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# Réponses adaptatives des anguilles tempérées à l'hétérogénéité environnementale : mécanismes évolutifs, menaces liées au changement global et conséquences pour la conservation

Maria Mateo Santos

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**Réponses adaptatives des anguilles tempérées à  
l'hétérogénéité environnementale : mécanismes évolutifs,  
menaces liées au changement global et conséquences  
pour la conservation**

Par María MATEO SANTOS

Sous la direction de : Hilaire DROUINEAU

(co-encadrement : Patrick LAMBERT et Stéphane TETARD)

Soutenue le 16 novembre 2017

Membres du jury :

M. RIVOT, Etienne (Maître de Conférences, Agrocampus Ouest)

M. SECOR, David (Professeur, Université de Maryland, U.S.)

Mme. CAM, Emmanuelle (Professeur, Université de Toulouse 3)

M. FEUNTEUN, Eric (Professeur, MNHN)

Mme. NEVOUX, Marie (Chercheur, INRA)

M. DROUINEAU, Hilaire (Ingénieur de recherche, Irstea)

M. TETARD, Stéphane (Ingénieur, EDF R&D)

Rapporteur

Rapporteur

Examinatrice

Examinateur

Examinatrice

Directeur de thèse

Invité



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**Adaptive responses of temperate eels to environmental  
heterogeneity: evolutionary mechanisms, threats due to  
global change and implications for conservation**

By María Mateo Santos

Thesis Director: Hilaire Drouineau

(co-supervision: Patrick Lambert and Stéphane Tétard)

Dissertation date: 16<sup>th</sup> November 2017

Jury members:

Researcher Etienne Rivot (Agrocampus Ouest, France)

Professor David Secor (University of Maryland, U.S.)

Professor Emmanuelle Cam (University of Toulouse 3, France)

Professor Eric Feunteun (MNHN, France)

Researcher Marie Nevoux (INRA, France)

Research engineer Hilaire Drouineau (Irstea, France)

Engineer Stéphane Tétard (EDF R&D, France)

Reviewer

Reviewer

Examiner

Examiner

Examiner

Thesis Director

Invited

*“According to Darwin’s Origin of Species, it is not the most intellectual of the species that survives; it is not the strongest that survives; but the species that survives is the one that is able best to adapt and adjust to the changing environment in which it finds itself.”*

Leon Megginson, Lessons from Europe for American business.

# Résumé étendu

## ► Chapitre 1 : Introduction générale

Différents mécanismes peuvent émerger comme réponse adaptative à l'hétérogénéité environnementale. Cette question de l'adaptation à l'hétérogénéité environnementale est particulièrement intéressante pour les anguilles tempérées, trois espèces catadromes et panmictiques qui se reproduisent en mer de Sargasses (l'anguille Européenne et l'anguille Américaine) (Schmidt, 1923; McCleave, 1993) et à l'ouest des îles Mariannes (l'anguille japonaise) (Tsukamoto, 1992). Cette reproduction est ensuite suivie d'un transport passif des larves par les courants océaniques jusqu'aux eaux continentales du Maroc à la Norvège pour l'anguille Européenne (Tesch, 2003), du Venezuela au Groenland pour l'anguille Américaine (Helfman *et al.*, 1987) et du nord des Philippines à la Corée pour l'anguille Japonaise (Tsukamoto, 1992). Ces particularités, panmixie et longue dérive larvaire, sont des freins à l'adaptation locale. Pour autant, des patrons d'histoire de vies corrélées aux gradients environnementaux sont observés à l'échelle de l'aire de répartition et à l'échelle des bassins versants. Une hypothèse est que, à défaut d'adaptation locale, ces patrons puissent émerger de réponses adaptatives à l'hétérogénéité environnementale sous la forme de plasticité phénotypique (Vollestad, 1992; Daverat *et al.*, 2006; Edeline, 2007; Geffroy and Bardonnnet, 2012), mais aussi de polymorphismes génétiques soumis à de la sélection spatialement variable et à de la sélection d'habitat sous influence génétique (Côté *et al.*, 2009, 2014, 2015; Pujolar *et al.*, 2011; Gagnaire *et al.*, 2012; Boivin *et al.*, 2015; Pavey *et al.*, 2015).

Comprendre les mécanismes adaptatifs qui expliquent la diversité phénotypique est essentiel pour la conservation et gestion des espèces (Brodersen and Seehausen, 2014). Les populations d'anguilles sont en déclin depuis les années 80-90, à tel point que l'anguille Européenne est classée aujourd'hui en danger critique d'extinction dans la liste rouge de l'UICN (Freyhof and Brooks, 2011) et les anguilles Américaine et Japonaise sont classées comme menacées (Jacoby *et al.*, 2014; Jacoby and Gollock, 2014a). Plusieurs facteurs ont été proposés pour expliquer ces déclin (Jacoby *et al.*, 2015), notamment les changements océaniques (Castonguay *et al.*, 1994), la contamination et la dégradation de l'habitat (Byer *et al.*, 2015; Belpaire *et al.*, 2016), le parasitisme (Feunteun, 2002), les pêcheries (Dekker, 2003a), la fragmentation et la perte massive d'habitat (Kettle *et al.*, 2011) et la mortalité induite par les turbines des centrales hydroélectriques (Castonguay *et al.*, 1994). Compte tenu de cette situation, les mesures de conservation se sont multipliées pour les trois espèces. La forte hétérogénéité spatiale des pressions anthropiques sur les populations combinée à la variabilité

phénotypique spatiale à l'échelle des bassins versants et de l'aire de répartition sont des défis majeurs pour la gestion de ces espèces.

Dans le contexte du changement global et des déclin des trois espèces, l'objectif principal de cette thèse était d'explorer l'écologie évolutive des anguilles tempérées pour comprendre les mécanismes impliqués dans leurs capacités d'adaptation à la variabilité environnementale et la manière dont ces capacités interagissent avec les pressions anthropiques. Dans ce but, la dynamique des populations d'anguilles a été analysée afin (i) de mieux comprendre les mécanismes évolutifs impliqués dans l'adaptation à l'hétérogénéité environnementale et de (ii) quantifier les effets de pressions anthropiques en prenant en compte ces mécanismes pour améliorer la conservation des anguilles tempérées.

## ► Chapitre 2

Dans ce contexte, une première approche de modélisation a été mise en œuvre dans le deuxième chapitre. GenEvEel (*Genetics & Evolutionary Ecology-based model for Eel*), la nouvelle version d'EvEel (Drouineau *et al.*, 2014), est un modèle individu-centré. Le modèle repose sur un postulat d'optimisation de fitness et vise à explorer le rôle des mécanismes adaptatifs dans l'émergence des patrons spatiaux d'histoire de vie chez l'anguille. Ce modèle fait suite aux observations de Côté *et al.* (2015), en ajoutant au modèle EvEel un polymorphisme génétique sur la croissance, via le distinguo entre des individus à croissance lente et des individus à croissance rapide. Ainsi, chaque individu est caractérisé par un taux de croissance ; en cherchant à maximiser la fitness espéré, il détermine son sexe, sélectionne son habitat de croissance dans un bassin versant, puis mature à une longueur optimale. En utilisant les paramètres de la littérature, le modèle est capable de reproduire les patrons spatiaux observés dans les bassins versants : à la fois ceux sur les traits de vie, mais aussi ceux sur la distribution des génotypes. Une exploration numérique a été réalisée pour déterminer dans quelles combinaisons des paramètres tous les patrons spatiaux sont reproduits et montre que ces patrons sont respectés à condition que les individus à croissance lente ne soient pas trop pénalisés par rapport aux individus à croissance rapide.

Nos résultats suggèrent que la sélection de l'habitat dépendant du génotype et la plasticité phénotypique peuvent être deux mécanismes adaptatifs complémentaires qui permettent à l'anguille de faire face à un environnement hétérogène. Le choix de l'habitat de croissance est le résultat du croisement entre les caractéristiques de l'environnement, le génotype de l'individu et la compétition intraspécifique. La plasticité phénotypique joue un rôle important dans la variabilité des traits d'histoire de vie et d'attributs démographiques induits par

l'environnement. Nos résultats aident à la compréhension de différentes stratégies de vie selon le sexe. Ils suggèrent que les individus choisiront leur stratégie selon leur croissance, qui elle-même présente une base génétique. Les individus à croissance rapide ont une mortalité plus élevée et choisissent préférentiellement des habitats à forte densité, une stratégie du temps minimal est favorisée. Les individus à croissance lente ont une mortalité intrinsèque plus faible et choisissent des habitats à plus faibles densités ce qui favorise une stratégie de taille maximale.

La question immédiate est de comprendre la répercussion des pressions anthropiques sur la population, car si elles peuvent être une source de mortalité accrue, elles peuvent également affecter les traits d'histoire de vie (taille à maturité) et les attributs démographiques (sexe-ratio) en jouant sur les effectifs et donc les mécanismes densité-dépendants ou sur les habitats accessibles, voir en affectant plus certains types d'individus que d'autres. Les conséquences de ces pressions seront différentes selon la nature des mécanismes adaptatifs qui modifient les caractères des individus : en favorisant des individus à croissance rapide (ou lente), en modifiant le sexe-ratio, la longueur à l'argenture ou la distribution spatiale.

Ces résultats ont fait l'objet d'un premier article publié au *Canadian Journal of Fisheries and Aquatic Sciences* (2017) : Mateo M., Lambert P., Tétard S., Castonguay M., Ernande B. et Drouineau H. « Cause or consequence? Exploring the role of phenotypic plasticity and genetic polymorphism in the emergence of phenotypic spatial patterns for the European eel ».

### ► Chapitre 3

Compte tenu de l'état actuel des anguilles tempérées et comme mentionné précédemment, les mesures de conservation se sont multipliées. Pour autant, celles-ci se limitent souvent à viser à une baisse globale des mortalités anthropiques, sans regarder plus finement les conséquences en termes de traits d'histoire de vie et d'attributs démographiques. Dans ce contexte, une méthode est indispensable pour évaluer l'impact des pressions anthropiques et donner des éléments pour prioriser les actions de gestion. L'objectif du troisième était d'explorer l'effet des pressions anthropiques en allant au-delà des études existantes, c'est à dire en ne se limitant pas à quantifier les mortalités directes ou le nombre de survivants (on parle d'échappement à la dévalaison) mais aussi en regardant les conséquences sur les attributs démographiques de cet échappement.

Ainsi, GenEveel a été adapté pour intégrer l'effet des pressions anthropiques au niveau des processus de colonisation et de dévalaison afin d'en quantifier les conséquences sur l'échappement des anguilles argentées, non seulement en termes de nombre d'anguilles, mais

aussi l'effet sur le sexe-ratio, les proportions des individus à croissance rapide/lente, la longueur à l'argenture et la production d'œufs, après une génération dans les eaux continentales soumises à différents types de pressions anthropiques. Le modèle a été donc structuré en représentant les événements et les processus du cycle de vie de l'anguille en milieux continentaux et en intégrant les effets des pressions anthropiques dans les simulations. La pêche civile et les obstacles à la montaison impactent la détermination du sexe, la sélection de l'habitat, et indirectement la survie à l'argenture. Les survivants sont ensuite impactés par des pêcheries d'anguilles argentées et des turbines qui tuent les migrantes en dévalaison. Une exploration numérique a permis de comparer les effets de différentes pressions anthropiques sur la population.

Nos résultats montrent que les impacts globaux sont complexes et que ce n'est pas forcément la pression qui tue le plus d'anguilles qui a le plus gros impact sur la biomasse féconde ou la production d'œufs. Nos résultats démontrent surtout que la plasticité permet de compenser les effets de certaines pressions (pêche civile et obstacles à la montaison) et est source de résilience pour la population, alors que d'autres pressions ne bénéficiaient d'aucun effet de compensation (pêche argentée et turbines à la dévalaison). La plupart des pressions, sauf la pêche civile, favorisent les individus à croissance rapide par rapport aux individus à croissance lente, démontrant que les pressions anthropiques peuvent être des pressions sélectives pour la population d'anguilles. Compte tenu du désavantage évolutif apparent des individus à croissance lente, on peut se demander comment ces individus ont pu être conservés par la sélection naturelle. Une explication plausible pourrait être que la plupart des femelles sont des individus à croissance lente avec une forte fécondité, ce qui peut devenir encore plus important dans un contexte de déclin de la population.

Afin d'explorer la question sur la préservation des individus à croissance lente et rapide au cours des générations, un modèle multigénérationnel à l'échelle de l'aire de distribution est nécessaire. Cela permettra d'étudier les conditions dans lesquelles la plasticité phénotypique et le polymorphisme génétique peuvent être sélectionnés comme réponse à l'hétérogénéité environnementale et d'aborder l'échelle de la population plutôt que l'échelle du bassin versant.

Ces résultats ont fait l'objet d'un deuxième article publié au Fisheries and Research (2017) : Mateo, M., Lambert, P., Tétard, B., Drouineau, H., « Impacts that cause the highest mortality of individuals do not necessarily have the greatest influence on temperate eel escapement ».



## ► Chapitre 4

Un des postulats sur lequel reposent EvEel et GenEvEel est que la plasticité phénotypique chez l'anguille est une réponse adaptative émergeant de la sélection naturelle. Cela implique qu'elle a, au moins un moment, procuré un avantage évolutif supérieur aux coûts liés. Ce postulat est indispensable pour justifier l'utilisation d'une approche d'optimisation de la fitness dans la simulation des processus biologiques de ces modèles, mais doit être validé. Dans ce contexte, Maxime Olsommer, étudiant M2 en Biologie Marine (Nice), a réalisé un stage dont l'objectif était d'explorer dans quelles conditions, la plasticité phénotypique a pu être sélectionnée, puis de voir si, dans un contexte d'effondrement de population comme celui que connaît l'anguille, la plasticité reste adaptative ou non.

MaxEel, un modèle individu-centré, a été développé afin de simuler l'évolution de normes de réaction, c'est-à-dire le range des phénotypes qu'un génotype peut produire en fonction des conditions environnementales, et de voir dans quelles conditions ces normes deviennent plastiques. Le modèle considère une population panmictique d'anguilles dont les individus colonisent aléatoirement trois bassins-versants contrastés en termes de croissance et de survie (selon la température du milieu). Dans le modèle, chaque individu est caractérisé par une norme de réaction propre (une longueur à argenture par bassin-versant) plus ou moins plastique (variance de ces longueurs à maturité). Au sein des bassins-versants, les individus ont une dynamique assez proche de celle décrite dans GenEveel : une croissance selon une courbe de von Bertalanffy, une survie densité-dépendante, et une maturation quand la taille à maturité (définie dans leur norme en fonction de leur bassin versant de résidence) est atteinte. Par contre, contrairement à GenEveel et Eveel, les bassins-versants ne sont constitués que d'une seule cellule (pas de gradient amont-aval), et contrairement à GenEveel, le polymorphisme sur les taux de croissance n'a pas été pris en compte. De plus, dans ce premier essai, seules les femelles ont été modélisées.

Les individus ayant survécu jusqu'à la taille à maturité se reproduisent ensemble. Les descendants possèdent la même norme que leur mère, avec une possible mutation aléatoire autour de cette norme. L'ensemble des individus produits au cours d'un pas de temps (une année) sont ensuite répartis aléatoirement au sein des trois bassins-versants, mimant ainsi une dérive larvaire aléatoire. L'opération est répétée sur plusieurs générations et les normes de réactions sélectionnées dans la population finale sont analysées. Les indicateurs choisis pour explorer l'évolution de la norme de réaction sont : la variance et l'amplitude des normes de réaction, et le coût qui y est lié. Une exploration numérique a été réalisée afin de déterminer l'impact de (i) la répartition des larves entre bassins-versants (soit homogène, soit biaisée vers

l'habitat le plus favorable, soit biaisée vers l'habitat le moins favorable), (ii) le degré d'hétérogénéité entre les environnements (contrastes plus ou moins forts des taux de croissance et de survie), (iii) la densité-dépendance (mortalité densité-dépendante plus ou moins forte), (iv) l'intensité de coût de plasticité et (v) le type de coût (maintenance ou production) de la plasticité sur l'émergence de la norme de réaction.

Sans surprise, c'est l'intensité de coût qui a l'effet le plus fort sur l'émergence ou non de la plasticité, c'est-à-dire le niveau de la variance de la norme de réaction. Ce résultat est logique puisque l'intensité du coût joue directement dans le trade-off avantage évolutif versus coût qui gouverne l'émergence de la plasticité (Pigliucci, 2005). Le second paramètre qui influence le plus est l'intensité de la densité-dépendance. Cela correspond bien aux résultats d'Ernande and Dieckmann (2004), qui avait démontré que la densité-dépendance était un facteur favorisant la plasticité phénotypique. Le type de coût représente le troisième paramètre plus impactant, les normes sont plus plastiques quand les coûts sont plus liés à des coûts de production plutôt qu'à des coûts de maintenance. Le degré d'hétérogénéité entre les bassins versants et la répartition des larves ont un effet moins important et quelques interactions peuvent moduler la valeur adaptative de la réponse plastique.

Les scénarios avec une intensité de densité-dépendance nulle peuvent aussi être interprétés comme des situations où la compétition intraspécifique devient négligeable, ce qui est le cas quand la population s'est effondrée. Dans les scénarios sans densité-dépendance, la plasticité phénotypique est encore présente, mais très largement atténuée (les normes sont beaucoup moins variables). Cela montre que la plasticité présente encore un avantage évolutif, y compris dans un contexte d'effondrement de la population, mais que la plasticité sélectionnée dans un contexte de forte d'abondance est sans doute trop forte dans un contexte d'effectifs réduits, engendrant des coûts superflus, ce qui à défaut d'être une mal-adaptation, n'est pas une situation optimale.

Finalement, un modèle démo-génétique a été décrit afin de déterminer dans quelles conditions écologiques, la plasticité phénotypique et le polymorphisme génétique (i) pourraient être sélectionnés par l'évolution et (ii) pourraient être maintenus dans le contexte actuel des populations effondrées. Les conditions écologiques à explorer sont: le gradient de température entre les bassins versants (comme un gradient latitudinal qui représente l'aire de distribution des anguilles), la variabilité spatiale dans les bassins versants (c'est-à-dire le gradient en amont et l'aval) et les paramètres démographiques, tels que l'abondance de la population. Pour analyser l'émergence évolutive de la plasticité phénotypique, nous explorons également l'effet

de ses coûts, car ils constituent des contraintes majeures pour l'avantage sélectif de ce mécanisme.

Cette nouvelle version est basée sur certains aspects de GenEveel afin de reproduire la phase continentale et de MaxEel afin de représenter la phase océanique. La nouveauté du modèle réside dans le codage génétique des traits quantitatifs ainsi que sa transmission à la descendance. Chaque individu est initialement caractérisé par un taux de croissance intrinsèque, une fertilité, et des paramètres décrivant sa norme de réaction (longueur à l'argenteure). Les descendants héritent de ses parents la valeur génétique de chaque un de ces traits, et une valeur stochastique est associée en représentant un bruit environnemental non hérité.

Le modèle couvre tout le cycle de vie des anguilles tempérées. Les descendants issus de la reproduction sont distribués aléatoirement parmi les trois bassins versants et ils sont affectés par la mortalité lors de la dérive larvaire. Cette mortalité dépend des caractéristiques intrinsèques des larves, de la durée de la dérive et de la température de l'eau. Lorsqu'ils pénètrent dans les eaux continentales, les individus sélectionnent leur habitat de croissance (saumâtre ou eau douce dans la rivière) et déterminent leur sexe (femelle ou mâle) en cherchant à maximiser la fitness attendue. Ensuite, les individus grandissent et meurent au cours de la phase continentale, avec une croissance et une mortalité qui dépendent des caractéristiques des individus, de l'habitat et de la densité-dépendance. Lorsqu'ils atteignent une longueur à l'argenteure, définie par une norme de réaction dépendante de l'environnement, ils migrent pour se reproduire. Les descendants héritent une partie des attributs de leurs parents et le cycle recommence. Le cycle est répété jusqu'aux patrons spatiaux sont stabilisés. Comme dans GenEveel, une approche par patron spatial est définie au sein des bassins versants (caractérisés par deux habitats, aval et amont), et entre bassins versants.

Ce modèle reste un prototype et n'a pas pu être utilisé au cours de cette thèse ; l'ODD présenté ici est donc susceptible d'être modifié dès que les premiers résultats seront disponibles. La présentation de ce modèle répond à différents objectifs. D'abord, le modèle résume les connaissances sur le fonctionnement de la population de l'anguille acquis à la fin de cette thèse, et en particulier sur son adaptation à l'hétérogénéité environnementale. Il est basé sur la compréhension de l'adaptation obtenue avec GenEveel, combiné avec la dynamique de la population à l'échelle de l'aire de répartition, ce qui donne une perspective évolutive en complétant le cycle de vie et en permettant des simulations multigénérationnelles. Finalement, la présentation du modèle permet de présenter les perspectives de ce doctorat, notamment les applications du modèle afin d'explorer différentes

questions sur l'effet des pressions anthropiques, de la résilience de la population ou des mesures de conservation.

