.05)
sd_n0 ~ dunif(0.01, 20)
tau_n0 <- 1 / (sd_n0 * sd_n0)
mu_logalpha ~ dnorm(0,0.1)
sd_logalpha ~ dunif(0.01,3)
tau_logalpha <- 1 / (sd_logalpha * sd_logalpha)
mu_logk ~ dnorm(0,0.1)
sd_logk ~ dunif(0.01, 3)
tau_logk <- 1 / (sd_logk * sd_logk)

#Parameters
for( S in 1 : nb.sp )
{
	for( i in 1 : nb.pop[S] )
	{
	logalpha[S , i] ~ dnorm(mu_logalpha, tau_logalpha)
	logk[S , i] ~ dnorm(mu_logk, tau_logk)
	k[S , i] <- exp(logk[S , i])
	alpha[S , i] <- exp(logalpha[S , i])
	n0[S,i] ~ dnorm(mu_n0, tau_n0)
	n1[S,i] ~ dnorm(mu_n1, tau_n1)
	}
}
#Observation variance on R and S
prec_obs_R<-1/sigma_obs_R
sigma_obs_R<-log(CV_obs_R*CV_obs_R+1)
prec_obs_S<-1/sigma_obs_S
sigma_obs_S<-log(CV_obs_S*CV_obs_S+1)

for( y in 1 : nb.obs )
{
#Prior on SReal
logSReal[y]<-log(SReal[y])
SReal[y]~dunif(0,10)

#observation equations, laurent corrected
logR[y]~dnorm(logRReal[y]-0.5*sigma_obs_R,prec_obs_R)
logS[y]~dnorm(logSReal[y]-0.5*sigma_obs_S,prec_obs_S)

#Link to data (prior on RReal )
logRReal[y] ~ dnorm(mu_R[y], tau_R[y])
mu_R[y]<-log(SReal[y]*k[sp[y],pop[y]]/((k[sp[y],pop[y]]/    alpha[sp[y],pop[y]])    +
SReal[y]))
#process variance model
tau_R[y] <- 1 / exp(n0[sp[y],pop[y]] + n1[sp[y],pop[y]] * SReal[y])
}
```

## Exemple de code JAGS pour le modèle de cycle de vie régionalisé de la sole de Manche Est

```
#Regional model with all data sources, z=regions, a=ages, t=years, Area=nurseries
#Date of observation of juvenile indices (in months)
obsJuvtime <- 8  # 1 sept

# Catchabilities

#IA JUVS
Logq_0 ~ dunif(-10,10)
q_0<-exp(Logq_0)
Logq_1 ~ dunif(-10,10)
q_1<-exp(Logq_1)
for(a in 1:max.a) {
SelecQ[a] <- Selec[a]
}

#IA BECBT
Logq_AgeSup_BECBT ~ dunif(-10,10)
q_AgeSup_BECBT <- exp(Logq_AgeSup_BECBT)
for(a in 1:max.a)
{
q_BECBT[a] <-  max(q_AgeSup_BECBT * SelecQ[a] ,1.0E-7)
 }

#IA UKCBT
Logq_AgeSup_UKCBT ~ dunif(-10,10)
q_AgeSup_UKCBT <- exp(Logq_AgeSup_UKCBT)
for(a in 1:max.a)
{
q_UKCBT[a] <-  max(q_AgeSup_UKCBT * SelecQ[a] ,1.0E-7)
}

#IA spatial
Logq_AgeSup_UKBTS ~ dunif(-10,10)
q_AgeSup_UKBTS <- exp(Logq_AgeSup_UKBTS)
for(a in 1:max.a) {
q_UKBTS[a] <-  max(q_AgeSup_UKBTS * SelecQ[a] ,1.0E-7)
}

# Fecondity
A_eggs <- 5.619
B_eggs <- 1.17

#Random walk on fishing effort (i.e. on F)
#year 1
for(z in 1:max.z)
{
log_Eff[1,z]~dnorm(0,0.1)
Effort[1,z]<-exp(log_Eff[1,z])
}
sd_Eff~dunif(0.01,0.5)
tau_Eff<-1/(sd_Eff*sd_Eff)

#next years
for(t in 2:max.t)
{
	for(z in 1:max.z)
	{
	log_Eff[t,z]~dnorm(log_Eff[t-1,z],tau_Eff) #modele autoregressif
	Effort[t,z]<-exp(log_Eff[t,z])
	}
}