## ► **Chapitre 5 : Discussion et perspectives**

Malgré le grand intérêt pour les anguilles tempérées et la littérature scientifique sur des aspects particuliers et la dynamique de population de ces espèces, la compréhension des mécanismes adaptatifs des anguilles face à l'hétérogénéité environnementale a connu des avancées très récentes. Depuis longtemps, de nombreuses études ont montré des corrélations entre les traits d'histoire de vie et des gradients environnementaux, comme la longueur à l'argenture, le sexe-ratio, et les effets de la densité sur la croissance. Récemment, d'autres études expérimentales ont mis en évidence la base génétique de la variation des traits d'histoire de vie comme la croissance et des corrélations entre les conditions environnementales et l'expression génétique. Cependant, peu d'études ont analysé toutes ces observations simultanément afin de trouver une signification adaptative commune.

Ce doctorat rassemble toutes les connaissances disponibles sur l'histoire de vie des anguilles afin d'analyser les caractéristiques vitales de cette espèce pendant sa phase continentale. À l'aide des modèles, nous avons donné un sens à toutes ces observations. Nous avons pu proposer un schéma général des mécanismes d'adaptation impliqués dans la réponse à l'hétérogénéité environnementale et fournir de nouvelles pistes pour la gestion.

Basé sur les résultats du deuxième et troisième chapitre, le chapitre quatre propose un modèle qui résume notre compréhension actuelle de cette espèce énigmatique. Ce type de modèle est un outil pertinent pour évaluer l'influence du changement global sur la population d'anguilles et pour informer les politiques de gestion et de conservation. Ce modèle est aussi utile pour illustrer comment la conservation de la diversité génétique et de l'habitat est cruciale pour la viabilité des espèces. C'est un bon candidat pour explorer la pertinence des stratégies de gestion, comme le repeuplement qui est l'une des principales mesures de gestion utilisées pour restaurer la population d'anguilles (Wickström and Sjöberg, 2014; Dekker and Beaulaton, 2016). Le modèle peut également être utilisé pour explorer le risque de sélection des traits d'histoires de vie induits par l'homme. Des recherches supplémentaires sur le rôle des pressions anthropiques comme pressions de sélection permettront d'analyser si les individus à croissance lente sont encore conservés par la sélection naturelle et artificielle.

La capacité d'adaptation des anguilles est basée sur la combinaison de la diversité génétique et la plasticité phénotypique qui sont source de la diversité des traits d'histoire de vie et permettent aux anguilles d'utiliser différents habitats. De ce fait, les anguilles représentent des

cas d'étude intéressants sur comment la diversité peut contribuer à la résilience et à la stabilité de la population. La grande variabilité des réponses à conditions environnementales pendant la phase continentale suggère que les mesures de gestion et de conservation devraient chercher à préserver la diversité des habitats, la diversité génétique et la diversité des traits de vie (Secor, 2015a). Ces diversités sont primordiales puisqu'ils sont source de *portfolio* et de *storage effects* (ICES, 2009; Secor, 2015b).

La plupart des espèces sont menacées par le changement global. Dans ce contexte il faut améliorer les connaissances sur la capacité des espèces à l'adaptation et leur vitesse d'adaptation pour orienter des stratégies de gestion et des politiques de conservation. Ces dernières années, de nombreuses études ont abordé ce sujet, en se focalisant sur les mécanismes évolutifs et les avantages de la sélection par rapport à la plasticité phénotypique sur le taux d'adaptation. Ce travail contribue à ce débat en utilisant les anguilles à titre d'exemple.

## Preface

The thesis is structured in five chapters. A “foreword” introduces the positioning of each chapter in the overall approach of the PhD and a “take home message” section summarizes the main findings and the questions raised by the corresponding chapter (except for the introduction and the discussion). The second and the third chapter are based on manuscripts that have been published on international reviewed journals:

- **Chapter 2:** Mateo M., Lambert P., Tétard S., Castonguay M., Ernande B., Drouineau H. 2017a. Cause or consequence? Exploring the role of phenotypic plasticity and genetic polymorphism in the emergence of spatial patterns of the European eel. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 987-999. doi: 10.1139/cjfas-2016-0214.
- **Chapter 3:** Mateo M., Lambert P., Tétard S., Drouineau H. 2017b. Impacts that cause the highest direct mortality of individuals do not necessarily have the greatest influence on temperate eel escapement. *Fisheries Research*, 193: 51-59. doi: 10.1016/j.fishres.2017.03.024.

Chapter four is partially based on the internship realised by Maxime Olsommer, a student (master level) that I supervised during six months in 2016 to explore the conditions in which phenotypic plasticity is adaptive. Chapter five is partially based on a manuscript submitted to *Fish and Fisheries*:

- Drouineau H., Durif C., Castonguay M., Mateo M., Rochard E., Verreault G., Youkouchi K., Lambert P. Collapse of temperate eels: when synergetic effects of the five components of global change outpace species adaptation capacity. Submitted to *Fish and Fisheries*.

Most of the contents of this work have been presented as oral presentations in international and national conferences:

- Mateo M., Lambert P., Tétard S., Drouineau H. Assessing the impact of anthropogenic pressures on temperate eels using Genetics & Evolutionary ecology-based model for eels. *13<sup>ème</sup> Colloque de l'AFH (Association Française d'Halieutique)*. Nantes (France), June 2017.
- Mateo M., Lambert P., Tétard S., Drouineau H. Assessing the impact of anthropogenic pressures on temperate eels using Genetics & Evolutionary ecology-based model for eels. *The 1<sup>st</sup> International Eel Science Symposium*. London (UK), June 2017.

- Mateo M., Lambert P., Tétard S., Drouineau H. Adaptation de l'anguille européenne à la variabilité environnementale : Mécanismes et conséquences. *Hynes meeting (Irstea-EDF team)*. Lyon (France), September 2016.
- Mateo M., Lambert P., Tétard S., Drouineau H. Genetics & Evolutionary Ecology-based model for Eel: GenEveel. *Life History Theory*, summer school. Groningen (Netherlands), September-October 2015.
- Mateo M., Lambert P., Tétard S., Drouineau H. La plasticité phénotypique adaptative et la sélection spatialement variable chez l'anguille européenne modifient-elles l'effet des pressions anthropiques sur la population ? *12<sup>ème</sup> Colloque de l'AFH (Association Française d'Halieutique)*. Montpellier (France), July 2015.
- Mateo M., Lambert P., Tétard S., Drouineau H. Consequences of adaptive phenotypic plasticity and local adaptation in the European eel: assessing population-level responses to anthropogenic pressures. *Models in Ecology and Evolution*. Montpellier (France), May 2015.

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**Chapter 1:**  
**Adaptation to environmental heterogeneity, the example of**  
**temperate eels**

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## **1.1. Species adaptation to environmental heterogeneity and new challenges due to global change**

### **1.1.1. Environmental heterogeneity: constraints and adaptive mechanisms**

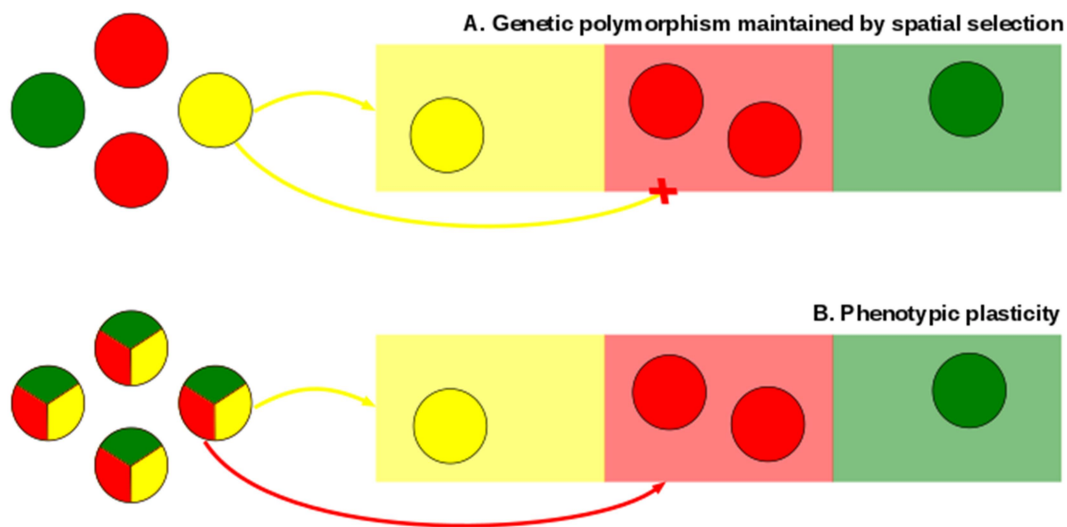
How organisms respond to their environment and the underlying mechanisms that allow these responses have always fascinated scientists. Nowadays, the Darwin evolutionary theory is the most accepted, becoming a milestone. Natural selection was defined by Darwin (1859) as the “principle by which each slight variation of a trait, if useful, is preserved”. This mechanism is based on (i) the variation of traits between individuals, (ii) the inheritance of individual variation from parents to offspring, and (iii) the competition for limited resources in a particular environment. Natural selection maintains and accumulates individual variation to allow the best reproductive success, or the expected number of offspring by individual. The increase in the frequency of this variation leads to adaptation of the population in their environment. At the individual scale, the fitness is a quantitative measure of the reproductive success of an individual, i.e. of its capacity to transmit its genotype or its phenotype to future generations.

Understanding the relationships between environmental heterogeneity of habitats and individual traits is a key issue. Environments can be heterogeneous in a variety of ways, in space and time, having different consequences on the response of individuals and influencing population dynamics. Spatial environmental heterogeneity refers to the uneven distribution of environments across a region and offer different and spatially structured habitats (Chesson, 2000; Oliver *et al.*, 2010). In such situation, individuals can choose to move between habitats (Forman, 1995), especially to find the one in which they increase their fitness by improving their growth and survival rates (Sergio and Newton, 2003). Alternatively, individuals can remain in a given habitat in which they merely survive and grow. Furthermore, natural selection that acts on an individual scale and includes the influence of environmental effects in the rate and sense of adaptation, needs to consider a coherent spatial scale with the species perception about their environments (Tews *et al.*, 2004) because they are able to detect the spatial changes in the quality of the habitat. In this context, the scale should provide the spatial region that describes the habitat (or mesohabitat) use by individuals and it is related to mobility and other life history traits (Wiens, 1989; Levin, 1992).

Individuals must adapt to changes of selective pressures induced also by temporal environmental variability. If the environment remains temporally constant, i.e. coarse grained environment, and the individuals are able to select their habitat, they will tend to be more and more adapted to a specific habitat. On the other hand, if environment is temporally variable, i.e. fine grained environment, and individuals are not able to select their habitats, they will tend to become adapted to a wide range of environmental conditions (Levins, 1968).

All organisms must adjust to conditions imposed by their environments in order to survive and reproduce. Adaptation refers to the progressive evolution of a trait that allows individuals to improve or maintain their fitness. The existence of a genetically determined phenotypic variation is necessary for the action of evolutionary processes (West-Eberhard, 2003). In fact, phenotypic differences between individuals may potentially induce differences of fitness and therefore have consequence on the evolutionary scale, favoring certain allelic variants over others. Within the mechanisms that maintain this genetic variation (soft sweeps, polygenic basis of adaptation, recurrent parallel evolution, epigenetics) (Bernatchez, 2016), balancing selection that benefits the variance of a phenotype and tends to generate or maintain genetic polymorphisms (multiple forms of a single gene), is likely to be the most useful mechanism within a population if the genetic variation is preserved by this mechanism (Whitlock, 2015). Examples of balancing selection include overdominance, frequency-dependent selection and temporal or spatial variation in selection (Mitchell-Olds *et al.*, 2007). The latter or spatially varying selection may be prevalent in species occupying heterogeneous environments (figure 1-1.A). Although this mechanism can be understood as a local adaptation because of the selective pressures imposed by the local environmental conditions, there are situations where local adaptation is impossible but adaptive genetic polymorphisms can be conserved by natural selection (Yeaman and Otto, 2011). In line with this, Bay and Palumbi (2014) studied the adaptation to climate change of table-top corals, and despite panmixia, they found genetic correlations with temperature suggesting that adaptive polymorphism would be maintained in heterogeneous habitats through balancing selection. However, phenotypic variability as a result of adaptation to heterogeneous environments is not exclusively due to genetic variability, but it may come from phenotypic plasticity or the capacity of an organism to produce different phenotypes by a single genotype in response to environmental changes (Pigliucci, 2005) (figure 1-1.B). This mechanism meets all the conditions required to be selected because it allows to increase the fitness of individuals and it can be inherited to offspring (Ernande *et al.*, 2004). Adaptive phenotypic plasticity has been demonstrated for several species (Schlichting, 1986; Sultan, 1987; Scheiner, 1993; Pigliucci, 2005). Nevertheless, there are costs associated to it: maintenance costs linked to the start-up of

sensorial receptors and regulatory mechanisms, and production costs related to the production of a specific phenotype. For been selected, the benefits provided by plasticity must therefore be greater than these associated costs (DeWitt *et al.*, 1998).



**Figure 1-1.** Schematic representations of two adaptations that deal with heterogeneous environments. The circles represent individuals with particular phenotypes (colours) in specific environments (rectangles). For example, a yellow individual can only survive in a yellow habitat, and therefore these phenotypes are determined genetically and local selection acts on them (A), or an individual can potentially express the phenotypes, and will express the phenotype corresponding to its habitat, so the phenotypes are induced environmentally by phenotypic plasticity (B).

Mechanisms of evolutionary adaptation exhibits different time-scales. Genetic evolution acts on a long time scale: the frequency of adapted genotypes will increase over generations while the frequency of maladapted genotypes will decrease or even irreversibly disappear. On the short time scale, phenotypic plasticity allows rapid and reversible phenotypic responses to environmental modifications (Charmantier *et al.*, 2008). In this situation, each individual is able to express different phenotypes with its own genotype depending on the environmental conditions. Contrary to natural selection, the phenotype is not transmitted to the offspring which remain plastic. More recently, epigenetics has proved to be an intermediate mechanism: it refers to modifications of the phenotypes without modification of the genotypes that occur at the individual scale (similarly to the phenotypic plasticity) but which are, at least partially, heritable (similarly to the genetic selection) (Bossdorf *et al.*, 2008). A possible non-genetic inheritance mechanism is the strategy of bet hedging, in which the unpredictable environmental variability favors genotypes that maximize the geometric mean of fitness, decreasing its variance (Hopper, 1999).

This thesis brings different approaches together to study the evolutionary mechanisms that determine the phenotypic variability to environmental heterogeneity and human impacts. Population genetics is the study of genetic variation within populations, investigating (genetic or phenotypic) changes in population distribution, under the influence of selective pressures (Hedrick, 2005; Hartl and Clark, 2007). R. Fisher, J. Haldane and S. Wright were the main founders of this field, conciliating Darwin's Theory of Evolution with Mendelian genetics. Evolutionary ecology focuses on how environment tend to favor specific phenotypic traits. It seeks to explain why some individual behavior, physiology or demography are more adapted to environmental conditions than others (Fox *et al.*, 2001). Therefore, by combining population genetics and evolutionary ecology, we simultaneously explain how genes control the variation of phenotypic characters and how environments influence the selection of those characters. Integrating the inheritance of phenotypic traits with the study of ecological features associated to those characters allow to determine their evolutionary potential and fitness of individuals.

Disentanglement of both mechanisms to explain the observed phenotypic variability facing to environmental heterogeneity remains a challenge that is even more crucial because human impacts on population dynamics could be different according to these evolutionary mechanisms.

### **1.1.2. Global change: a challenge for species adaptation capacities**

Global change refers to the deep modifications of ecosystems due to anthropogenic activities (Steffen *et al.*, 2005). There are five main components of global change: (i) global warming and oceanic changes, which are due to increased greenhouse gas emission by human activities (IPCC and Pachauri, 2015) and is the most well-documented, (ii) the increasing nutrient, contaminant and pesticide loads in the ecosystem due to industries, agriculture and urbanization (Verhoeven *et al.*, 2006), (iii) the fragmentation of aquatic and terrestrial ecosystems and the modification of habitats due to anthropogenic land use (Collinge, 1996; Fischer and Lindenmayer, 2007; Brook *et al.*, 2008), (iv) biological invasion and biodiversity modifications (Vitousek *et al.*, 1997; Occhipinti-Ambrogi and Savini, 2003; Ricciardi, 2007), (v) the over-exploitation of natural resources (Brook *et al.*, 2008).

In the current context of global change, one of the central questions is whether species will survive by adapting to the new environmental conditions (Lavergne *et al.*, 2010; Hoffmann and Sgrò, 2011). Indeed, the intensity and the rate of variations due to global changes are a

challenge for species adaptation (Spurgeon, 2000; Donner *et al.*, 2005; Visser, 2008; Cahill *et al.*, 2012; Urban, 2015): to survive, they must cope with the new constraints by displaying adaptive responses (Hughes, 2000). Hughes (2000) listed different responses to the global change: physiological modifications, phenological changes, modifications of distribution area or local adaptation. This question of adaptation to new conditions has been raised for a great amount of species (Collins and Bell, 2004; Hendry *et al.*, 2008; Ozgul *et al.*, 2009; Van Doorslaer *et al.*, 2009; Boutin and Lane, 2014; Charmantier and Gienapp, 2014; Crozier and Hutchings, 2014; Reusch, 2014). This thesis focuses on temperate eels' responses to environmental challenges, species that have proved strong adaptation capacities but are now considered to be critically endangered.

### **1.1.3. A conceptual framework: from life history theory to population dynamics**

In the previous section, we detailed how population genetics (gene frequency) and evolutionary ecology (trait) explore adaptation mechanisms to deal with environmental heterogeneity. Life history theory, a branch of evolutionary ecology, analyzes the evolution of all the components of fitness, or the contribution of an individual to new generations in terms of offspring (McNamara and Houston, 1992; Giske *et al.*, 1998). This theory focuses on specific life history traits, i.e. characters that affect directly the reproductive potential of an individual through its life, by modifying its survival or fecundity rates. Examples of life history traits include size at birth, growth, age and size at maturity, number and size of offspring, lifespan and reproductive investment (Roff, 1992).

Life history traits evolve as a result of the interaction between two factors (Stearns, 2000): the direct ecological impact of the trait on the life cycle of individuals and the linkage among life history traits that constrain each other, i.e. trade-offs. A classical trade-off is the onset of reproduction, which usually restricts other traits such as growth, survival and even future reproductions (Reznick, 1983). Furthermore, natural selection acts under these trade-offs that will determine a specific combination of life history traits, defining a particular strategy. These life history strategies refer to the different adaptations that control how individuals allocate their available resources in reproduction and survival in face of a particular environment (Stearns, 1992).

A classical approach to study the life history evolution is optimality (Parker and Maynard Smith, 1990). This approach studies how the design of phenotypes varies to achieve strategies that optimize fitness in a given environment (Mayhew, 2006). For example, the Optimal

Foraging Theory, described by MacArthur and Pianka (1966) postulates that natural selection favors the traits that minimize the energy expended to acquire a quantity of food. The limitations of optimality models have led to consider other theories. The Theory of Games is used to include ecological scenarios with frequency-dependence and study what happens when one or more phenotypes compete with others within a population (Maynard Smith, 1982). In this case, natural selection tends to favor the most competitive genotype. Moreover, density-dependent processes, such as the competition of resources in the space or trade-offs between survival and fecundity, are strongly linked to the fluctuations on size of the population and its productivity which determines population dynamics (Wennersten and Forsman, 2012). This is considered in the adaptive dynamics or the evolutionary invasion analysis that includes the frequency-dependent processes (from the Theory of Games) with population dynamics to examine the selective pressures induced by population fluctuations in its environment, which generates eco-evolutionary feedbacks. This kind of model studies how an increase in fitness of a phenotype will depend in the frequency of others phenotypes within the population (Mylius and Dieckmann, 1995; Dieckmann, 1997).

## **1.2. Temperate eels: three old species that display fascinating life-cycles**

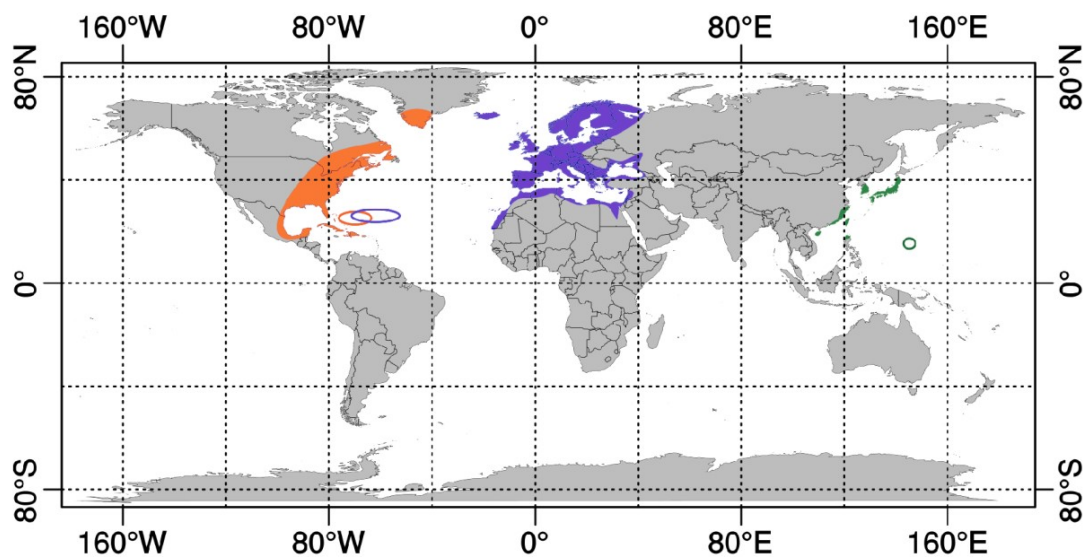
### **1.2.1. Overview of phylogeny and distribution of the species**

Freshwater eels belong to the superorder Elopomorpha, an ancient group of teleost fishes that share the leptocephalus larval stage and dwell in varied marine habitats. Among the four orders of this group, Anguilliformes comprises more than 800 species and relates to the genus *Anguilla*. The genus includes 16 species and three subspecies that occupy areas all over the world except the coasts of South Atlantic and eastern Pacific. The genus *Anguilla* or freshwater eels appeared about 50 million years (Tsukamoto and Aoyama, 1998). Freshwater eels display remarkable migrations between freshwater and marine habitats, spend most of their lives in freshwater during the growth phase while the reproduction takes place in open ocean areas. This migratory behavior, called catadromy, could be inherited from Pleistocene glaciations, during which individuals that spent time in inland waters to build energy reserves would guarantee the migration from the refuge areas to the spawning grounds (Kettle *et al.*, 2011).

According to their geographical distributions (figure 1-2), freshwater eels are divided into temperate and tropical eels. There are three temperate and 11 tropical eels. The three



temperate eels are: *Anguilla japonica* (Japanese eel) in the Pacific Ocean, *A. rostrata* (American eel) and *A. anguilla* (European eel) in the Atlantic Ocean. Spawning areas are located at tropical latitudes: the Sargasso Sea for *A. anguilla* and *A. rostrata* (Schmidt, 1923; McCleave, 1993) and west of the Mariana Islands for *A. japonica* (Tsukamoto, 1992). Their growth stage take place from Morocco to Norway (Tesch, 2003) for the European eel, from Venezuela to Greenland for the American eel (Helfman *et al.*, 1987) and from Northern Philippines to Korea for the Japanese eel (Tsukamoto, 1992). Historically, *A. japonica* appeared about 15 million years (Lin *et al.*, 2001), while *A. rostrata* and *A. anguilla* diverged about three million years ago because of the emergence of the Isthmus of Panama (Jacobsen *et al.*, 2014). Specifically, the European eel have survived strong changes until now such as ice ages and the continental drift that has separated the spawning grounds from the nursery grounds (Knights, 2003).

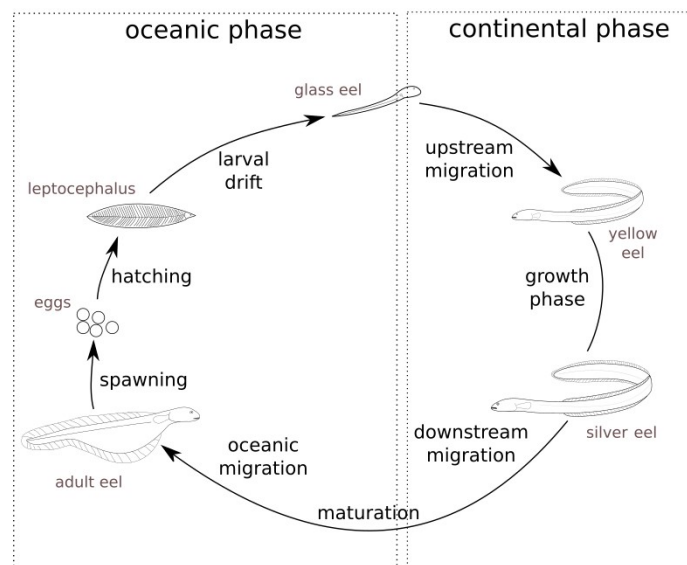


**Figure 1-2.** Distribution of temperate eels: American eel distribution is represented in orange, European eel distribution in purple and Japanese eel distribution in green. The supposed spawning grounds are indicated by circles (adapted from Drouineau *et al.*, submitted).

### 1.2.2. Description of the life cycle

The three species display very similar life history (Daverat *et al.*, 2006; Edeline, 2007). As mentioned earlier, temperate eels are catadromous species (figure 1-3). Since 1998, different studies have analyzed the ratio of strontium and calcium in otoliths of eels and showed that freshwater eels can spend their entire lifetime in brackish or saltwater, and therefore catadromy would be facultative (Tsukamoto and Arai, 2001). While reproduction takes place at sea, leptocephali larvae are subject to a long and passive trans-oceanic drift which duration is not perfectly known but estimates vary from seven months to more than two years

(Bonhommeau *et al.*, 2010). Larvae metamorphose into glass eels when arriving on the continental shelf. Then glass eels enter into continental water and progressively become pigmented yellow eels (Tesch, 2003). The continental phase that corresponds to the growth phase, lasts between three to 30 years, depending on the region and the sex (Vollestad, 1992). Under the influence of environmental factors, as temperature or photoperiod, yellow eels metamorphose again into silver eels that are ready to migrate at the end of the summer. The seaward migration stage is then triggered by environmental factors that generate stronger water discharge and low light conditions (Trancart *et al.*, 2017). Their sexual maturation is achieved while the eels migrate back to the spawning grounds. During this reproduction migration, silver eels do not eat. Consequently, they need sufficient lipid stores to achieve the migration and oocytes maturation (van Ginneken and van den Thillart, 2000; van den Thillart *et al.*, 2004; Belpaire *et al.*, 2009). The duration of this oceanic migration is still poorly known but recent observations suggest that it lasts several months and that eels make large (up to 600m) diel vertical migrations (Béguer-Pon *et al.*, 2015; Righton *et al.*, 2016). Although spawning has never been observed for the American and European eels - a first direct observation of a mature individual on the spawning ground occurred in 2012 for the Japanese eel (Tsukamoto *et al.*, 2013) - they are supposed to die after reproduction.



**Figure 1-3.** Life cycle of temperate eels (adapted from Drouineau *et al.*, submitted and Dekker, 2000a)

### 1.2.3. How does environmental variability shape life history of temperate eels?

The species capacity to occupy and use a wide range of habitats is possible due to the establishment and maintenance of a population genetic structure, the upkeep of panmixia, and the acquisition of adaptive phenotypic plasticity for several life history traits linked to the

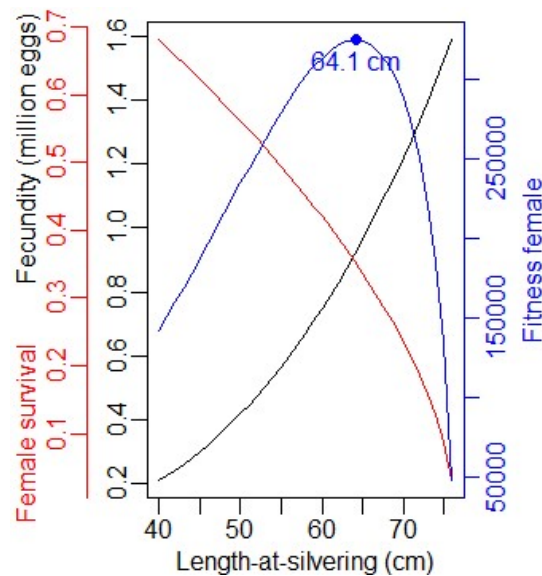
development of the species (Via and Conner, 1995; Via *et al.*, 1995; Pelletier *et al.*, 2007). Temperate eels can face very heterogeneous environments because of its large distribution area. Even at the river catchment scales, eels can be found in highly contrasted habitats: from marine waters, brackish estuaries to upstream freshwater habitats. How does the eel address this environmental heterogeneity? The three species are panmictic: all genotypes are randomly mated during the reproduction leading to a genetically uniform population (Palm *et al.*, 2009; Han *et al.*, 2010; Als *et al.*, 2011a; Côté *et al.*, 2013). Furthermore, eels cannot “select” a specific river catchment because of the passive larval drift. The combination of these panmixia and passive larval drift impairs the possibility of local adaptation by natural selection. However, life history of temperate eels is highly variable and extreme phenotypic variations, in terms of sex ratio (due to sex determination), growth rate and size at maturity are observed. Indeed, spatial patterns of life-history traits are correlated to environmental gradients at the distribution area and the river catchment scales (Vélez-Espino and Koops, 2010), raising the question of whether they are the result of adaptive responses to environmental heterogeneity.

► **Sex ratio spatial patterns: adaptive environmental sex-determination**

Sex determination begins in the yellow eel stage and is metagamic, i.e. determined by the environmental conditions (Davey and Jellyman, 2005; Geffroy, 2012; Geffroy and Bardonnnet, 2015). Environmental sex determination is promoted when the fitness of males and females differ because of environmental factors, such as temperature, density or social interactions (Devlin and Nagahama, 2002; Mayhew, 2006). The influence of density on eel sex determination has been proposed because a male-biased sex ratio is observed at high density, while females predominate at low density (Tesch, 2003). This was confirmed by observations of fluctuations of sex ratio in natural catchments as a result of density modifications (Parsons *et al.*, 1977; Poole *et al.*, 1990; De Leo and Gatto, 1996; Roncarati *et al.*, 1997; Tesch, 2003), and in controlled environment experiments (Colombo and G. Grandi, 1996; Beullens *et al.*, 1997; Holmgren *et al.*, 1997). The global quality of the environment was also proposed as a factor that affects this mechanism (Geffroy, 2012).

This question of sex-determination is especially important since males and females are supposed to have different life history strategies (Helfman *et al.*, 1987). The reproductive success of males mostly depends on their survival to a minimum length that ensure successful migration: it corresponds to time-minimizing strategy in which males maximize their fitness by minimizing the time before their reproduction, and consequently their survival rate (Vollestad, 1992; Oliveira, 1999; Van Den Thillart *et al.*, 2007). On the other hand, the

female reproductive success depends on their size, since fecundity increases with body size (Barbin and McCleave, 1997). Therefore, the reproductive success of females is the result of a trade-off between fecundity and survival to the size at maturity and females follow a size maximizing strategy. Drouineau *et al.* (2014) estimated the optimal length-at-silvering that is constrained by the trade-off of fecundity and survival (figure 1-4). Highly skewed sex ratios are observed at different spatial scales: in a latitudinal gradient, females are concentrated in the northern part of the distribution area, while males are concentrated in the southern part (Kettle *et al.*, 2011). At the catchment scale, a male biased sex ratio is observed in downstream habitats (table 1.1) (Oliveira and McCleave, 2000; Tesch, 2003).



**Figure 1-4.** Trade-off between fecundity, which increases with length-at-silvering, and survival, which decreases with length-at-silvering. The product between them estimates the resulting female fitness with the optimal length-at-silvering (Drouineau *et al.*, 2014).

► **Patterns in habitat use: an adaptive trade-off between growth and survival?**

During the growth phase of eels, growth patterns depend on numerous factors, i.e. latitude, temperature, sex, population size and habitat characteristics that vary considerably according to the habitat used by the species. The influence of latitude reveals higher growth rates at Southern latitudes, regardless of sex (table 1-1) (Oliveira, 1999). Furthermore, the distance between the spawning ground and the inland waters plays also an important role since eels can settle in a wide range of habitats (from saltwater of coasts and brackish water of estuarine to freshwater of upstream habitats or lakes) (Tsukamoto *et al.*, 1998; Daverat *et al.*, 2006; Arai and Chino, 2012). Growth in saline conditions like marshes and estuaries is higher because these habitats are more accessible and favorable in terms of resources thus, enables a high density of eels (Lobón-Cerviá *et al.*, 1995; Melià *et al.*, 2006a; Daverat *et al.*, 2012). In

the other hand, low growth is observed in upper habitats of river catchments, which would be compensated by low mortality through reduced intraspecific competition. The choice of these habitats is suggested as a conditional evolutionary strategy, in which individuals reach the same fitness adopting different migratory tactics (Edeline, 2007). However, Cairns *et al.* (2009) did not observe these variations in mortality rates between habitats.

Latitude		Life history traits and demographic attributes	Distance from the sea	
North	South		Saltwater	Freshwater
↗	↘	Proportion of females	↘	↗
↗	↘	Female size at maturity		
↗	↘	Male age at maturity		
↗	↘	Longevity		
↘	↗	VPL Growth coefficients		
↘	↗	Somatic growth rates	↗	↘
		Density	↗	↘
		Fecundity	↘	↗
		Mortality	↘	↗
		Average of seaward migration	↘	↗
		Average body size	↘	↗
		Average age	↘	↗

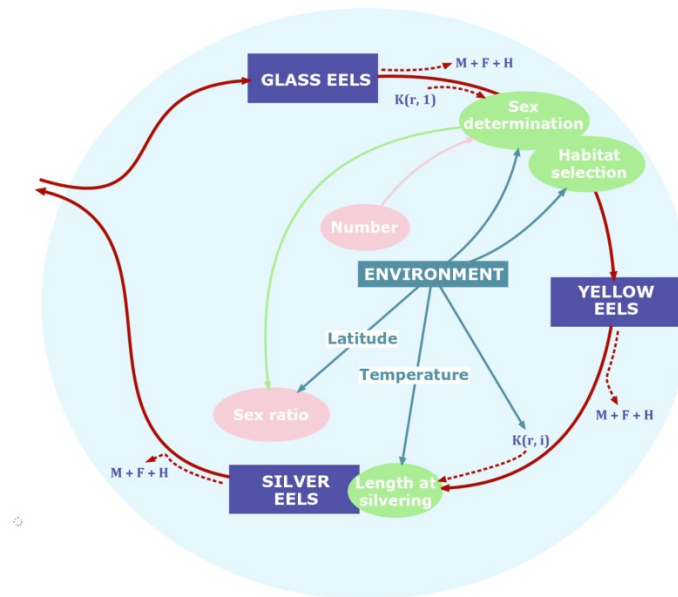
**Table 1-1.** Patterns described by Vélez-Espino and Koops (2010) about life history traits and demographic attributes through different gradients, the latitude and the distance from the sea (differentiated by saltwater and freshwater).

► **Spatial patterns in length-at-silvering: adaptive trade-off between fecundity and survival due to specific life strategies?**

Closely related to the difference in life strategies of males and females are the spatial patterns of length-at-silvering that occur at the distribution area and the catchment scales (table 1-1). The difference in strategies explain why length-at-silvering is rather constant for the males (Vollestad, 1992; Oliveira, 1999) and correlated with the latitude for the females (Helfman *et al.*, 1987; Davey and Jellyman, 2005; Jessop, 2010). In upstream habitats or in Northern habitats, length-at-silvering is generally longer than in Southern or downstream habitats. Indeed, in upstream and Northern habitats, slow growth rates are outweighed by lower mortality rates, so that females (which are predominant in such habitats) are thought to delay their maturation to increase their fecundity. Conversely, individuals (especially males) are thought to mature at smaller length to increase their survival.

Figure 1-5 summarizes the life history traits and tactics characterized by spatial patterns and correlated to environmental gradients. It also outlines the possible relationships between

traits, tactics and demographic parameters that are influenced by environmental conditions and that would be maintained by adaptive mechanisms.



**Figure 1-5.** Life cycle of temperate eels with life history traits and tactics that show spatial patterns depending on different environmental factors. In each stage, the individual mortality (M: natural mortality, F: fishing mortality, H: other kinds of anthropogenic mortality), the initial growth rate,  $K(r, 1)$ , and the growth rate through river catchment,  $K(r, i)$ , appeared.

## 1.2.4. Adaptive mechanisms to deal with environmental heterogeneity

### ► Phenotypic plasticity

The panmictic population of eels with the long and passive larval drift, and the broad distribution area promote the emergence of phenotypic plasticity rather than local genetic adaptation as an adaptive response to natural and anthropogenic changes in spatially structured environments (Hutchings *et al.*, 2007). This mechanism has been proposed for several life history traits and tactics: the migratory behaviour of facultative catadromy (Tsukamoto and Arai, 2001; Daverat *et al.*, 2006; Edeline, 2007; Thibault *et al.*, 2007a), the head shape (Ide *et al.*, 2011; De Meyer *et al.*, 2015), the sex determination and the subsequent sex ratio (Davey and Jellyman, 2005), the growth rate (De Leo and Gatto, 1995; Côté *et al.*, 2009; Geffroy and Bardonnnet, 2012), and the length-at-silvering (Vollestad, 1992). These features have been analyzed independently or by pairs and Drouineau *et al.* (2014) developed the first model, Eveel, which considers life history traits and tactical choices as adaptive response to spatially structured environments and density-dependence. Their results suggest that sex-determination, length-at-silvering and growth habitat use may be interpreted as the

result of adaptive phenotypic plasticity that maximizes individual fitness in high variable environments.

► **Genetic polymorphism maintained by natural selection (spatially varying selection and habitat selection)**

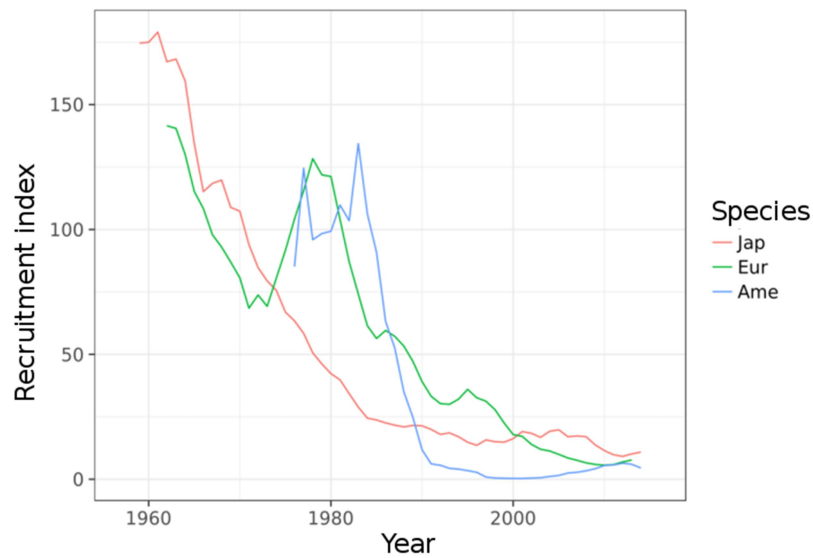
Despite panmixia, Pujolar (2014) showed correlations between allele frequencies at some loci and environmental variables in the European eel, and suggested that the selected polymorphisms would be maintained by spatially varying selection. Same results were found by Gagnaire *et al.* (2012) in American eel, although on different loci, probably because of different selection pressures (Ulrik *et al.*, 2014). Pavey *et al.* (2015) demonstrated a polygenic basis of freshwater and brackish/saltwater ecotypes in the American eel. They assumed that spatially varying selection (imposed by local environmental conditions) do not result in a local adaptation because each disruption of allelic proportions would be deleted in each new generation during the reproduction. Common garden experiments tested the hypothesis on genetic versus environmental factors to the origin of phenotypic differences in glass eels from different origins. The results revealed genetic patterns of growth rates related to geographic zones in American eel (Côté *et al.*, 2009, 2014, 2015). In line with this results, Boivin *et al.* (2015) studied how salinity and geographic origin influenced growth and habitat selection in the same species, and that differences in growth between glass eels reared in different areas had a genetic basis.

### **1.3. Contemporary dynamics of eel populations and implications for management**

#### **1.3.1. Status of temperate eels: dramatic declines and conservatory initiatives**

Over the last three decades, a worldwide decline of the temperate eel populations has been observed at all their life stages (figure 1-6) (Dekker, 2009; Dekker and Casselman, 2014; Jacoby *et al.*, 2015). As a consequence of this, the IUCN classified the European eel (*Anguilla anguilla*) as critically endangered (Jacoby and Gollock, 2014b) and the American eel (*A. rostrata*) and the Japanese eel (*A. japonica*) as endangered (Jacoby and Gollock, 2014a; Jacoby *et al.*, 2014). Several factors have been proposed to explain these declines (Jacoby *et al.*, 2015) such as changes in oceanic conditions (Castonguay *et al.*, 1994), contamination and habitat degradation (Byer *et al.*, 2015; Belpaire *et al.*, 2016), parasitism (Feunteun, 2002;

Kirk, 2003), fishing pressure (Dekker, 2003b), fragmentation including massive habitat loss (Kettle *et al.*, 2011), and hydroelectricity induced mortality (Castonguay *et al.*, 1994).