# Logistic selectivity in data
```

```
#Combined F
CV_F ~ dunif(0.00001, 0.99999)
a_F <- 1 / (CV_F*CV_F)

for(t in 1:max.t)
{
       for(z in 1:max.z)
       {
              for(a in 1:max.a)
              {
              mean_F[a,t,z] <- Selec[a] * Effort[t,z]
              b_F[a , t,z] <- (1 / (CV_F*CV_F)) * (1/mean_F[a,t,z])
              F[a,t,z] ~ dgamma(a_F, b_F[a, t,z])
              }
       F3_8[t,z] <- mean(F[3:8,t,z])
       }
}

#informative prior on alpha
mu_log_alpha~dnorm(-3,100)
log_tau_log_alpha~dnorm(-1.272966,100)
tau_log_alpha<-exp(log_tau_log_alpha)

for(Area in 1:max.Area){
log_alpha[Area]~dnorm(mu_log_alpha,tau_log_alpha)T(-50,0)
alpha[Area]<-exp(log_alpha[Area])
log_K[Area]~dnorm(mu_log_k,tau_log_k)
K[Area]<-exp(log_K[Area])
}

#uninformative prior on K
mu_log_k~dnorm(4,15)
log_tau_log_k~dnorm(0.2,100)
tau_log_k<-exp(log_tau_log_k)
log_k~dnorm(mu_log_k,tau_log_k)

# Process error on SR (post larvae to age 0)
log_sigma2_SR ~ dunif(-10,10)
sigma2_SR  <- exp(log_sigma2_SR)
Tau_SR <- 1 / sigma2_SR

# Initialisation of the number at all ages for year 1 (x1000)
for(z in 1:max.z)
{
mean_logN1_NoSpace[1,z]<-log(sum(N1[,1]*N1_inits_dummy[,,z]))  #same  as  doing  sums
of regional nurseries withing each adjacent region
Na1[1,z] ~  dlnorm(mean_logN1_NoSpace[1,z], Tau_P)
N[1, 1,z]  <- Na1[1,z]
P[1,1,z] <- 1
}

for(a in 2:max.a)
{
       for(z in 1:max.z)
       {
       Na1[a,z] ~ dunif(1.0E-7, 1.0E7)
       N[a,1,z] <- Na1[a,z]
       P[a, 1,z] <- 1
       }
}

# Initialisation of number of Age 0 and Age 1 on Areas for year 1
# No need for age 0 as it is correlated to Larvae
for(Area in 1:max.Area)
{
N1[Area,1] ~ dunif(1.0E-7, 1.0E7)
}
```

```
# Population dynamics
#  ---------------------------

# Process error on dynamic equations (to speed up the sampling process)
# (correponds to a (very low) Normal variability in the natural mortality)
Tau_P <- 1000

#Dirichlet multinomial on larvae allocation, same results as fixed matrix
corr<-0.001 #dispersion coefficient

for(z in 1:max.z)
{
eta[z]<-(1/corr)-1
eps[z]<-0.01
}

for(t in 1:max.t)
{
    for(z in 1:max.z)
    {
    eta_star[t,z]<-Eggs[t,z]*(eta[z]+1)/(eta[z]+Eggs[t,z])-1
        for(Area in 1:(max.Area+1))
        {
        a[Area,t,z]<-Key_6[Area,t,z]*eta_star[t,z]+eps[z] #peut etre tirer une
moyenne mu[Area,t,z] sur la key
        }
    theta1[1:(max.Area+1),t,z]~ddirich(a[1:(max.Area+1),t,z])
        for(Area in 1:max.Area)
        {
        Larvae_inc[Area,t,z]<-Eggs[t,z]*theta1[Area,t,z]
        }
    }

    for(Area in 1:max.Area)
    {
    Larvae_EConly[Area, t]<-sum(Larvae_inc[Area,t,])
    Larvae[Area,t]<-Larvae_EConly[Area,t]+Larvae_NS[Area,t] #add NS larvae, in
data

    # Berverton&Holt recruitment function --> age 0
    L_star[Area,t] <- Larvae[Area,t] / Sstar[Area]
    mean_N0[Area,t] <- (K[Area] * L_star[Area,t]) / ((K[Area]/alpha[Area])+
L_star[Area,t])
    mean_logN0[Area, t] <- log(mean_N0[Area, t])
    LogN0[Area, t] ~ dnorm(mean_logN0[Area, t], Tau_SR)
    resSR[Area,t] <- LogN0[Area, t] - mean_logN0[Area, t]
    N0[Area, t] <- exp(LogN0[Area, t])*Sstar[Area] #on passe en global