**Figure 1-6.** Recruitment trends for temperate eels (adapted from Drouineau *et al.*, submitted)

In view of this recruitment decline, conservation regulations have been established for the three species. For the European eel, the European Commission enforced a regulation (Council of the European Union, 2007) in which each member state has to implement management measures to recover the stock reducing all anthropogenic mortalities and ensuring the escapement of at least 40% of the silver eel pristine biomass (best estimate of escapement that would have existed if no anthropogenic pressures had impacted the stock). In order to meet this target, EU countries have proposed measures such as: limiting fisheries, re-establishing connectivity through inland waters and restocking suitable inland habitats with young eels. For the latter, EU countries with glass eels fisheries need to reserve 60% of their catches for restocking. For the American eel, it was classified as “endangered” in 2008 under the Ontario Endangered Species Act, which provides advice and recommendations to governments in order to protect and restore suitable habitats, and reduce mortality (prohibiting fishing and trading) to enhance silver eel escapement (MacGregor *et al.*, 2013). At the same time in Newfoundland and Labrador, the species was also listed as “vulnerable” under Endangered Species Act (Wildlife Division, 2010). According to these designations, the Canadian Government is conducting a consultation process on whether the species should be listed as “threatened” under the federal Species at Risk Act. The Japanese Ministry of Environment added the Japanese eel on its Red List in 2013, prohibiting the catches of juvenile and silver eels.



Among the challenges to assess the species status, the panmixia, the inter-individual variability in growth, the size dependent biological parameters, the density dependent process and the variable recruitment confound the current conservation efforts. Furthermore, to distinguish between local effects and stock status is difficult because of the contrast in life history traits and tactics displayed by eels to deal with heterogeneous environments and anthropogenic pressures at different scales. Finally, the fractal dimension of eel stock also challenges the assessment for the continental phase and a large scale management is necessary (Dekker, 2000a).

### **1.3.2. Should management consider adaptive mechanisms: anthropogenic pressures as a selective pressure**

In population dynamics, the impact of anthropogenic pressures is often assessed by quantifying mortality rates. The European eel Regulation falls within this approach: it sets a target as a number (or a proportion) of escapees and enforces measures to reduce anthropogenic mortalities and to increase inland waters colonization and production (fishways, restocking). As such, the European Regulation mainly focuses on the number of spawners that survive to anthropogenic pressures, regardless their sex, size or quality (i.e. capacity to contribute to the next generation). This was thought to be consistent with a panmictic population in which all individuals were thought to be equivalent. However, adaptive mechanisms undermine this theory. All individuals are not strictly equivalent: individuals display different genotypes. Moreover, phenotypic plasticity may lead to modifications in demographic attributes such as sex ratio or average fecundity. In this context, it seems necessary to improve our understanding of adaptive mechanisms to inform on potential indirect effects of anthropogenic pressures on eel populations and ensure that mortality estimation is enough.

Such knowledge would also contribute to the debate about restocking, one of the main controversial management measures used for the conservation of the species (Brämick *et al.*, 2016; Dekker and Beaulaton, 2016). For years, managers have restocked eels in specific areas where growth and survival were thought to be good. For example, a restocking plan was carried out in Canada by stocking glass eels caught in Nova Scotia and New Brunswick in Lake Ontario (Pratt and Threader, 2011). However, since all eels are not strictly equivalent, restocking may lead to unattended results, and Lake Ontario produced for the very first time very small silver eels whereas it had always produces very large females (Verreault *et al.*, 2010; Stacey *et al.*, 2015).

## 1.4. Aims and outlines of the thesis

In the context of global change and dramatic declines, the purpose of this thesis was to explore the evolutionary ecology of temperate eels to understand the mechanisms involved in their adaptation capacities, and how these capacities interact with anthropogenic pressures. In this purpose, we focused on how interactions among individuals, and interactions between individuals and their environment shape the eel population dynamics through adaptation mechanisms. We finally analyze the consequences of the resulting evolutionary processes on population dynamics.

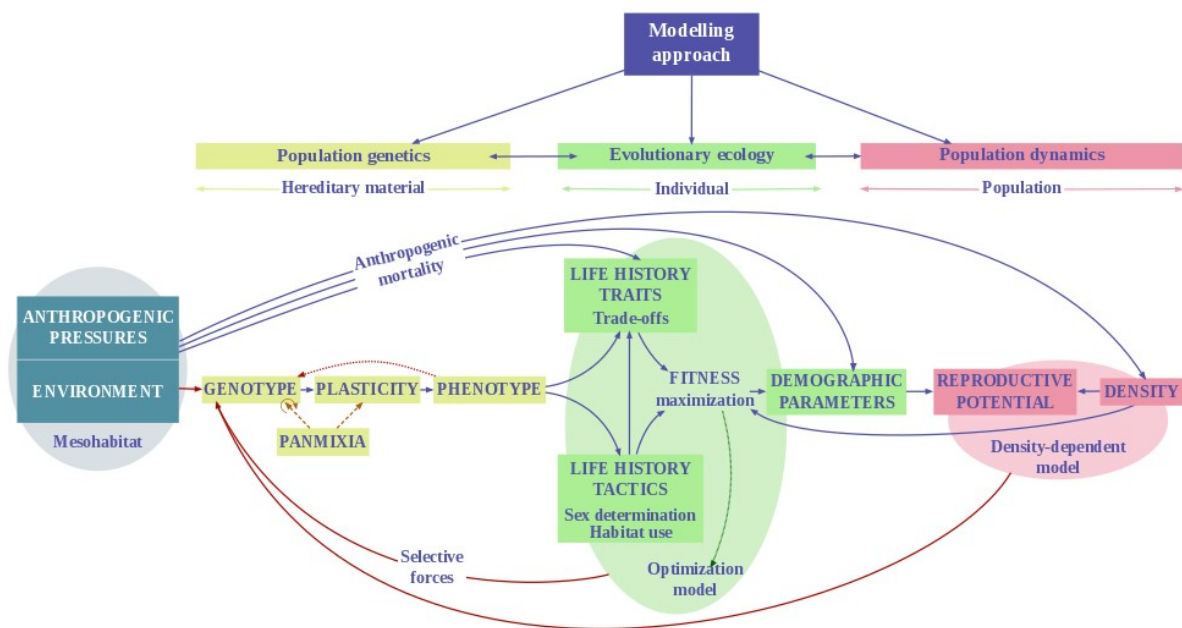
The approach adopted throughout the thesis is outlined in figure 1-7. Based on the phenotypic variability, adaptive responses can emerge to face environmental heterogeneity: different phenotypes in different environments induce differences in fitness of individuals throughout life history traits and strategies. The responses are provided by two mechanisms: individuals can genetically adapt to environmental conditions favoring allelic variants and the best genotypes are selected, or the responses are determined by the environment through phenotypic plasticity. Through fitness, life history traits and strategies also induce changes in demographic parameters of population, and therefore in the population structure, which will depend on the adaptation mechanisms implemented by individuals. Simultaneously, variation in demographic parameters influences life history traits, and consequently there is a feedback between life history and population dynamics mediated by the environment. In a context of global change, human activities lead to mortality of individuals that modifies the structure of population. The impacts of these activities in the environment also lead to changes in life history traits and strategies of individuals, which ultimately affect their fitness and can be selective pressures for the population.

In this context, the aims of this study were to:

- (i) Improve the understanding of adaptation mechanisms to deal with environmental heterogeneity. For that, chapter two seeks to answer whether phenotypic plasticity and genetic polymorphism are adaptive responses for temperate eels that occupy heterogeneous environments.
- (ii) Quantify the effects of anthropogenic pressures considering previous mechanisms. On account of this, chapter three investigates how adaptive responses influence the impact of human activities on eel population dynamics.
- (iii) Explore the emergence and the evolution of adaptive responses of temperate eels. In chapter four, a first study focuses on the ecological conditions that favor the

selection of phenotypic plasticity and if this mechanism is still adaptive in the current context of depleted population of eels. This chapter also proposes the design of a demo-genetic model to study not only the emergence of plasticity, but also genetic polymorphism.

To achieve these aims, a modelling approach is used, crossing concepts from evolutionary ecology, population dynamics and population genetics. In chapter two and three, the model is based on an optimality approach (with the basis of population genetics) to specify the adaptive mechanisms (phenotypic plasticity and genetic polymorphism) and validate them through the comparison of observed life history traits and strategies in heterogeneous environments. The integration of these mechanisms in a population dynamics model allows to quantify the impact of anthropogenic pressures. In chapter four, the approach is slightly different because the aim is the exploration of eel adaptations origin.



**Figure 1-7.** Scheme of the thesis outline.

**Chapter 2:**

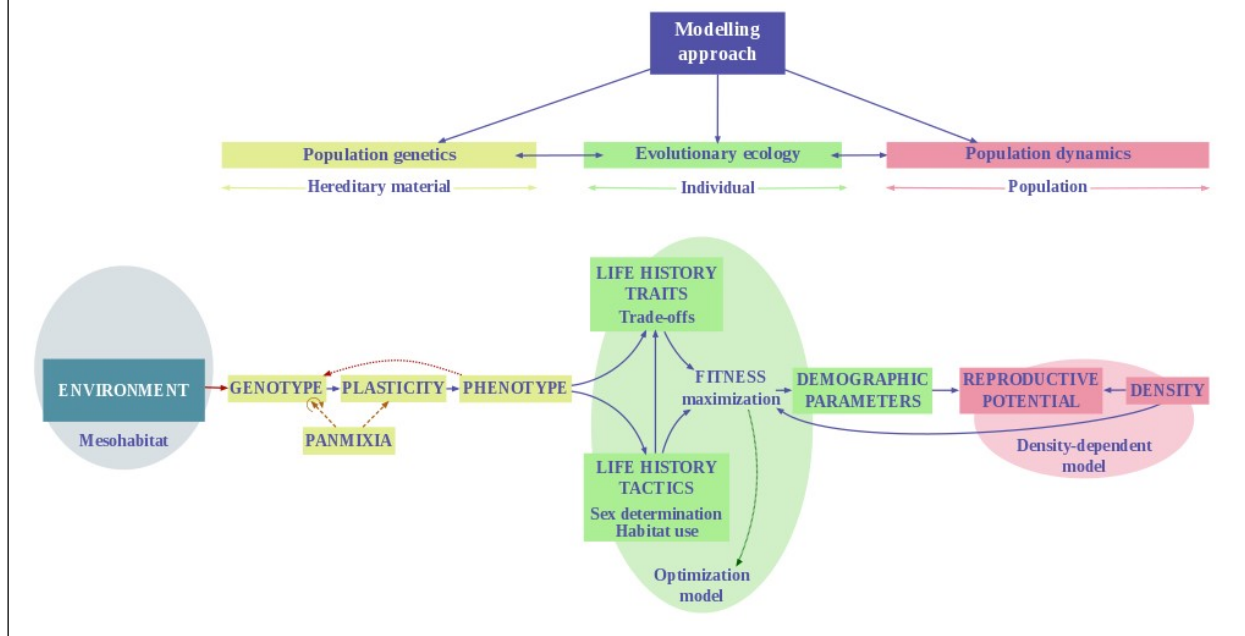
**Cause or consequence? Exploring the role of phenotypic plasticity and genetic polymorphism in the emergence of phenotypic spatial patterns of the European eel**

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*Published article:* Mateo, M., Lambert, P., Tétard, S., Castonguay, M., Ernande, B. and Drouineau, H. 2016. Cause or consequence? Exploring the role of phenotypic plasticity and genetic polymorphism in the emergence of phenotypic spatial patterns of the European eel. *Canadian Journal of Fisheries Aquatic Sciences*, 74: 987-999.

## Foreword

In a context of rapid global change and dwindling populations, the adaptation of temperate eels to environmental heterogeneity is becoming a crucial question. In view of this, a multidisciplinary approach is necessary to improve our understanding of the processes involved in the large phenotypic variability of those panmictic species, especially in correlation between life history traits and environmental gradients. In this chapter, we addressed the evolutionary mechanisms involved in this adaptation. We also explored whether life history spatial patterns can be mimicked. To do so, an optimization modelling approach was used. It incorporated eel population dynamics in the river basin and postulated both genetic polymorphism and adaptive phenotypic plasticity. In this individual-based population model, each individual is characterized by an intrinsic growth rate, it determines its sex, selects its growth habitat within the catchment and its length-at-maturity to optimize its density-dependent fitness. GenEveel uses a pattern modelling approach that carries out a numerical exploration to validate different assumptions, which are based on optimal foraging and life history theories. The approach can provide new insights on the continental phase of these species. The following figure summarizes the positioning of this chapter within the overall PhD project.



## 2.1. Abstract

The European eel (*Anguilla anguilla*), and generally, temperate eels, are relevant species for studying adaptive mechanisms to environmental variability because of their large distribution areas and their limited capacity of local adaptation. In this context, GenEveel, an individual-based optimization model, was developed to explore the role of adaptive phenotypic plasticity and genetic-dependent habitat selection, in the emergence of observed spatial life-history traits patterns for eels. Results suggest that an interaction of genetically and environmentally controlled growth may be the basis for genotype-dependent habitat selection, whereas plasticity plays a role in changes in life-history traits and demographic attributes. Therefore, this suggests that those mechanisms are responses to address environmental heterogeneity. Moreover, this brings new elements to explain the different life strategies of males and females. A sensitivity analysis showed that the parameters associated with the optimization of fitness and growth genotype were crucial in reproducing the spatial life-history patterns. Finally, it raises the question of the impact of anthropogenic pressures that can cause direct mortalities but also modify demographic traits, and act as a selection pressure.

*Keywords:* phenotypic plasticity, *Anguilla anguilla*, genetic polymorphism, life history theory, modeling

## 2.2. Introduction

Life-history theory posits that the schedule and duration of life-history traits are the result of natural selection to optimize individual fitness (Clark, 1993; Giske *et al.*, 1998). Optimal solutions greatly depend on environmental conditions, and consequently, living organisms have developed different adaptive mechanisms to address environmental variability. Among them, local adaptation theory posits that natural selection favors the most well adapted genotypes in each type of environment. In a context of limited genetic exchange between environments, this may lead to isolation and speciation (Williams, 1996; Kawecki and Ebert, 2004). Phenotypic plasticity might also be an adaptive response to an heterogeneous environment (Levins, 1963; Gotthard and Nylin, 1995; Pigliucci, 2005). Phenotypic plasticity refers to the possibility of a genotype to produce different phenotypes depending on environmental conditions. In some cases, increases in fitness occur because of plastic phenotypes compared to non-plastic ones, and that consequently, phenotypic plasticity may be selected by natural selection (Schlichting, 1986; Sultan, 1987; Travis, 1994).

Adaptation to environment heterogeneity is a key issue for temperate anguillids, *Anguilla anguilla*, *A. japonica*, *A. rostrata*, three catadromous species that display remarkable similarities in their life-history traits (Daverat *et al.*, 2006; Edeline, 2007). The European eel (*A. anguilla*) is widely distributed from Norway to Morocco, grows in contrasting environments, and displays considerable phenotypic variation. The species displays a complex life cycle: reproduction takes place in the Sargasso Sea, larvae (or leptocephali) are transported by ocean currents to European and North African waters, where they experience their first metamorphosis to become glass eels. These juveniles colonize continental waters and undergo progressive pigmentation changes to become yellow eels. The growth phase lasts between two and 20 years depending upon the region and sex of the eels (Vollestad, 1992). At the end of this stage, yellow eels metamorphose again into silver eels, which mature during the migration to their spawning area in the Sargasso Sea. The population is panmictic, resulting in a homogeneous population, from a genetic viewpoint (Palm *et al.*, 2009; Als *et al.*, 2011b; Côté *et al.*, 2013). This panmixia combined with a long and passive larval drift limit the possibility of adaptation to local environments. However, spatial patterns of different life traits, including growth rate (Daverat *et al.*, 2012; Geffroy and Bardonnnet, 2012), sex (Helfman *et al.*, 1987; Tesch, 2003; Davey and Jellyman, 2005), length at maturity (Vollestad, 1992; Oliveira, 1999), and habitat use (De Leo and Gatto, 1995; Daverat *et al.*, 2006; Edeline, 2007) are observed and correlated with environmental patterns.

Growth rates greatly vary depending on latitude, temperature, sex (Helfman *et al.*, 1987) but also on habitat characteristics (Cairns *et al.*, 2009). Indeed, eel can settle in a wide range of habitats (De Leo and Gatto, 1995; Daverat *et al.* 2006; Geffroy and Bardonnnet, 2012) and faster growth is observed in brackish waters than in freshwater (Daverat *et al.*, 2012). Slower growth in freshwater habitats is sometimes assumed to be compensated for by lower mortalities and Edeline (2007) suggested that habitat choice could be the result of a conditional evolutionary stable strategy. However, Cairns *et al.* (2009) questioned this assumption because they did not observe strong variation in mortality rates between habitats. Spatial patterns were also observed with respect to sex ratios, with female biased sex ratios in the upper part of river catchments (Tesch, 2003) and in the northern part of the distribution range (Helfman *et al.*, 1987; Davey and Jellyman, 2005). However, sex is not determined at birth but is determined by environmental factors (Oliveira, 2001; Davey and Jellyman, 2005; Geffroy and Bardonnnet, 2012). Population density also plays a role in this mechanism: males are favored at high densities, whereas low densities favor females (Tesch, 2003). This is important because males and females have different life-history strategies (Helfman *et al.*, 1987). The reproductive success of a male does not vary with body size, and consequently, males are assumed to follow a time-minimizing strategy, leaving continental waters as soon as they have enough energy to migrate to the spawning grounds (Vollestad, 1992). However, a female's reproductive success is constrained by a trade-off between fecundity, which increases with length, and survival, which decreases with length. Consequently, females are assumed to adopt a size-maximizing strategy (Helfman *et al.*, 1987). Strong differences in female length at silvering were observed among habitats and latitudes (Oliveira, 1999).

Because local adaptation is impossible, this raises two questions: (i) are those life-history trait patterns resulting from an adaptive response to environmental heterogeneity, and (ii) which adaptation mechanisms have been selected. Despite panmixia, previous researchers (Gagnaire *et al.*, 2012; Ulrik *et al.*, 2014; Pavey *et al.*, 2015) have detected genetic differences correlated with environmental gradients and assumed that those differences were reshuffled at each generation. Common garden experiments have been used to test the respective contributions of genetic and plastic mechanisms on phenotypic differences observed in glass eels found in distinct locations. The results revealed genetic patterns related to geographic zones in American eels, whereas individual growth rates had a genetic basis and could be sex-dependent (Côté *et al.*, 2009, 2014, 2015). Building on this, Boivin *et al.* (2015) studied the influence of salinity preferences and geographic origin on habitat selection and growth in American eels, demonstrating genetic-based differences for growth between glass eels from different origins. However, these experiments also confirmed the contribution of phenotypic



plasticity that allowed individuals to develop quick and effective responses to environmental variability (Hutchings *et al.*, 2007). Several traits have been proposed as plastic: growth habitats (Daverat *et al.*, 2006; Edeline, 2007), growth rates (Geffroy and Bardonnnet, 2012), and length at silvering (Vollestad, 1992). Understanding the adaptive mechanisms that explain this diversity is crucial to environmental conservation and management (Brodersen and Seehausen, 2014).

As a result of a decline observed since the 1980s, the European eel is now listed as critically endangered in the IUCN Red List (Jacoby and Gollock, 2014c) and the European Commission enforced a European Regulation, which requires a reduction in all sources of anthropogenic mortality (obstacles, loss of habitat, fisheries, pollution, and global change) (Council of the European Union, 2007). However, those anthropogenic pressures are not uniformly distributed (Dekker, 2003a) and acts on specific fractions of the stock isolated in river catchments (Dekker, 2000a), with heterogeneous life-history traits because of the spatial phenotypic variability. This strong spatial heterogeneity of anthropogenic pressures affecting the eel population in Europe combined with this spatial phenotypic variability at both the distribution area and river catchment scales causes specific challenges for management, because it impairs our ability to assess the effect of anthropogenic pressures on the whole stock and to coordinate management actions (Dekker, 2003a, 2009).

Recently, a model called EvEel (evolutionary ecology-based model for eel) was developed to explore the contribution of adaptive phenotypic plasticity in the emergence of observed phenotypic patterns: sex ratio, length at silvering, and habitat use (Drouineau *et al.*, 2014). Assuming fitness maximization, the model was able to mimic most observed patterns at both river catchment and distribution area scales. The result confirmed the probable role of adaptive phenotypic plasticity in response to environmental variability. However, recent findings demonstrated the existence of genetic differences in growth traits in a wide range of different habitats (Côté *et al.*, 2009, 2014, 2015; Boivin *et al.*, 2015). Building on these new results, we developed GenEveel, a new version of EvEel, which introduces a bimodal growth distribution (fast and slow growers) for individuals, as observed by Côté *et al.* (2015), and considers phenotypic plasticity in life-history traits and demographic attributes as in EvEel. Because individuals have different intrinsic growth and mortality rates, they can be favored differently among environments, opening the door to conditional habitat selection. In this study, we used GenEveel to test whether simultaneously considering genetically distinct individuals and phenotypic plasticity improves model performance. Pattern orienting

modelling was used to detect the reproduced spatial patterns of EvEel and other patterns based on the distribution of the different types of individuals.

## 2.3. Materials and methods

### 2.3.1. Model description

The model description follows the Overview, Design concepts, and Details (ODD) protocol (Grimm *et al.*, 2006, 2010):

#### 2.3.1.1. Overview

##### 2.3.1.1.1. Purpose

GenEveel is a model based on a former model called EvEel (Drouineau *et al.*, 2014), but includes a genetic component. It is an individual-based population model that predicts emergent life-history spatial patterns depending on adaptive mechanisms and environmental heterogeneity. Emergent patterns can later be compared to observed spatial patterns in freshwater life stages of European eels in order to (i) confirm that observed phenotypic patterns can plausibly result from adaptive responses to environmental heterogeneity, (ii) validate that phenotypic plasticity for length at silvering, sex determination, habitat choice, and genetic polymorphism (slow growers and fast growers) with conditional habitat selection can explain those patterns.

##### 2.3.1.1.2. State variables and scales

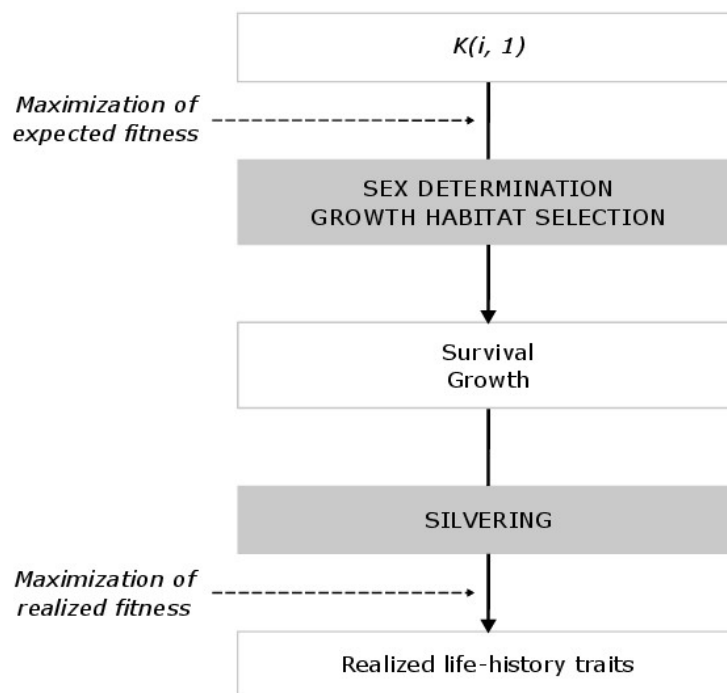
*Temporal scales:* the model simulates a population generation. It has no sensu stricto time steps, but rather successive events: sex-determination and habitat selection, survival, and growth until maturation.

*Entities and spatial scales:* a von Bertalanffy growth function is assumed for individual growth. Each individual  $i$  is characterized by an intrinsic Brody growth coefficient  $K_i$  and a natural mortality rate  $M_i$ . Based on Côté *et al.* (2015), who observed two clusters in growth rates, we build a simple quantitative-genetic model assuming that growth is coded for by a single gene with two variations. Therefore, we assumed that there are two types of individuals called (i) fast-growing individuals for which  $K_i = K_{fast}$  and  $M_i = M_{fast}$  and (ii) slow-growing individuals for which  $K_i = K_{slow}$  and  $M_i = M_{slow}$ . At the end of the simulation, individuals are characterized by a sex, length at silvering, corresponding fecundity (if female), position in the river catchment, and survival rate until silvering.

The river catchment environment was represented by a sequence of cells of the same size. The first cell represents the river mouth, whereas the  $n$ th cell represents the source of the river. Because it was observed that an individual grows faster downstream than upstream (Acou *et al.*, 2003; Melià *et al.*, 2006), we assumed that realized growth rate in a cell depends on both intrinsic growth rate and position in the catchment (i.e., cell) (see submodel section). Realized natural mortalities depend both on individual intrinsic mortality rates, position of the cell in the catchment, and number of individuals in the catchment (to mimic density-dependent mortality).

### 2.3.1.1.3. Process overview and scheduling

The model has two main steps. In a first step, individuals select their growth habitat (a cell in the catchment) and determine a sex (male or female) one after another (random order). To do that, fitness is calculated for each combination of sex and cell (a quasi-Newton algorithm is used to estimate the lengths at silvering that optimize female fitness in each cell). Individuals are assumed to select the combination with highest fitness given the choices made by former individuals. Once this step is finished (i.e., all individuals have a growth habitat and sex), using the quasi-Newton algorithm we estimated the optimal length at silvering for all females (males have a constant length at silvering) given the positions of fishes from step 1, and then compute corresponding survival rates until silvering and fecundity determination (figure 2-1).



**Figure 2-1.** Flow chart representing the fish biological pathway.

The process mentioned above is defined by the computer algorithm (figure 2-2):

(1) For each individual  $i$ :

- For each cell  $x$ :
  - Compute  $\pi m(x)$  given positions of individuals  $\{1, \dots, i-1\}$
  - Compute  $\max_{L_{sf}} \pi_f(x, L_{sf})$  given positions of individuals  $\{1, \dots, i-1\}$
- Put individual and determine sex by selecting maximum values within  $\max_{L_{sf}} \pi_f(x, L_{sf})$  and  $\pi m(x)$

(2) For each individual  $i$ :

- For each cell  $x$ :
  - if  $\text{sex}(i) = \text{male}$   
 $L_s(i) = L_{sm}$
  - else  
 $L_s(i) = \arg L \max (\pi f(x, L_{sf}))$  given positions of individuals  $\{1, \dots, n\}$

where fitness is defined in equations 0 and 0 for females and males respectively.

## 2.3.1.2. Design concept

### 2.3.1.2.1. Basic principles

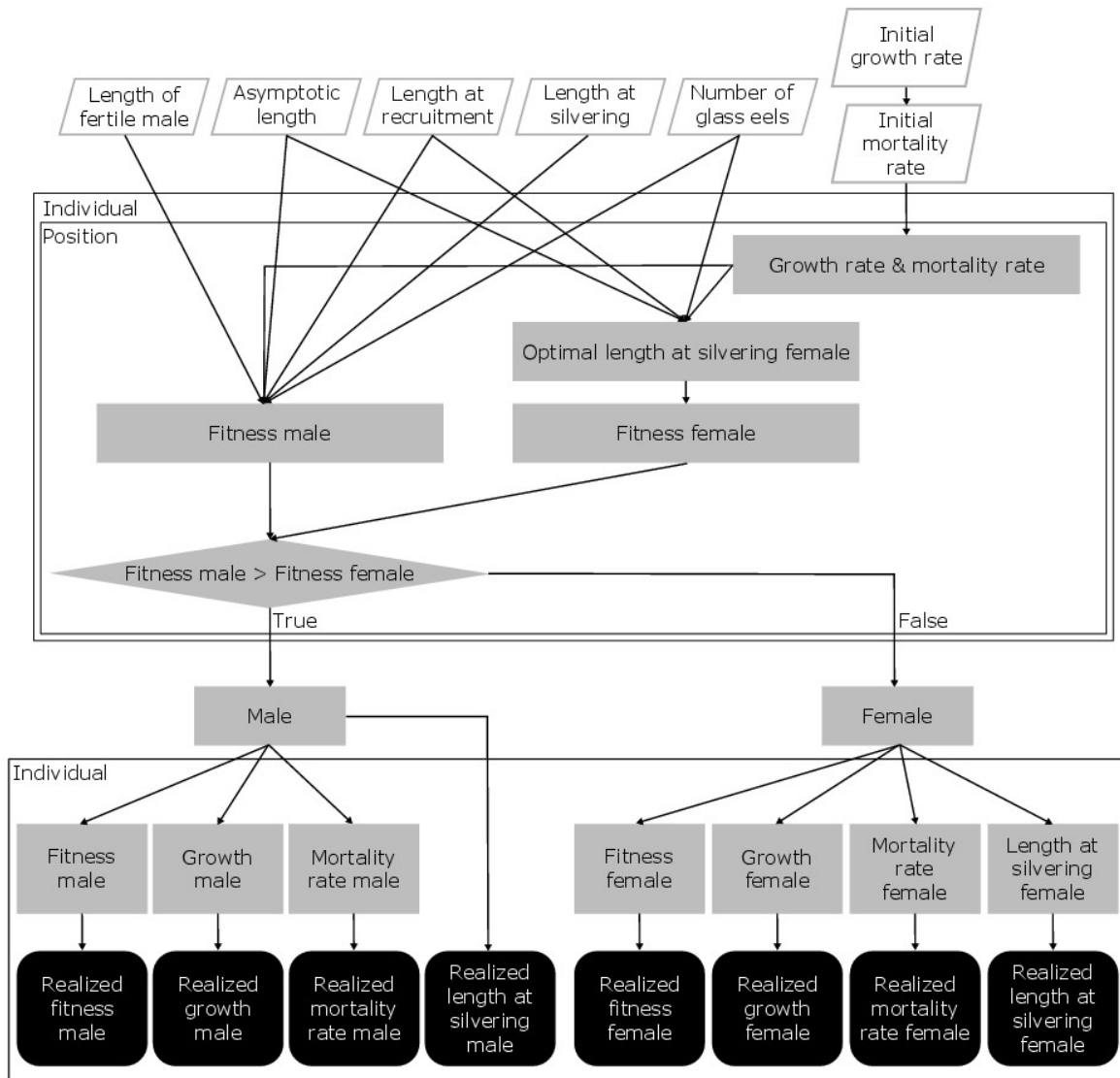
Consistent with life-history theory and optimal foraging theory, the model uses an optimization approach in which individuals “respond to choices” so as to select and fix the adaptive traits, maximizing their expected fitness given their environment (Parker and Maynard Smith, 1990; McNamara and Houston, 1992; Giske *et al.*, 1998; Railsback and Harvey, 2013).

### 2.3.1.2.2. Emergence

Using the pattern-oriented modelling approach (Grimm and Railsback, 2012), GenEveel compares predicted spatial patterns with those observed in real river catchments. Five emergent population spatial patterns were analyzed from the literature:

- (i) higher density downstream than upstream
- (ii) higher length at silvering upstream than downstream
- (iii) male-biased sex ratio downstream and female-biased sex ratio upstream
- (iv) more individuals characterized with the fast-growing genotype downstream than upstream, which was mainly characterized by the slow-growing genotype

(v) the phenotypic response led to faster growth rate downstream than upstream.



**Figure 2-2.** Algorithm of the model GenEveel.

### 2.3.1.2.3. Adaptation

Individuals have three adaptive traits: sex-determination, length at silvering for females, and choice of growth habitat (cell in the grid). These traits are assumed to maximize the predicted objective function (i.e., the individual fitness).

### 2.3.1.2.4. Predictions

We assumed that individuals could perfectly predict expected fitness given previous choices and could make the most appropriate choices.

### 2.3.1.2.5. Sensing

In the model, individuals are able to “sense” fitness, which was a function of a density-dependent mortality and growth rate. In the real world, temperature and density would

probably be the proximal cues because natural mortality and growth rates are strongly influenced by temperature (Bevacqua *et al.*, 2011; Daverat *et al.*, 2012).

#### **2.3.1.2.6. Interaction**

Interactions occurred through growth habitat selection, sex determination, and density-dependent mortality.

#### **2.3.1.2.7. Stochasticity**

Stochasticity occurred at two levels. First, individuals were randomly affected by a slow-growing genotype ( $Pr = 0.5$ ) or by a fast-growing genotype ( $Pr = 0.5$ ). Then stochasticity occurred in the order of individuals for step 1.

#### **2.3.1.2.8. Observations**

Five spatial patterns were computed at the end of the simulation:

- (i) number of individuals per cell
- (ii) mean length at silvering per cell
- (iii) sex ratio (proportion of females) per cell
- (iv) ratio of fast-growing genotype per cell
- (v) phenotypic response of mean realized growth rate per cell.

These five patterns corresponded to five patterns available in the literature. Simulated patterns (i), (iv), (v) was said to be consistent with the literature when a negative trend from downstream to upstream was observed, whereas patterns (ii), (iii) were said to be consistent with the literature when a positive trend was observed from downstream to upstream.

### **2.3.1.3. Details**

#### **2.3.1.3.1. Initialization**

At the beginning of the simulation, the catchment was empty.  $N$  individuals were created and attributed to the slow-growing or fast-growing genotype with probability 0.5 and had a length 7.5 cm. They had not yet entered the river catchment.

#### **2.3.1.3.2. Input data**

We tested the model using a reference simulation. Values of parameters were obtained from the literature (table 2-1). The outputs of the model were identified based on spatial patterns as previously defined in *Observations*.

### 2.3.1.3.3. Submodels

Most of the submodels were similar to submodels from EvEel. Consequently, we provide here only the novelties and the equations that are required for a better understanding of the model. Further details are provided in Drouineau *et al.* (2014).

*Growth and silvering*: growth rate was assumed the outcome of an intrinsic Brody growth coefficient ( $K_i$ ), which is modulated by an environmental effect. This combination resulted in a phenotypic growth rate. Within the river, growth rates were significantly faster downstream than upstream (even for the same individual). Therefore, we assumed that individual  $i$  would have a growth rate  $K(i, x)$  in cell  $x$  given by:

$$(1) K(i, x) = r_K \cdot K(i, n) + (K(i, 1) - r_K \cdot K(i, n)) \cdot \text{cauchit}\left(\frac{x}{n}, \gamma_K\right)$$

$$(2) \text{cauchit}(x, \gamma) = 1 - \frac{2}{\pi} \cdot \text{atan}\left(\frac{x^2}{\gamma}\right)$$

where  $r_K$  defined the ratio between upstream and downstream growth rate,  $K(i, 1)$  is the growth rate in cell 1,  $n$  is the total cells in the river catchment and *cauchit* was a mathematical function similar to the sigmoid function, but which allowed asymmetrical patterns (by modifying the parameter  $\gamma$ ) to model, for example, a small brackish area in the downstream part of the catchment and a large freshwater zone upstream.

Individual's growth was simulated by a von Bertalanffy function:

$$(3) L(t, i, x) = L_\infty \left[ 1 - e^{-K(i, x)(t - t_0)} \right]$$

where  $L(t, i, x)$  was the length at time  $t$  and  $L_\infty$  and  $K(i, x)$ , the von Bertalanffy parameters in cell  $x$  for individual  $i$ .

From this equation, we could calculate the time required to reach the length at silvering.

$$(4) A_s(i, x) = \frac{1}{K(i, x)} \cdot \log\left(\frac{L_\infty - L_g}{L_\infty - L_s(i, x)}\right)$$

where  $L_g$  was the length at recruitment and  $L_s(i, x)$  was the length at silvering, which was constant for males, and a fitness maximizing variable for females.

*Survival*: mortality rate was assumed the result of three factors: density-dependence, intrinsic growth rate, and  $M_i$  modulated by an environmental effect. Because natural mortality was

sometimes assumed to be smaller upstream than downstream (Moriarty, 2003; Daverat and Tomás, 2006), we assumed that the instantaneous natural mortality without density-dependence in cell  $x$  for individual  $i$ ,  $M(i, x)$  was:

$$(5) M(i, x) = r_M \cdot M(i, n) + (M(i, 1) - r_M \cdot M(i, n)) \cdot \text{cauchit}\left(\frac{x}{n}, \gamma_M\right)$$

where  $r_M$  is the ratio between upstream and downstream instantaneous mortality rate and  $M(i, 1)$  was the natural mortality in cell 1.

To account for the additional density-dependent mortality, we assumed that natural mortality increased linearly with an intensity of density  $\alpha$  as in EvEel:

$$(6) M_d(i, x) = M(i, x) + N(i, x) \cdot \alpha$$

where  $N$  was the number of competitors in cell  $x$ . An eel was assumed a competitor if it had an intrinsic growth rate greater or equal to  $Ki$ . This corresponded to an asymmetric growth rate with larger individuals harassing smaller individuals. The basis of this assumption was the intraspecific competition, which leads to compete for limited resources between individuals of different sizes (Francis, 1983; Juanes *et al.*, 2002).

Given equation 0 and this survival rate, we could calculate the probability of surviving until silvering as:

$$(7) p(i, x) = e^{-M_d(i, x) \cdot A_s(i, x)} = \left( \frac{L_\infty - L_g}{L_\infty - L_s(i, x)} \right)^{\frac{-M_d(i, x)}{K(i, x)}}$$

*Fitness*: in any optimization model, an important component is the computation of the fitness. Because sexes adopt different life strategies, and following Drouineau *et al.* (2014), we assumed sex-specific fitness functions. Males were known to adopt a time minimizing strategy (Helfman *et al.*, 1987), with constant length at silvering. Therefore, male fitness was proportional to survival rate until length at silvering. However, females follow a size-maximizing strategy in which length at silvering was constrained by a trade-off between survival and fecundity (Helfman *et al.*, 1987). Consequently, we assumed that female fitness was the product of fecundity at an optimal length at silvering (based on an allometric relationship, fecundity is assumed to be a power function of length) multiplied by the probability of survival until this length at silvering. In the model, individuals were assumed to determine their sex according to the relative potential male and female fitness. To make fitness values comparable, we rescaled male fitness (which was the probability of survival) into an expectation of egg production (the scale of female fitness). To do that, we multiplied



the male survival by a constant that would be similar to fertility. Hence, we had to specify a value for fertility with an order of magnitude similar to fecundity. The first solution might be to fix the fertility value equal to the fecundity of silver females having a length equal to male length at silvering. However, with this solution, female fitness will always be greater (because females can optimize their length at silvering). Consequently, fertility has to be slightly greater such that male fitness can be sometimes be greater than female fitness (but not too much, to avoid male fitness always being superior). These resulted in the following equations:

$$(8) \text{ fecundity} \left( L_{S_f}(i, x) \right) = \left( a_1 + a \cdot L_{S_f}(i, x)^b \right)$$

where  $a_1$ ,  $a$  and  $b$  are the parameters of the allometric relationship linking fecundity and female length at silvering  $L_{S_f}(i, x)$  (Andrello *et al.*, 2011; Melia *et al.*, 2006).

$$(9) \pi_f(i, x) = \text{fecundity} \left( L_{S_f}(i, x) \right) \cdot \left[ \frac{L_\infty - L_g}{L_\infty - L_{S_f}(i, x)} \right]^{\frac{-M_f(i, x)}{K(i, x)}}$$

$$(10) \pi_m(i, x) = \text{fertility} \cdot \left[ \frac{L_\infty - L_g}{L_\infty - L_{S_m}(i, x)} \right]^{\frac{-M_m(i, x)}{K(i, x)}}$$

## 2.3.2. Model exploration

### 2.3.2.1. Reference simulation

The reference simulation consisted of a simulation using parameter values in table 2-1, i.e. the best set of values found in the literature. After simulating this scenario, we analyzed the different patterns. Mann-Kendall tests were implemented on each pattern to detect a monotonic upward or downward trend of the variable of interest confirming the spatial patterns previously defined. The correlation coefficient of this non-parametric test was denoted by  $\tau$ .

### 2.3.2.2. Experimental design

Simulation design is a classical tool to explore complex models. Typically, the goal is to assess the sensitivity of results to uncertain model parameters. We developed such an experimental design to (i) assess the influence of uncertain parameters on the simulated

patterns (table 2-1) and (ii) derive environmental and population dynamics for all the patterns that were correctly modelled.