    # Survival to age 1 (quasi deterministic)
    mean_LogN1[Area, t+1] <- log(N0[Area, t] * exp(-M0[Area] * (1-
(obsJuvtime/12))))
    N1[Area, t+1] ~ dlnorm(mean_LogN1[Area, t+1], Tau_P)
    }

S_yoy[t] <- sum(N0[,t]) / sum(Larvae[,t]) #global survival of YoY

    for(z in 1:max.z)
    {
    # Sum age 1 over space (quasi deterministic)
        for(area in 1:max.Area)
        {
        N1_out[area,z,t+1]<-N1[area,t+1]*conn_JA[area,z] #conn_JA=connectivity
matrix from nurse areas to adult zones in data
        }
    mean_logN1_NoSpace[t+1,z] <- log(sum(N1_out[,z,t+1]))
    N[1, t+1,z] ~ dlnorm(mean_logN1_NoSpace[t+1,z], Tau_P)
    P[1, t+1,z] <- 1
```

```
        # Dynamic equation - Age 1 : max
        # (quasi deterministic)

        # N by cohorts
                for(a in 1:(max.a))
                {
                Row[a, t,z] <- step(t - a - 1) * (1) + step(a - t) * (a - t +1)
                Col[a, t,z] <- step(t - a - 1) * (t - a + 1)  + step(a - t) * (1)
                N_C[a, t - a + max.a,z] <- N[a,t,z]
                }

                for(a in 1:(max.a-1))
                {
                log_mean_P[a + 1, t + 1,z] <- log(P[a,t,z] * exp(-M[a]-F[a,t,z]) )
                P[a + 1, t + 1,z] ~ dlnorm(log_mean_P[a + 1, t + 1,z], Tau_P)
                #N[a +1 , t +1,z] <-  P[a +1, t +1,z] * N[Row[a, t,z], Col[a, t,z],z]
                alpha_manty[a+1,t+1,z]<-P[a  +  1,  t  +  1,z]*(N[Row[a,  t,z],  Col[a,
t,z],z]+1)+0.1
                beta_manty[a+1,t+1,z]<-(1-P[a  +  1,  t  +  1,z])*(N[Row[a,  t,z],  Col[a,
t,z],z]+1)+0.1

        p_manty[a+1,t+1,z]~dbeta(alpha_manty[a+1,t+1,z],beta_manty[a+1,t+1,z)
                N[a +1 , t +1,z]<-p_manty[a+1,t+1,z]*N[Row[a, t,z], Col[a, t,z],z]
                }
        }

        # Fecundity (relation weight-at-age <-> number of eggs)
        #(W_Stock in the data)
        for(a in 1:max.a)
        {
        Fec[a, t] <- exp(A_eggs + B_eggs * log(W_Stock[a, t] * 1000))
        }

  # SSB
        for(z in 1:max.z)
        {
                for(a in 1:max.a)
                {
                W_Nb[a, t,z] <- N[a,t,z] * W_Stock[a, t] * step(a - 3)
                }
      SSB[t,z] <- sum(W_Nb[,t,z])
      }
        SSBtot[t]<-sum(SSB[t,])

        # Number of eggs (x 1000) (After P_Period% mortality ~ spawning period)
        for(a in 1:max.a)
        {
                for(z in 1:max.z)
                {
                Nb_eggs[a,  t,z]  <-  N[a,  t,z]  *  exp(P_Period[t]*(-M[a]-F[a,t,z]))  *
Pf[a] * Fec[a,t] * step(a - 3)
                }
        }

        for(z in 1:max.z)
        {
        Eggs[t,z] <- sum(Nb_eggs[ ,t,z])
        }

} # end loop on years

# For max.t+1, we use catches and fecundity of the previous year
for(a in 1:max.a)
{
    for(z in 1:max.z)
    {
```

```
       Nb_eggs[a,  (max.t  +  1),z]  <-  N[a,  (max.t  +  1),z]  *  exp(P_Period[max.t]*(-
M[a]-F[a,max.t,z])) * Pf[a] * Fec[a,max.t] * step(a - 3)
       }
}