Parameter	Description	Reference value	(-) modality	(+) modality	Reference
$n$	Cells of river catchment	30	24	36	(Drouineau <i>et al.</i> , 2014)
$N$	Number of glass eels that colonize freshwater	30 000	24 000	36 000	(Drouineau <i>et al.</i> 2014)
$a_l$	Regression coefficient from fecundity at length	8 846	-	-	(Andrello <i>et al.</i> , 2011)
$a$	Regression coefficient from fecundity at length	1.3877119	-	-	(Melià <i>et al.</i> , 2006b; Andrello <i>et al.</i> , 2011)
$b$	Regression exponent from fecundity at length	3.22	2.576	3.864	(Melià <i>et al.</i> , 2006b)
$L_\infty$ (cm)	Asymptotic length	76.2	60.96	91.44	(De Leo and Gatto, 1995)
$L_{sm}$ (cm)	Male length at silvering	40.5	38.15	42.85	(Vollestad, 1992)
$L_g$ (cm)	Length at recruitment	7.5	6	9	(Desaunay and Guerault, 1997; Dekker, 1998; Desaunay <i>et al.</i> , 2012)
$fertility$	Constant of male fertility	43	40.5	45.5	-
$K_{fast}(i, l), year^{-1}$	Fast intrinsic growth rate	0.315	0.295	0.335	(De Leo and Gatto, 1995)
$K_{slow}(i, l), year^{-1}$	Slow intrinsic growth rate	0.253	0.233	0.273	(De Leo and Gatto, 1995)
$propK$	Proportion of individuals that grow slowly	0.5	0.4	0.6	-
$M_{fast}(i, l), year^{-1}$	Fast intrinsic mortality rate	0.38	0.405	0.355	-
$M_{slow}(i, l), year^{-1}$	Slow intrinsic mortality rate	0.138	0.15	0.127	(Dekker, 2000a)
$\alpha$	Intensity of density-dependence	0.0001	0.00008	0.00012	(Drouineau <i>et al.</i> , 2014)
$r_K$	Ratio between upstream and downstream growth rate	0.5	0.4	0.6	(Drouineau <i>et al.</i> , 2014)
$r_M$	Ratio between upstream and downstream mortality rate	1	0.8	1.02	(Drouineau <i>et al.</i> , 2014)
$Y_K$	Shape parameter of growth	0.05	0.049	0.051	(Drouineau <i>et al.</i> , 2014)
$Y_M$	Shape parameter of mortality	0.05	0.049	0.051	(Drouineau <i>et al.</i> , 2014)

**Table 2-1.** GenEveel parameter descriptions with reference values and modalities (- and +) for the 17 parameters involved in the experimental design.

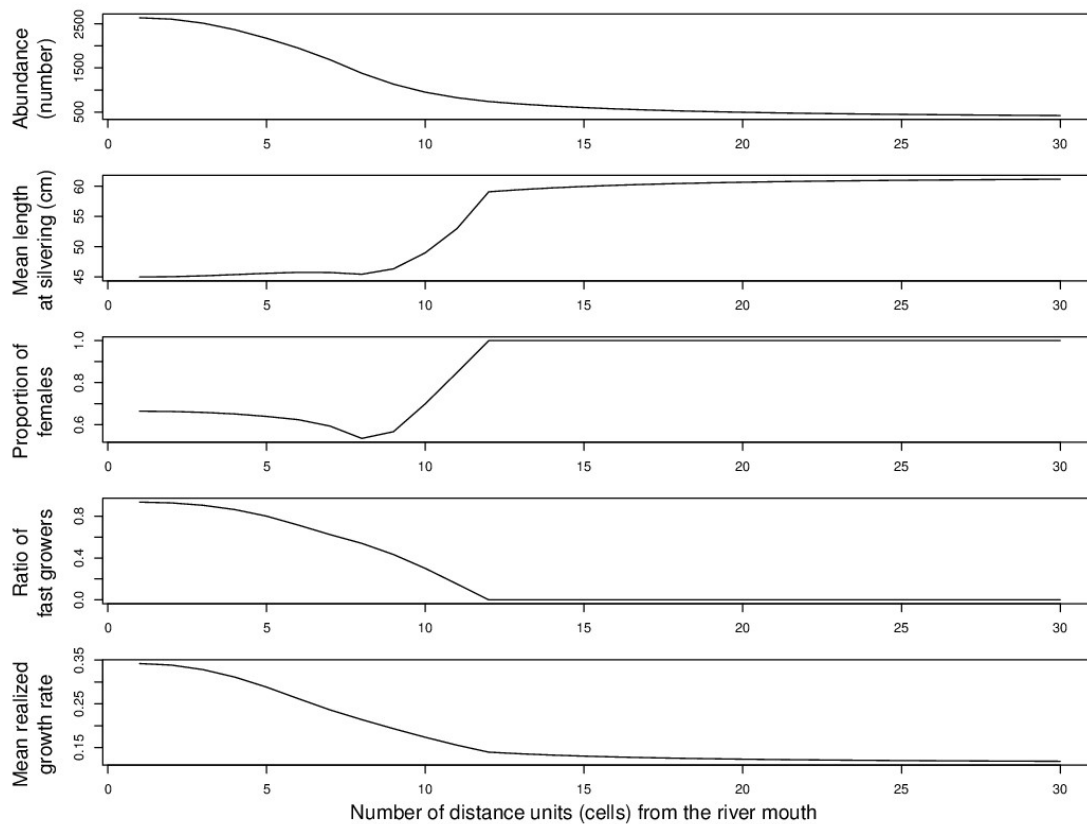
Seventeen uncertain parameters were identified in the model (table 2-1) and they were dispatched into twelve groups: number of glass eel entering the catchment freshwater ( $N$ ), parameters that impact the male fitness (*fertility* and male length at silvering,  $L_{sm}$ ), fast growing genotype ( $K_{fast}(i, l)$  and  $M_{fast}(i, l)$ ), slow-growing genotype ( $K_{slow}(i, l)$  and  $M_{slow}(i, l)$ ), proportion of individuals that grow slowly ( $propK$ ), intensity of density-dependence ( $\alpha$ ), cells of river catchment ( $n$ ), regression coefficient from fecundity at length ( $b$ ), asymptotic length ( $L_{\infty}$ ), length at recruitment ( $L_g$ ), ratio between upstream and downstream instantaneous growth and mortality rates ( $r_K$  and  $r_M$ ), and the shape parameter of growth and mortality ( $\gamma_K$  and  $\gamma_M$ ). Groups were composed of parameters that have are assumed to influence the model in similar directions, a method called group-screening (Kleijnen, 1987). A low and high value was set for each parameter around the reference value, with 20% variation (Drouineau *et al.*, 2006; Rougier *et al.*, 2015), except for three sets of parameters: *fertility* and  $L_{sm}$  (as a minimum value, *fertility* corresponded to the fecundity of a female with a length at silvering equals to male length at silvering; otherwise, female fitness would always be superior to male fitness), and growth genotypes (to avoid overlap between them), where the range of variation was less. We then conducted a fractional factorial design of resolution V ( $2^{12-4} = 256$  combinations). This kind of orthogonal designs allows to explore main effects and first order interactions without confusion. To account for model stochasticity, we conducted 10 replicates for each of the 256 combinations leading to 2560 simulations. The five patterns were calculated for each simulation producing an output table with 2560 lines (one per simulation) and five columns containing the tau value of the Mann-Kendall trend tests for each pattern (a negative tau value indicates a negative trend from downstream to upstream while a positive tau indicates a positive trend from downstream to upstream).

## 2.4. Results

### 2.4.1. Reference simulation

In the reference simulation, GenEveel mimicked the five spatial patterns at the catchment scale (figure 2-3). Males were concentrated in the downstream section of the river where density was higher (Helfman *et al.*, 1987; Tesch, 2003; Davey and Jellyman, 2005). Fast growers preferentially settled in downstream habitats, whereas slow growers tended to move upstream to avoid competition (De Leo and Gatto, 1995; Daverat *et al.*, 2006, 2012; Drouineau *et al.*, 2006; Edeline, 2007; Geffroy and Bardonnnet, 2012). Regarding mean length at silvering (for males and females), a smaller size at maturity was simulated in the

downstream section of the river, whereas larger lengths were occurred gradually throughout the catchment (Vollestad, 1992; Oliveira, 1999).



**Figure 2-3.** Output values for the five spatial patterns resulting from the reference simulation.

The Mann-Kendall test confirmed that the five patterns were mimicked in the simulation. More specifically, negative tau values confirmed a decreasing trend for density, ratio of fast growers and mean realized growth rate; while positive tau values pointed to an increasing trend for ratio of females and mean length at silvering (table 2-2).

Spatial pattern	Tau
Abundance	-1
Mean length at silvering	0.98
Sex ratio (proportion of females)	0.57
Ratio of fast growers	-0.78
Mean realized growth rate	-1

**Table 2-2.** Results of Mann-Kendall test of reference simulation.

## 2.4.2. Model exploration

For each combination, the 10 replicates provided the same results, confirming that the patterns were not sensitive to stochasticity.

Interestingly, 310 simulations produced only females while 640 simulations produced only males. Simulations with only females corresponded to simulation where density-dependence  $\alpha$ ,  $L_\infty$  and the fecundity exponent  $b$  were simultaneously strong. Conversely, simulations with only males corresponded to simulations with a low  $b$  and a low  $L_\infty$ . With only one sex, it was not possible to calculate a spatial trend in sex ratio and with only males, it was not possible to calculate a trend of length at silvering.

Two questions were addressed here. In a first time, we compared the five patterns to see which of those patterns were frequently mimicked and which were less frequently mimicked. Then, we compared the sensitivity of the model to each group of parameters. To quantify this sensitivity to a group of parameters values, we compared the number of simulations that reproduce a given pattern when the group had modality (-) with the number of simulations and when the group had modality (+). A strong discrepancy indicated a high sensitivity to the group of parameters.

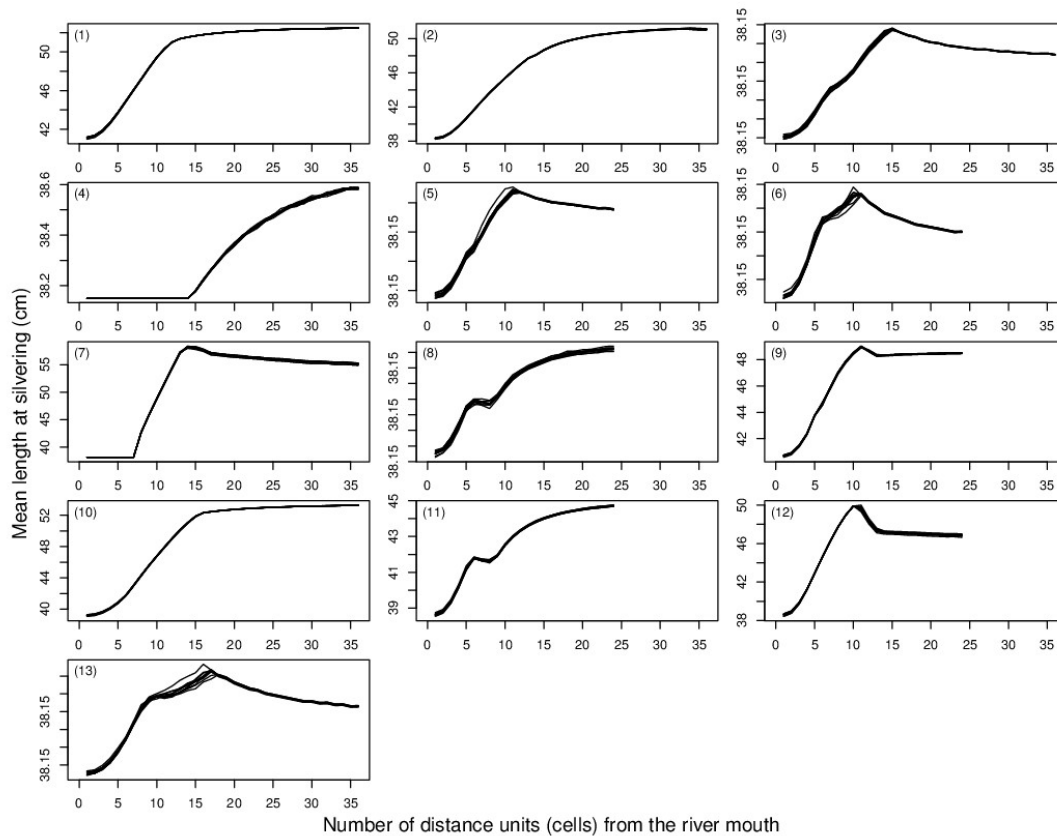
The Mann-Kendall tests of spatial patterns confirmed that the simulated patterns of abundance, ratio of fast growers, and mean realized growth rate were consistent with the literature in each of the 2560 combinations (table 2-3). This result indicates that these model outputs do not depend on parameters values in the parameter space considered. Consequently, the assumptions about asymmetrical density-dependence and growth genotypes were enough to simulate catchment colonization.

Regarding length at silvering pattern, patterns were consistent in 1300 simulations of the 1920 simulations for which it was possible to calculate a pattern (table 2-3, figure 2-4 for several examples). This meant that, in situations where some females were produced, the pattern was consistent in about 2/3 of the simulations. Length at silvering pattern appeared to be sensitive to most of the parameters. The two most important were  $L_\infty$  and  $b$ : consistent pattern were much more frequent with a modality (+) (respectively 990 and 940 simulations) for these two parameters than with modality (-) (respectively 310 and 360 simulations). This is not surprising since with modality (-) for those parameters, the model produced only males in 640 simulations. Two other groups of parameters had a strong influence: male fertility/ male length at silvering and density-dependence. Consistent patterns were more frequent with low

male fertility and length at silvering (800 with modality (-) vs 500 with modality (+)), and with limited density dependence (810 with modality (-) vs 490 with modality (+)).

Parameters group	Abundance 2560	Mean length at silvering 1920	Sex ratio (proportion of females) 1610	Ratio of fast growers 2560	Mean realized growth rate 2560	The five spatial patterns 1610
$N$	(-) 1280/1280	(-) 650/960	(-) 70/800	(-) 1280/1280	(-) 1280/1280	(-) 70/800
	(+) 1280/1280	(+) 650/960	(+) 60/810	(+) 1280/1280	(+) 1280/1280	(+) 60/810
<i>fertility and</i> $L_{sm}$	(-) 1280/1280	(-) 800/960	(-) 130/800	(-) 1280/1280	(-) 1280/1280	(-) 130/800
	(+) 1280/1280	(+) 500/960	(+) 0/810	(+) 1280/1280	(+) 1280/1280	(+) 0/810
$K_{fast}(i, I)$ and $M_{fast}(i, I)$	(-) 1280/1280	(-) 650/960	(-) 70/810	(-) 1280/1280	(-) 1280/1280	(-) 70/810
	(+) 1280/1280	(+) 650/960	(+) 60/800	(+) 1280/1280	(+) 1280/1280	(+) 60/800
$K_{slow}(i, I)$ and $M_{slow}(i, I)$	(-) 1280/1280	(-) 710/960	(-) 0/810	(-) 1280/1280	(-) 1280/1280	(-) 0/810
	(+) 1280/1280	(+) 590/960	(+) 130/800	(+) 1280/1280	(+) 1280/1280	(+) 130/800
$propK$	(-) 1280/1280	(-) 650/960	(-) 90/810	(-) 1280/1280	(-) 1280/1280	(-) 90/810
	(+) 1280/1280	(+) 650/960	(+) 40/800	(+) 1280/1280	(+) 1280/1280	(+) 40/800
$\alpha$	(-) 1280/1280	(-) 810/960	(-) 60/960	(-) 1280/1280	(-) 1280/1280	(-) 60/960
	(+) 1280/1280	(+) 490/960	(+) 70/650	(+) 1280/1280	(+) 1280/1280	(+) 70/650
$n$	(-) 1280/1280	(-) 660/960	(-) 60/810	(-) 1280/1280	(-) 1280/1280	(-) 60/810
	(+) 1280/1280	(+) 640/960	(+) 70/800	(+) 1280/1280	(+) 1280/1280	(+) 70/800
$b$	(-) 1280/1280	(-) 360/640	(-) 10/640	(-) 1280/1280	(-) 1280/1280	(-) 10/640
	(+) 1280/1280	(+) 940/1280	(+) 120/970	(+) 1280/1280	(+) 1280/1280	(+) 120/970
$L_{\infty}$	(-) 1280/1280	(-) 310/640	(-) 120/640	(-) 1280/1280	(-) 1280/1280	(-) 120/640
	(+) 1280/1280	(+) 990/1280	(+) 10/970	(+) 1280/1280	(+) 1280/1280	(+) 10/970
$L_g$	(-) 1280/1280	(-) 650/960	(-) 60/800	(-) 1280/1280	(-) 1280/1280	(-) 60/800
	(+) 1280/1280	(+) 650/960	(+) 70/810	(+) 1280/1280	(+) 1280/1280	(+) 70/810
$r_K$ and $r_M$	(-) 1280/1280	(-) 630/960	(-) 40/810	(-) 1280/1280	(-) 1280/1280	(-) 40/810
	(+) 1280/1280	(+) 670/960	(+) 90/800	(+) 1280/1280	(+) 1280/1280	(+) 90/800
$\gamma_K$ and $\gamma_M$	(-) 1280/1280	(-) 730/960	(-) 60/810	(-) 1280/1280	(-) 1280/1280	(-) 60/810
	(+) 1280/1280	(+) 570/960	(+) 70/800	(+) 1280/1280	(+) 1280/1280	(+) 70/800

**Table 2-3.** Number of simulations with consistent patterns for each modality of the groups of parameters, over the number of simulations for which it was possible to calculate a pattern. The columns represent the spatial patterns and the numbers of simulations for which it was possible to estimate a pattern.



**Figure 2-4.** Simulated mean length at silvering patterns in the 13 combinations of parameters that consistently mimic the pattern described in the literature. These 13 combinations correspond to the 13 combinations that generate consistent patterns for all the five spatial patterns. Each plot stands for a combination (the number is an identifier of the combination that can be found in table 2-4) and each line stands for a replicate.

For the female ratio pattern, 130 simulations produced consistent patterns over the 1610 simulations for which it was possible to calculate a pattern (table 2-3). This pattern was mostly sensitive to four groups of parameters which correspond to the four most influential groups for the pattern of length at silvering. Patterns were consistent only when male fertility/length at silvering had modality (-) whereas  $K_{slow}/M_{slow}$  had modality (+). Moreover, consistent patterns were more frequent when  $L_{\infty}$  had a modality (-) and  $b$  a modality (+).

On the whole, 130 of the 2560 combinations produced results which were consistent for all the five patterns (table 2-4, figure 2-4 and table S2-1). These 130 simulations corresponded exactly to the 130 simulations that produced consistent sex ratio patterns, demonstrating that this last pattern was the more constraining (figure 2-5). Consequently, the interpretation regarding sensitive parameters was similar.

N	fertility,		Kfast(i, 1), Mfast(i, 1)	Kslow(i, 1), Mslow(i, 1)	propK	a	n	b	L <sub>∞</sub>	L <sub>g</sub>	r <sub>K</sub> , r <sub>M</sub>	γ <sub>K</sub> , γ <sub>M</sub>	Abundance	Sex ratio	
	L <sub>sm</sub>												Ratio of fast growers	$\overline{LS}$	
														$\overline{K(l, x)}$	
1	-	-	-	+	+	+	+	+	-	-	+	+	↘	↗	
2	+	-	-	+	-	+	+	+	-	+	+	+	↘	↗	
3	+	-	-	+	+	-	+	+	-	+	+	-	↘	↗	
4	-	-	-	+	-	-	+	+	-	-	+	-	↘	↗	
5	+	-	+	+	+	-	-	+	-	-	+	-	↘	↗	
6	+	-	-	+	-	-	-	+	-	+	-	-	↘	↗	
7	-	-	-	+	-	+	+	-	+	+	+	+	↘	↗	
8	-	-	+	+	-	-	-	+	-	+	+	-	↘	↗	
9	-	-	+	+	+	+	-	+	-	+	+	+	↘	↗	
10	-	-	+	+	-	+	+	+	-	+	-	+	↘	↗	
11	+	-	+	+	-	+	-	+	-	-	+	+	↘	↗	
12	-	-	-	+	-	+	-	+	-	-	-	+	↘	↗	
13	+	-	+	+	-	-	+	+	-	-	-	-	↘	↗	

**Table 2-4.** Results of the 13 combinations that generated five consistent patterns. The signs +/- refer to the modalities of the parameters groups. The two last columns represent the five spatial patterns. An ascendant arrows stands for positive Mann-Kendall tau value (increasing trend from downstream to upstream). Conversely, a descendant arrow stands for a negative Mann-Kendall tau value.

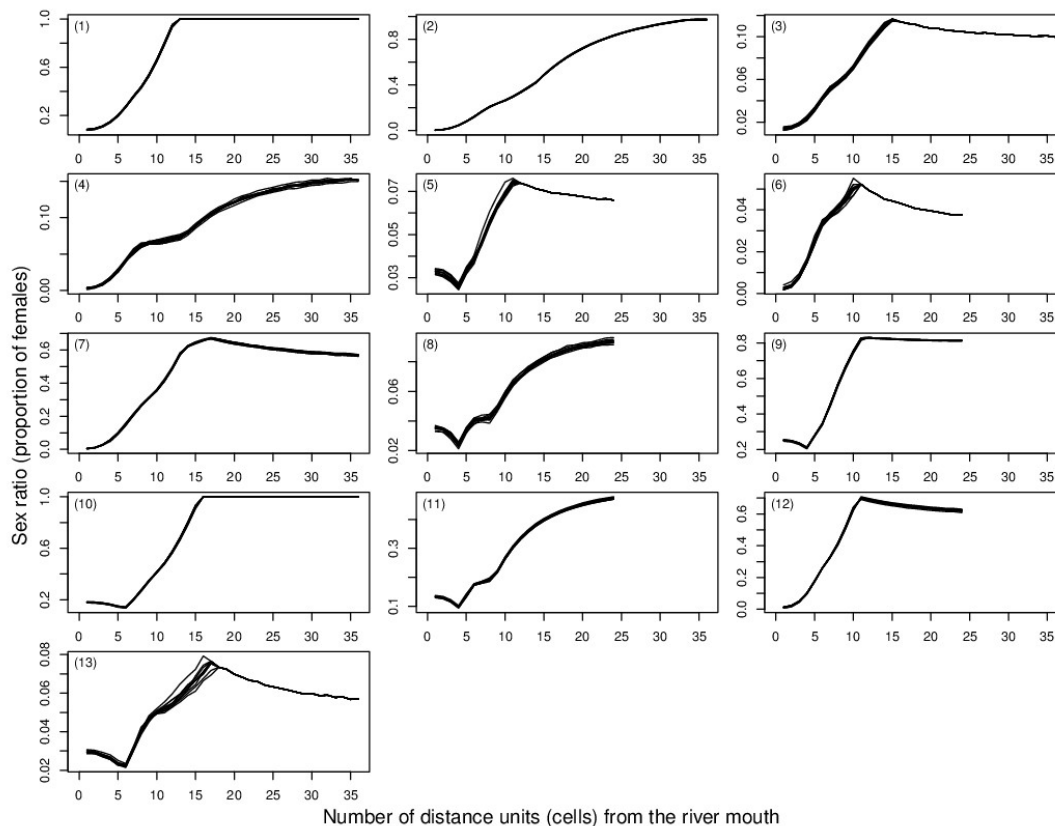
To make a summary of those results: in situations where females' fitness was favored because of a strong  $L_{\infty}$  or a strong  $b$ , i.e. a high fecundity, the model produced only females. Conversely, when females were too penalised, model produced only males. Therefore, an equilibrium was required between males and females fitnesses to mimic all patterns. The patterns in length at silvering and sex ratio were the two most constraining patterns and were mainly sensitive to four groups of patterns.

These groups of parameters set the equilibrium between males and females fitnesses (male fertility and length at silvering,  $b$  and  $L_{\infty}$ ) and the advantages between slow and fast growers. Density-dependence was also important regarding the pattern on length at silvering. We can observe that the five patterns were consistent mostly when slow growers and females were not too penalized with respect to males and fast-growers.

Some of the patterns were indeed very constrained by model assumptions so it is hardly surprising that they were mimicked by the model. For example, our constraints on mortality and growth really constrained the distribution of fishes and probably the pattern of realized growth rates in the catchment. However, those constraints were based on various observations in the literature that have rarely been considered together to see if they make sense in a



context of adaptive response. We do not specify any constraints on the sex ratio, length at maturity and relationships between sex ratio and slow/fast growers. Those results are really emerging patterns that are consistent with the literature.



**Figure 2-5.** Simulated sex ratio (proportions of females) patterns in the 13 combinations of parameters that consistently mimic the pattern described in the literature. These 13 combinations correspond to the 13 combinations that generate consistent patterns for all the five spatial patterns. Each plot stands for a combination (the number is an identifier of the combination that can be found in table 2-4) and each line stands for a replicate.

## 2.5. Discussion

### 2.5.1. Adaptation to environmental variability: phenotypic plasticity and genetic polymorphism of European eel

The European eels, and more generally, temperate eels, display fascinating characteristics: catadromy with a long larval drift, large distribution area with contrasted growth habitats, panmixia, and strong phenotypic and tactic variability at different spatial scales. Consequently, this species is relevant to explore adaptive mechanisms to environmental variability. Phenotypic plasticity has been proposed as one such mechanism because of random mating and larval dispersal that prevent local selection pressures to generate habitat-

specific adaptations, or local adaptation, from one generation to the next. Drouineau *et al.* (2014) developed the first model to explore the major role of phenotypic plasticity in both life-history traits and tactical choices as an adaptive response to spatially structured environments and density dependence. However, recently Gagnaire *et al.* (2012), Pujolar *et al.* (2014), Boivin *et al.* (2015), Côté *et al.* (2015) and Pavey *et al.* (2015) demonstrated the existence of genetic differences correlated with the environment, suggesting that part of the observed phenotypic variability had a genetic basis.

Based on the approach developed by Drouineau *et al.* (2014), the objective of this study was to propose a model based on life-history theory and optimal foraging theory to explore the role of both adaptive phenotypic plasticity and genetic polymorphism with genetic-dependent habitat selection, in the emergence of phenotypic patterns. To that end, we used a pattern-oriented modelling approach, as developed by Grimm *et al.* (1996). This kind of approach compared field observed patterns to simulated patterns and postulated that those patterns are similar, the model is likely to contain the mechanisms generating these patterns.

### **2.5.2. In which conditions were the patterns mimicked?**

Similarly to Eveel, a main limitation of our approach was that it was based on a simulation model with a pattern-oriented approach. Consequently, our results demonstrated that our assumptions were plausible, but did not demonstrate that they were correct. Such a demonstration would require demonstrating underlying mechanisms, for example by conducting complementary controlled experiments.

We built a full experimental design to explore the model. This type of approach is classical in complex model exploration (de Castro *et al.*, 2001; Faivre *et al.*, 2013). For example, in the context of sensitivity analysis of complex simulation models (Drouineau *et al.*, 2006). Our exploration goals were to generate simulations from the parameter space and analyze the qualitative differences in the model output to (i) study the impact of parameters on the model output, (ii) determine which parameters were the most important, and (iii) identify the combinations of parameters required to mimic all observed spatial patterns. In this study, 17 parameters grouped in 12 set of parameters, were chosen to define the region of the parameter space where all spatial patterns were reproduced.

To assess the influence of stochasticity, we made 10 replicates per combination. This can appear limited, however, it was impossible to increase the number of simulations and we preferred to have a better exploration of uncertainty due to uncertain parameters rather than

on stochasticity which is rather limited in our model. Stochasticity occurs during the initialization process when randomly building slow or fast value with a given probability. This corresponds to a binomial distribution which has, given the large number of individuals, a very small variance. Stochasticity also occurs in the order of individuals for step 1, but this is closely linked to the previous process and consequently also has a limited variability. This limited effect of stochasticity was confirmed by our results since patterns per combination were always consistent among replicates (figure 2-4 and 2-5).

One hundred thirty simulations among the 2560 mimicked the five spatial patterns. The fourth pattern stated that fast growers and slow growers had different spatial distributions. Fulfilling this pattern demonstrated that genetically different individuals have different habitat selection strategies to maximize their respective fitnesses. Consequently, fulfilling the five patterns suggested that, at least in certain conditions, genotype-dependent habitat selection and phenotypic plasticity could explain observed phenotypic patterns. The level of sensitivity was variable among groups of parameters, but four main groups of parameters were crucial: males' fertility and length at silvering, growth and mortality rates of slow growers, fecundity, and  $L_{\infty}$ . Density-dependence was also an important parameter regarding length at silvering. In summary, the patterns were mimicked in simulations with dominants and dominated but when dominated individuals, mainly females, were not too penalized with respect to dominants, mainly males.

Regarding the spatial patterns, higher density, higher proportions of fast growers, and faster growth rates in downstream regions were mimicked for all combinations of parameters. This suggested that in the range of variation considered, none of the parameters had effects on model outputs. This probably means that the gradient in environmental conditions and the population dynamics in the model were sufficient to reproduce these patterns, regardless of the competitive advantage of fast growers with respect to slow growers, confirming that phenotypic plasticity plays an important role in environmentally induced changes in life-history traits and demographic attributes. Concerning the two other patterns (sex ratio and length at silvering), additional hypotheses are needed regarding competition and genetic polymorphism. They were fulfilled in conditions of weak competition and when growth differences were not too strong between the two genotypes.

### **2.5.3. Consequences of intra-specific competition**

In our model, we assumed the existence of asymmetrical density dependence between fast and slow growers. We assumed that smaller individuals would avoid engaging in competition

with larger ones (regardless of sex) and would consequently be more affected by density dependence. This assumption seems ecologically realistic. Asymmetrical density dependence has been observed in plants (Weiner, 1990), insects (Varley *et al.*, 1973), and fish (Dingsør *et al.*, 2007). Intraspecific competition is a very common mechanism of density dependence, favoring large body size in fishes (Francis, 1983; Juanes *et al.*, 2002). In anguillid eels, this may be manifested through agonistic interactions (Knights, 1987; Bardonnet *et al.*, 2005), including cannibalism (Edeline and Elie, 2004). Such behaviors have been observed in yellow eels under artificial rearing conditions (Peters *et al.*, 1980; Degani and Levanon, 1983; Knights, 1987).

We modelled this asymmetric competition by specifying different levels of density-dependent mortality for slow and fast growers. Interestingly, the spatial patterns were still reproduced when setting these parameters to a similar value (not presented here). Indeed, even with similar intensity of density dependence, slow growers needed more time to reach their length at silvering and consequently, suffered competition longer. Thus, even if competition has the same impact on instantaneous mortality rates of slow and fast-growers, density dependence produces asymmetric impacts on their respective fitness. In EvEel, Drouineau *et al.* (2014) assumed the existence of asymmetric competition between males and females, with females being more affected by competition. Interestingly, we observed in our results that females had a higher proportion of slow growers than males. This means that the gender-based asymmetry proposed by Drouineau *et al.* (2014) may be an indirect result of an asymmetry between two genetically distinct types of individuals with respect to growth.

The asymmetric competition implies that fitness of individuals having a given growth genotype depends on the number of individuals having the other growth genotype, which may lead to frequency-dependent selection (Heino *et al.*, 1998). This has several implications. In the model, we assumed that individual fitness corresponded to the lifetime reproductive success called  $R_0$ , and that this fitness is maximized. However, in a frequency-dependent selection context (i) natural selection does not necessarily lead in fitness maximization (Mylius and Diekmann, 1995; Metz *et al.*, 2008), and (ii) fitness may need to be defined as an invasion criterion (Metz *et al.*, 1992). Even when fitness maximization applies,  $r$ , the population growth rate, may be a more appropriate measure of fitness than  $R_0$  depending on how density-dependence acts (Mylius and Diekmann, 1995). To ensure that our assumptions about fitness definition and maximization were valid would require a multi-generational model at the scale of the population distribution area. This would allow computing fitness for the whole life-cycle across all potential habitat types of the distribution area while accounting

for population structure in terms of genotypes or clusters. At this point, it would be interesting to explore the heritability of the different traits and the intra-generational spatially varying selection, a mechanism suggested by the SNP differences according to latitude (Pujolar *et al.*, 2011; Gagnaire *et al.*, 2012; Ulrik *et al.*, 2014).

This was not possible because of difficulties to develop a whole life-cycle model. More specifically, the fractal dimension of the eel population makes it very difficult to develop a population dynamics model for the continental phase at the distribution area scale. Moreover, such a model would require the use of stock-recruitment relationships, which is very difficult for the European eels because of insufficient data, long larval drift, and different recruitment trends through the distribution area. In this context, we had to use intra-generational model and a R0 fitness function, restricted to a single catchment and a portion of the whole life-cycle, and to postulate that this R0 was maximized.

#### **2.5.4. Reinterpreting the time-minimizing and size-maximizing strategies**

To summarize the results for combinations of parameters that mimicked observed patterns, we observed a high proportion of individuals, mainly fast growers, in the downstream environment, which corresponded to marine or brackish water. These individuals were mainly males with a constant length at silvering. In upstream areas, we found mainly slow growers, primarily females with higher length at silvering. This can aid in the reinterpretation of gender difference in life tactics (i.e., males with a time-maximizing strategy and females with a size-maximizing strategy). Our results suggest that these tactics were possibly based on the existence of two genotypes for growth. Fast growers grow fast but suffer higher mortality (because they inhabit downstream habitats with higher mortality and density); a time-minimizing strategy is suitable for them. Slow growers grow slowly but suffer lower mortality, consequently they can stay longer in continental habitats, and a size-maximizing strategy is suitable for them.

Another interesting question is whether cues are used by individuals to select their growth habitat. In the model, individuals were omnipotent and omniscient: they were able to assess the potential fitness in each cell and move in the most suitable cell. This would mean that they were able to assess the natural mortality, growth rate, and density in each cell. *Drouineau et al.* (2014) suggested that temperature might be one of the main proximal cue used by individuals to assess the suitability. Regarding density-dependence, reaction to aggressiveness (Geffroy and Bardonnnet, 2012) or cons-specific odors (Schmucker *et al.*, 2016) were observed

on growth and propensity to migrate. Vélez-Espino and Koops (2010) also revealed temperature as main factor explaining variation in life-history traits. Our model suggested that density in various habitats was also probably a main cue, especially for slow growers, which tended to minimize competition.

### **2.5.5. Perspectives**

#### **► Exploring conditions in which phenotypic plasticity is adaptive**

It has been demonstrated that phenotypic plasticity allows short-term adaptation to environmental heterogeneity for many species (Schlichting, 1986; Sultan, 1987; Scheiner, 1993; Pigliucci, 2005). However, the fitness gain arising from phenotypic plasticity should overcome its cost to be selected. This last point has not been demonstrated for eels. One possibility would be to simulate the evolution of a plastic reaction norm, for example length at silvering, close to the model developed by Marty *et al.* (2011). Following Ernande *et al.* (2004) and based on adaptive dynamics models (Mylius and Diekmann, 1995), it would be interesting to explore in which environmental and density-dependence conditions, phenotypic plasticity may be selected as an adaptive mechanism despite its costs, and if plasticity is still adaptive in a context of low densities after a population collapse.

#### **► Assessing the impact of anthropogenic pressures at the distribution area scale**

Another perspective is to assess the impact of anthropogenic pressures on eel populations. Drouineau *et al.* (2014) mentioned that, because of phenotypic plasticity, anthropogenic pressures are not only a source of mortality, but may also affect sex ratio or mean length at silvering. The existence of two genotypes for growth suggests that anthropogenic activities may act as selective forces. Recently, Podgorniak *et al.* (2015) demonstrated that human-induced obstacles to migration could act as an evolutionary pressure. Concerning this, Boulenger *et al.* (2016) highlighted that human pressures impact survival, leading to different life-history strategies.

To conclude, our model provided new insights on eel adaptive mechanisms to heterogeneous environments. Phenotypic plasticity and genotype-dependent habitat selection are two types of mechanisms that can explain the patterns in life-history traits observed in natural environments at the river catchment scale. A better understanding of these mechanisms is crucial to interpret the observations made in the environment, the effects of anthropogenic pressures on the population, and to understand if eels are still adapted in the context of depleted population size and climate change.

## **2.6. Acknowledgements**

This study was supported by the Hynes project between Irstea and EDF R&D. We would like to thank Christian Rigaud and Laurent Beaulaton and two anonymous referees for their contribution to the discussion.

## ***Take-home messages***

- ✓ **Phenotypic plasticity** and **genotype-dependent habitat selection** maintained by **genetic polymorphism** may be complementary **adaptive mechanisms** to deal with environmental heterogeneity. In such a scheme:

Phenotypic plasticity plays an important role in the spatial correlations between life history traits, demographic parameters and environmental gradients. Habitat selection and sex-determination are the result of an interaction between the environmental conditions, the genotype of individuals and the intraspecific competition.

- ✓ The different **life history strategies** used by **males** and **females** could be **reinterpreted**:

Sex determination, which subsequently determines individual life strategies, is partially related to growth that is under the influence of environmental conditions and individual genotypes. In the model, fast-growing individuals had higher intrinsic mortality rates and tend to settle in habitats with high densities, favoring a time-minimizing strategy. Conversely, slow-growing individuals had lower intrinsic mortality rates and avoid competition by settling habitats with lower densities, favoring a size-maximizing strategy.

- ✓ **Spatial patterns** are **mimicked** in particular **conditions** of parameters:

In the reference simulation all spatial patterns were mimicked. The model exploration shows that patterns are especially sensitive to a set of parameters: all patterns were mimicked with parameters that ensure slow-growing individuals and females were not too penalized with respect fast-growing individuals and males.

## ***To go further***

These results raise an immediate question about the consequences of anthropogenic pressures on the population. Since anthropogenic pressures take place in different habitats and affect different types of individuals, they are likely to interplay with adaptive mechanisms and have indirect consequences on life history traits, such as size at maturity, or demographic parameters, such as sex ratio in addition to be sources of direct mortality. The consequences of these pressures will be different and in accordance to the adaptive mechanisms that modify the traits of individuals.



**Chapter 3:**

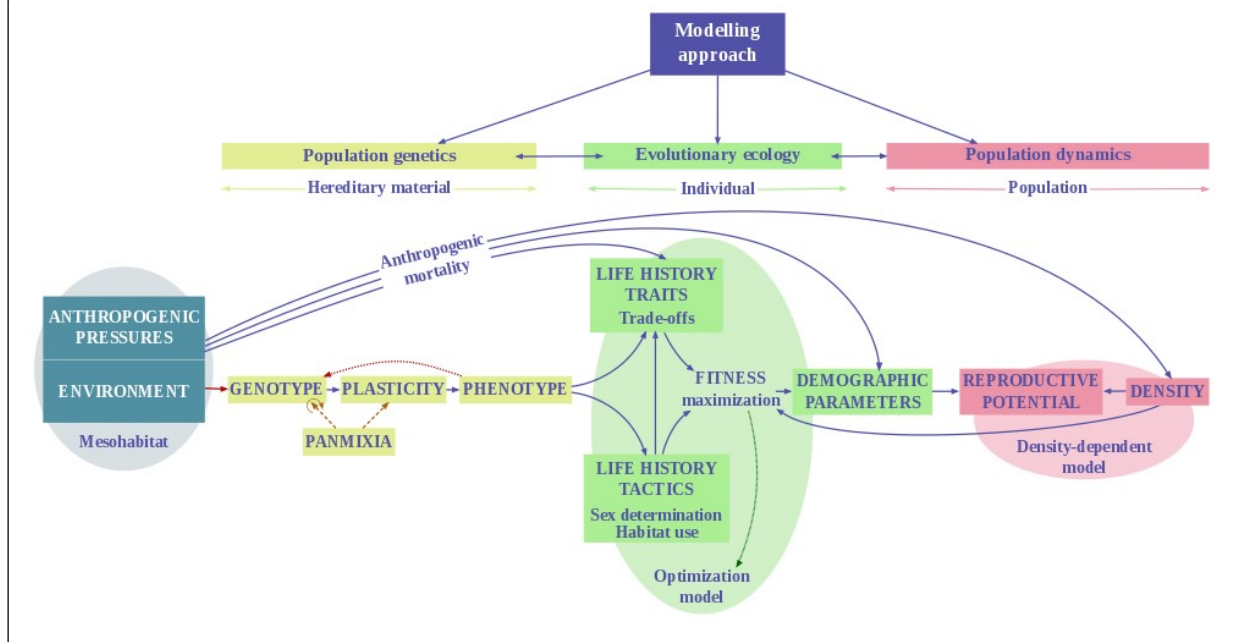
**Impacts that cause the highest direct mortality of  
individuals do not necessarily have the greatest influence  
on temperate eel escapement**

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*Published article:* Mateo, M., Lambert, P., Tétard, B., Drouineau, H., 2017. Impacts that cause the highest mortality of individuals do not necessarily have the greatest influence on temperate eel escapement. *Fisheries Research*, 197: 51-59.

## Foreword

Given the current status of temperate eels, conservation initiatives have flourished to reduce sources of anthropogenic mortalities. In this context, there is a need of a method to assess the impact of those pressures to prioritize management actions. However, most studies and the management target enforced by the EU Regulation, focus on direct mortality rates that neglects the adaptive processes shaping individuals' response to their environment and exploitation. In view of this, we incorporated different anthropogenic pressures within GenEveel: glass eel and silver eel fisheries, obstacles to upstream migration and hydropower facilities. Each anthropogenic pressure affects specific life stages in specific habitats of the river basin. A numerical exploration of the model was carried out using a Latin Hypercube Sampling design and General Additive Model. These analyses assessed the impact of each anthropogenic pressure, in terms of mortalities rates, and on other life history traits and demographic parameters (sex ratio, proportion of slow-growing individuals, average length-at-silvering and overall egg production). The following figure summarizes the positioning of this chapter within the overall PhD project.