#  Observation equations
#  ------------------------------
#observation variances fixed in data
# Catches

sigma2LogC  <- log(CV_C*CV_C+1)
tauLogC<- 1/sigma2LogC

# Abundance Indices

sigma2LogIA_UKCBT<-log(CV_IA_UKCBT*CV_IA_UKCBT+1)
tauLogIA_UKCBT<-1/sigma2LogIA_UKCBT

sigma2LogIA_BECBT<-log(CV_IA_BECBT*CV_IA_BECBT+1)
tauLogIA_BECBT<-1/sigma2LogIA_BECBT

sigma2LogIA_UKBTS<-log(CV_IA_UKBTS*CV_IA_UKBTS+1)
tauLogIA_UKBTS<-1/sigma2LogIA_UKBTS

sigma2LogIAJuv<-log(CV_IAJuv*CV_IAJuv+1)
taulogIAJuv <- 1/sigma2LogIAJuv


# Catches  (X 1000)
for(t in 1:(max.t))
{
       for(a in 1:max.a)
       {
              for (z in 1:max.z)
              {
              C_mean[a, t,z] <-   (N[a, t,z] * ( F[a, t,z] / (F[a, t,z] + M[a]))   *
(1 - exp(-1 * (M[a] + F[a, t,z]))) )
              C_meancor[a, t,z] <- C_mean[a,t,z] * exp(- 0.5*sigma2LogC)
              logCmean[a,t,z]<-log(C_meancor[a,t,z])
             }
    Cmeantot[a,t] <- sum(C_meancor[a,t,])
       }
       for (z in 1:max.z)
       {
              for(a in 1:10)
              {
              C_obs_spat[a,t,z] ~ dlnorm(logCmean[a,t,z], tauLogC)
              }
       C_mean11Plus[t,z] <- sum(C_meancor[11:max.a,t,z])
       logC_mean11Plus[t,z] <- log(C_mean11Plus[t,z])
       C_obs11Plus_spat[t,z] ~ dlnorm(logC_mean11Plus[t,z], tauLogC)
       }
}

for(t in 1:(max.t))
{
       for (z in 1:max.z)
       {
       C_meanzon[t,z]<-sum(C_meancor[,t,z])
      }
}

# Abundance indices CBT at EC scale
for(t in 1:(max.t))
{
       for(a in 2:max.a)
       {
```

```
        #Abundance indices including selectivity of the fishery
        #SelecQ[a] included in q[a]

        #BECBT
        log_IA_BECBT[a,  t]  <-  log(q_BECBT[a]  *  sum(N[a,  t,]))          #whole  EC
        BECBT[a, t] ~ dlnorm(log_IA_BECBT[a, t], tauLogIA_BECBT)


        #UKCBT
        log_IA_UKCBT[a, t] <- log(q_UKCBT[a] * sum(N[a, t,]))      #whole EC
        UKCBT[a, t] ~ dlnorm(log_IA_UKCBT[a, t], tauLogIA_UKCBT)
        }
}

#Spatial abundance indices
for(t in 1:max.t)
{
        for(z in 1:max.z)
        {
                for(a in 2:10)
                {
                log_IA_UKBTS[a,t,z]<-log(q_UKBTS[a]*N[a,t,z]) #q specifique
                IA_spatial_obs[a,t,z]~dlnorm(log_IA_UKBTS[a,t,z], tauLogIA_UKBTS)
                }
        }
}

# Abundance for juveniles
for(Area in 1:max.Area)
{
        for(t in 1:max.t)
        {
        log_N0[Area, t] <- log(q_0 * N0[Area, t]/Sstar[Area]) #par surface
        IA_Age0[Area, t] ~ dlnorm(log_N0[Area,t], taulogIAJuv)
        resIA_Age0[Area,t] <-     log(IA_Age0[Area, t]) - log_N0[Area, t]
        log_N1[Area,    t]    <-    log(q_1    *    N1[Area,t]/Sstar[Area]    *    exp(-
(M[1]+mean(F[1,t,]))*(obsJuvtime/12)))
        IA_Age1[Area,t] ~ dlnorm(log_N1[Area,t], taulogIAJuv)
        resIA_Age1[Area, t] <-    log(IA_Age1[Area, t]) - log_N1[Area, t]
        }
sdAge0[Area] <- sd(resIA_Age0[Area, ])
sdAge1[Area] <- sd(resIA_Age1[Area, ])
#Residuals of the SR relationship
sdSR[Area] <- sd(resSR[Area,])
}

# Number of eggs
# /! Eggs_obs of year 1991 = Eggs_spawned by SSB of year 1990
# Here, eggs observed only at year 10, so for t = 9
for(t in 1:(max.t))
{
log_Eggs[t] <- log(sum(Eggs[t,]))
Eggs_obs[t] ~ dlnorm(log_Eggs[t], 20)
}
#End of model
```