### 3.1. Abstract

Temperate eels are three panmictic catadromous species with a long period of oceanic passive larval drift and large distribution areas in contrasting environments. Spatial patterns of life history traits have been observed, and are correlated with environmental gradients, and may arise from both adaptive phenotypic plasticity and genetic polymorphism. This raises the question of the effect of spatially heterogeneous anthropogenic pressures on these populations. In this context, we used GenEveel, an individual-based optimization model that includes both phenotypic plasticity and genetic polymorphism, to explore the effects of different kinds of anthropogenic pressures: glass eel and silver eel fisheries, obstacles to upstream migration, and turbine mortality. More specifically, we analyzed the effects of these pressures on five output variables: the number of escapees, the proportion of females, the proportion of slow growers, the mean length-at-silvering and the resulting egg production. Our results suggest that phenotypic plasticity could act as a compensatory mechanism that mitigates the effects of some pressures (glass eel fishery and obstacles to upstream migration) and could be a source of resilience for the population, while other pressures did not show any compensatory effect (silver eel fishery and turbine mortality). Therefore, global impacts are very hard to assess, and the pressure that kills the most individuals does not necessarily have the biggest impact on the spawning biomass.

*Keywords:* Temperate eels; anthropogenic pressures; adaptive mechanisms; life history traits; modeling

### 3.2. Introduction

Temperate eels (*Anguilla rostrata*, *A. anguilla*, *A. japonica*) are three catadromous species that reproduce at sea and grow in continental waters. They display remarkable similarities in life history traits (Daverat *et al.*, 2006; Edeline, 2007). The three populations are panmictic (Als *et al.*, 2011; Han *et al.*, 2010; Pujolar, 2013). Reproduction occurs in the Sargasso Sea for *A. anguilla* and *A. rostrata* (McCleave, 1993; Schmidt, 1923) and west of the Mariana Islands for *A. japonica* (Tsukamoto, 1992). Larvae (known as leptocephali) are subject to a long and passive trans-oceanic drift. When arriving on the continental shelves, leptocephali metamorphose into young and transparent eels, called glass eels (Tesch, 2003), and enter continental waters, where they become pigmented yellow eels, the immature adult stage. After a variable period, generally lasting from three to 15 years, yellow eels metamorphose again into silver eels (this metamorphosis is generally called “silvering”), the seaward migration stage. They achieve their sexual maturation while migrating back to spawning grounds. Because of the long larval drift, their distribution area is very large, and the growth phase can occur in very heterogeneous river basins, from Morocco to Norway (Tesch, 2003) for the European eel, from Venezuela to Greenland for *A. rostrata* (Helfman *et al.*, 1987), and from the northern Philippines to Korea for *A. japonica* (Tsukamoto, 1992).

Concomitantly to this environmental heterogeneity, temperate eels display remarkable life history trait patterns at both distribution and river catchment scales (Vélez-Espino and Koops, 2009). Among them, the sex ratio is highly variable at different spatial scales: female-biased sex ratios are generally observed in the northern part of the distribution area, while male-biased sex ratios are observed in the southern part (Kettle *et al.*, 2011). At the catchment scale, sex ratios are male biased in downstream habitats (Oliveira and McCleave, 2000; Tesch, 2003). This question of sex ratio is relevant since eel sex is not genetically determined, but depends on environmental conditions (Davey and Jellyman, 2005; Geffroy, 2012; Geffroy and Bardonnet, 2015), and males and females display very different life history tactics (Helfman *et al.*, 1987). Males are assumed to have a time-minimizing strategy; since their reproductive success does not depend on their size, they are assumed to leave continental waters as soon as they reach the minimal size required to successfully migrate back to spawning grounds (Oliveira, 1999; Van Den Thillart *et al.*, 2007; Vollestad, 1992). On the other hand, female reproductive success is assumed to be a trade-off between size at maturity (known as length-at-silvering) and survival, called a size-maximizing strategy. This size-maximizing strategy assumption is supported by the observation of larger females in the

northern part of the distribution area (slow growth but lower mortality) than in the southern part (Davey and Jellyman, 2005; Helfman *et al.*, 1984).

Indeed, eels display a large range of tactics in terms of habitat use for growth, with some settling in estuarine waters, while others moving far upstream in river catchments (Arai and Chino, 2012; Daverat *et al.*, 2006; Tsukamoto *et al.*, 1998). Higher densities are observed in downstream habitats, which are the most accessible and the most favorable in terms of growth rates (Daverat *et al.*, 2012; Helfman *et al.*, 1984; Melià *et al.*, 2006). However, other eels also settle in the upper parts of river catchments. Edeline (2007) proposed that more limited intraspecific competition may overcome migratory energy costs, such as loss in growth rate. This assumption was challenged by Cairns *et al.* (2009), who did not observe a decrease in natural mortality in upstream habitats that would outweigh the cost of migration and the decrease in growth rate.

Few studies have explored whether the observed spatial phenotypic patterns are the result of adaptive mechanisms to environmental variability, and they therefore remain poorly understood. The panmixia and long and passive larval drifts impair the possibility of local adaptation. Phenotypic plasticity has been proposed as an adaptive response to environment variability for many species (Gotthard and Nylin, 1995; Levins, 1963; Pigliucci, 2005), and Ernande and Dieckmann (2004) demonstrated that density dependence favors the selection of plastic phenotypes. In this context, assuming that phenotypic plasticity is an adaptive response to environmental variability, Drouineau *et al.* (2014) developed an optimization model that was able to mimic most of the observed patterns at both the distribution area and river catchment scales. The existence of correlations between genotypic patterns and environmental conditions have been observed (Boivin *et al.*, 2015; Côté *et al.*, 2015, 2014, 2009; Gagnaire *et al.*, 2012; Pujolar *et al.*, 2014; Ulrik *et al.*, 2014). Côté *et al.* (2014, 2009) and Boivin *et al.* (2015) observed differences in growth rates depending on eel origin that were preserved after several months in common garden experiments. Pujolar *et al.* (2014), Gagnaire *et al.* (2012) and Ulrik *et al.* (2014) observed patterns in single-nucleotide polymorphisms correlated with environmental conditions. They assumed that individual genetic differences contribute to the emergence of phenotypic spatial patterns because of differential selection by the environment, but that these differences are reshuffled in each generation because of panmixia. In this context, Mateo *et al.* (2017a) developed a new model, called GenEveel that was able to mimic all observed patterns assuming the existence of genetic polymorphism in growth rate and adaptive phenotypic plasticity. It suggested that the genetic polymorphism and phenotypic plasticity may have been selected by natural selection as an adaptation to environmental

heterogeneity and density dependence. In this context, selection of growth habitats, length-at-silvering and sex determination would be plastic traits that enable individuals to optimize their fitness in a wide range of environments.

This issue of adaptation to environmental variability is presently crucial because temperate eels have suffered dramatic collapses (Dekker, 2009; Dekker and Casselman, 2014; Jacoby *et al.*, 2015), and *A. anguilla* is classified as critically endangered by the IUCN (Jacoby and Gollock, 2014b), while *A. rostrata* and *A. japonica* are classified as endangered (Jacoby *et al.*, 2014; Jacoby and Gollock, 2014ba). Several factors have been proposed to explain these declines (Jacoby *et al.*, 2015), including changes in oceanic conditions (Castonguay *et al.*, 1994), contamination and habitat degradation (Belpaire *et al.*, 2016; Byer *et al.*, 2015), parasitism (Feunteun, 2002; Kirk, 2003), fishing pressure (Dekker, 2003a), fragmentation including massive habitat loss (Kettle *et al.*, 2011), and hydroelectricity-induced mortality (Castonguay *et al.*, 1994). In view of this situation, the European Commission introduced European Regulation N° 1100/2007, imposing a new set of measures designed to reverse the decline. Since eel management is under the responsibility of member states, each member state was required to implement Eel Management Plans, enforcing management measures to decrease all sources of anthropogenic mortalities. Because of the heterogeneity in anthropogenic pressures, these measures are quite heterogeneous, targeting different types of pressures among countries and regions. The impact of anthropogenic pressures is indeed generally assessed by quantifying the induced mortality rates. Indeed, the European Regulation uses the biomass of escapees as a management target (the Regulation required that management measures should be implemented to ensure that silver eel escapement is at least 40% of the escapement in pristine conditions). However, in the presence of genetic polymorphism and phenotypic plasticity, anthropogenic pressures can have a wide range of effects in terms of life history traits. They can be a selective pressure advantaging fast or slow growers or have consequences in terms of the sex ratio, length-at-silvering or spatial distribution by affecting plastic traits.

In view of this, we decided to use GenEveel (Mateo *et al.*, 2017a) to assess the impact of anthropogenic pressures on silver eel escapement, not only by quantifying the number of escapees, but also by assessing their effect on the sex ratio, the proportions of slow and fast growers, the length-at-silvering and the resulting egg production after a generation in continental waters exposed to different kinds of anthropogenic pressures. We chose to focus on four kinds of anthropogenic pressures: (i) the glass eel fishery, (ii) obstacles to upstream migration, (iii) turbine mortality during downstream migration, and (iv) the silver eel fishery.

(i) Glass eel fishing is a widespread activity in France, the UK, Spain, Portugal and Italy (ICES, 2016), in some North American rivers (Cairns *et al.*, 2008; Dutil *et al.*, 2009; Jessop, 1998) and in Asian waters (Tatsukawa, 2003). In the Bay of Biscay, the glass eel fishery used to be the most important fishery in France in terms of turnover (Castelnaud, 2000), and the Bay of Biscay is assumed to receive the main part of the total recruitment (Dekker, 2000). These fisheries harvest young, sexually undetermined individuals entering continental waters. In some river basins, the glass eel fishery can catch nearly all individuals entering the basins, such as in the Vilaine River, where the recruitment rate is less than 5% some years (Briand *et al.*, 2005). (ii) Fragmentation by human-induced obstacles can impact upstream migration (Drouineau *et al.*, 2015; Tremblay *et al.*, 2016). By blocking individuals during their upstream migration, they confine them into restricted parts of river basins (Kettle *et al.*, 2011). (iii) During downstream migration, they can impair migration to the sea (Drouineau *et al.*, 2017; Tremblay *et al.*, 2016), especially because of mortality induced by passage through hydropower facilities (Pedersen *et al.*, 2012; Winter *et al.*, 2006). (iv) Finally, silver eel fishing is a widespread activity (Aalto *et al.*, 2016; Amilhat *et al.*, 2008; Bernotas *et al.*, 2016; Verreault *et al.*, 2012; Westerberg and Wickström, 2016) that targets large silvers when they migrate back to sea.

We adapted the GenEveel model and developed five output indicators (number of escapees, proportion of females, egg production, length-at-silvering, and proportion of slow growers) to consider the impact of anthropogenic pressures on population dynamics. We carried out a numerical exploration of the model and fitted statistical models to assess the effects of the anthropogenic pressures on the outputs. This enables us to quantify the impact of pressures on the different components and to discuss the implications.

### **3.3. Materials and methods**

#### **3.3.1. GenEveel**

GenEveel is an individual-based model. It postulates that the population is composed of two types of individuals (slow and fast growing) based on a genetic polymorphism and that individuals determine their sex and select their growth habitat and length-at-silvering to optimize their fitness. Assuming that males follow a time-minimizing strategy, their fitness is assumed to be proportional to their survival rate until a constant length-at-silvering is reached. On the other hand, females are assumed to follow a size-maximizing strategy, and their fitness is constrained by a trade-off between fecundity at length-at-silvering and the survival rate to this length, with the length-at-silvering selected to optimize this trade-off. Growth is assumed

to be a combination of intrinsic growth rates (slow and fast growers) modulated by environmental effects, with faster growth rates in downstream habitats. Survival is a product of environmental effects and density dependence.

The environment, a single river catchment, is represented by 30 contiguous cells (growth habitat) with prespecified effects on individual growth and mortality rates. One by one, individuals determine their sex and select their growth habitat and length-at-silvering based on the combination that maximizes fitness.

A complete description of the model can be found in Mateo *et al.* (2017a). We parameterized the model as in the reference simulation in Mateo *et al.* (2017a) for this study, which consisted of the best set of values found in the literature for the European eel. Seventeen parameters were used in the model to characterize the environment (as cells in the river catchment) and individuals (demographic, growth and fitness parameters).

### **3.3.2. Impacts of anthropogenic pressures**

#### **3.3.2.1. Glass eel fishery**

The glass eel fishery was characterized by the catch rate,  $g$ , i.e., the proportion of individuals caught by the fishery. The glass eel fishery was assumed to harvest individuals before sex determination and habitat selection. Consequently, if  $N$  eels entered the catchment, glass eel catches were assumed to follow a binomial distribution,  $binomial(N, g)$ , and the number of survivors was the complement.

#### **3.3.2.2. Obstacles to upstream migration**

We used two obstacles (0.66 and 0.1, respectively, according to the relative distance along the river and referring to the 20<sup>th</sup> and 3<sup>th</sup> cells of the 30 that represent the river catchment) characterized by their blockage rates ( $b_{0.66}$  and  $b_{0.1}$ , respectively) and locations ( $po_{0.66}$  and  $po_{0.1}$ , respectively, which represent cells of the catchments). For each individual, we restricted the possible combinations of growth habitat, length-at-silvering and sex to cells near the river mouth,  $po_{0.1}$ , with a probability  $b_{0.1}$  and to cells near the river source,  $po_{0.66}$ , with probability  $(1-b_{0.1}) \cdot (1-b_{0.66})$ .



### 3.3.2.3. Turbine mortality

The two obstacles also had turbine mortality rates ( $t_{0.66}$  and  $t_{0.1}$ , respectively). Each individual located upstream of the obstacle and that survived until length-at-silvering were killed by turbines, with a probability corresponding to the mortality rates.

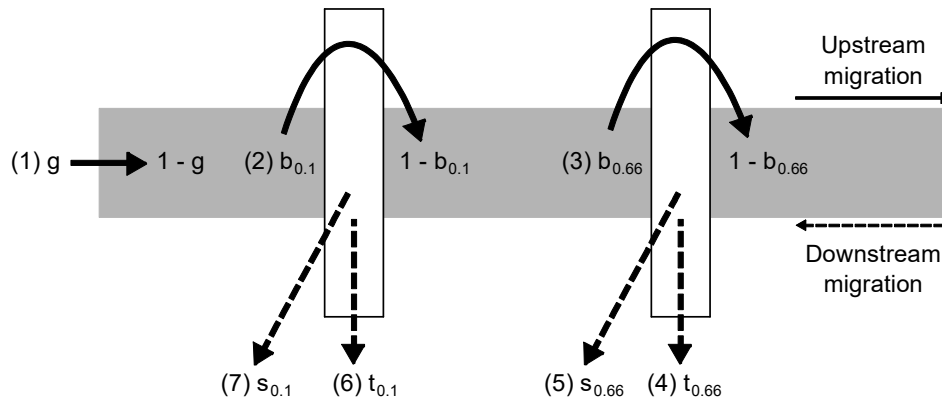
### 3.3.2.4. Silver eel fishery

The silver eel fishery was assumed to affect eels in a similar way to the mortality due to turbines. We assumed that two successive silver eel fisheries occur, one located near the river source at position  $ps_{0.66}$  and one near the river mouth at position  $ps_{0.1}$ . These fisheries were characterized by catch rates of  $s_{0.66}$  and  $s_{0.1}$ , respectively. Each individual located upstream of the obstacle and that survived until length-at-silvering were caught by silver eel fisheries with a probability corresponding to the catch rates.

### 3.3.3. Model sequence

The glass eel fishery occurred first, as it is the first source of mortality encountered by young eels. Then, GenEeel was used to position individuals in the catchment with restrictions due to obstacles to determine their sex, length-at-silvering and survival probability to length-at-silvering. The survivors that reached maturity in the upper parts of the river migrated downstream and were impacted by the silver eel fishery and the turbine located near the river source. The remaining fish were then impacted by the silver eel fishery and the turbine located near the river mouth.

Figure 3-1 represents the model sequence. A proportion,  $g$ , of recruits was first harvested by the glass eel fishery. Among the  $1-g$  individuals that escaped the glass eel fishery, a proportion,  $b_{0.1}$ , was constrained to settle downstream of the first obstacle, and only  $(1-b_{0.1}) \cdot (1-b_{0.66})$  were free to settle in the whole catchment. After sex determination and habitat selection (the combination that maximized the expected fitness), individuals underwent downstream migration and were harvested with a given probability if they passed a silver eel fishery or a turbine.



**Figure 3-1.** Conceptual representation of the catchment, indicating the seven anthropogenic pressures considered in the study: 1)  $g$ : catch rate by the glass eel fishery, 2)  $b_{0.66}$  and 3)  $b_{0.1}$ : blockage rates (located near the river source and the river mouth, respectively), 4)  $t_{0.66}$  and 6)  $t_{0.1}$ : turbine mortality rates (located near the river source and the river mouth, respectively), 5)  $s_{0.66}$  and 7)  $s_{0.1}$ : catch rates by the silver eel fisheries (located near the river source and the river mouth, respectively).

We computed five indicators based on the survivors (escapees):

1. number of escapees ( $Ns$ );
2. mean length-at-silvering ( $Ls$ );
3. proportion of females (sex ratio) ( $SR$ );
4. egg production (sum of female fecundity among survivors) ( $E$ ); and
5. proportion of slow growers ( $Sl$ )

The first indicator is the traditional indicator for quantifying mortality and is generally used as a proxy of the spawning biomass, although not accounting for trait modifications. The next two indicators aim to measure the effect of anthropogenic pressures on two plastic traits. The fourth indicator quantifies the total effects of pressures on egg production and is a more direct proxy than the number of escapees because it combines both induced mortality and trait modifications. The last indicator is used to quantify the selective pressure induced by each anthropogenic pressure.

### 3.3.4. Numerical exploration of the model and results analysis

#### 3.3.4.1. Experimental design

Our objective was to compare the intensity of effects of anthropogenic pressures rather than locations. Therefore, we chose a set of parameters that were similar among pressures. For locations, pressure positions were set at the same cells in the catchment:  $ps_{0.66}=po_{0.66}=20$  and  $ps_{0.1}=po_{0.1}=3$ . To explore the effect of pressure intensity, we used Latin hypercube sampling (LHS) (Iman and Conover, 1980; McKay, 1988; McKay *et al.*, 2000). LHS is classical tool used to carry out global sensitivity analysis of models (Blower and Dowlatabadi, 1994;

Helton *et al.*, 2005; Helton and Davis, 2003; Manache and Melching, 2004). It allows an efficient exploration of the input parameter space; estimation of output statistics, such as sensitivity indices; and variance decomposition. It subdivides each parameter into  $X$  intervals and then samples those intervals with probability  $1/X$  (random sampling within intervals), ensuring that each parameter interval is sampled only once and that two parameters are not sampled in the same interval in the same experiment. By doing this, LHS ensures a random association of parameter values and allows their respective effects to be disentangled.

In our LHS, the resulting design matrix is made up of all anthropogenic pressures ( $g, b_{0.66}, b_{0.1}, s_{0.66}, s_{0.1}, t_{0.66}, t_{0.1}$ ) in columns, defined at an interval of 0 (no pressure) to 1 (impact all individuals). Intervals were then subdivided into 100 subintervals, corresponding to simulations in rows. We built 100 independent LHSs to account for model stochasticity, resulting in 10,000 simulations.

### 3.3.4.2. Results analysis

For each output  $Y$ , we fitted a generalized additive model on the 10,000 simulations using  $Y$  as a dependent variable and the anthropogenic pressures ( $g, b_{0.66}, b_{0.1}, s_{0.66}, s_{0.1}, t_{0.66}, t_{0.1}$ ) as explanatory variables:

$$(1) Y \sim s(g) + s(s_{0.1}) + s(s_{0.66}) + s(b_{0.1}) + s(b_{0.66}) + s(t_{0.1}) + s(t_{0.66})$$

with  $s()$  as a smoother function.

The Gaussian family was used for the number of escapees ( $Ns$ ), length-at-silvering ( $Ls$ ) and egg production ( $E$ ) (a log transformation was used for  $Ns$  and  $E$  to normalize the distribution), while the binomial family was used for the proportion of females ( $SR$ ) and slow growers ( $SI$ ).

Generalized additive models (GAMs) were fitted using the package `mgcv` (Wood, 2011) in R (R Development Core Team, 2011). Plots of marginal effects were used to explore the relations between pressures and outputs. The signs of the regression coefficients indicated whether the pressure has a positive or negative impact on the indicator. The proportion of explained variance was used to compare the strength of the effects of anthropogenic pressures.

We computed the partial rank correlation coefficients (PRCC) (Saltelli *et al.*, 2000) to assess the global effects of pressures on each output variable using the package `sensitivity` (Pujol *et al.*, 2016). These coefficients assessed the degree of association between an output variable and a predictor after removing the effects of other predictors.

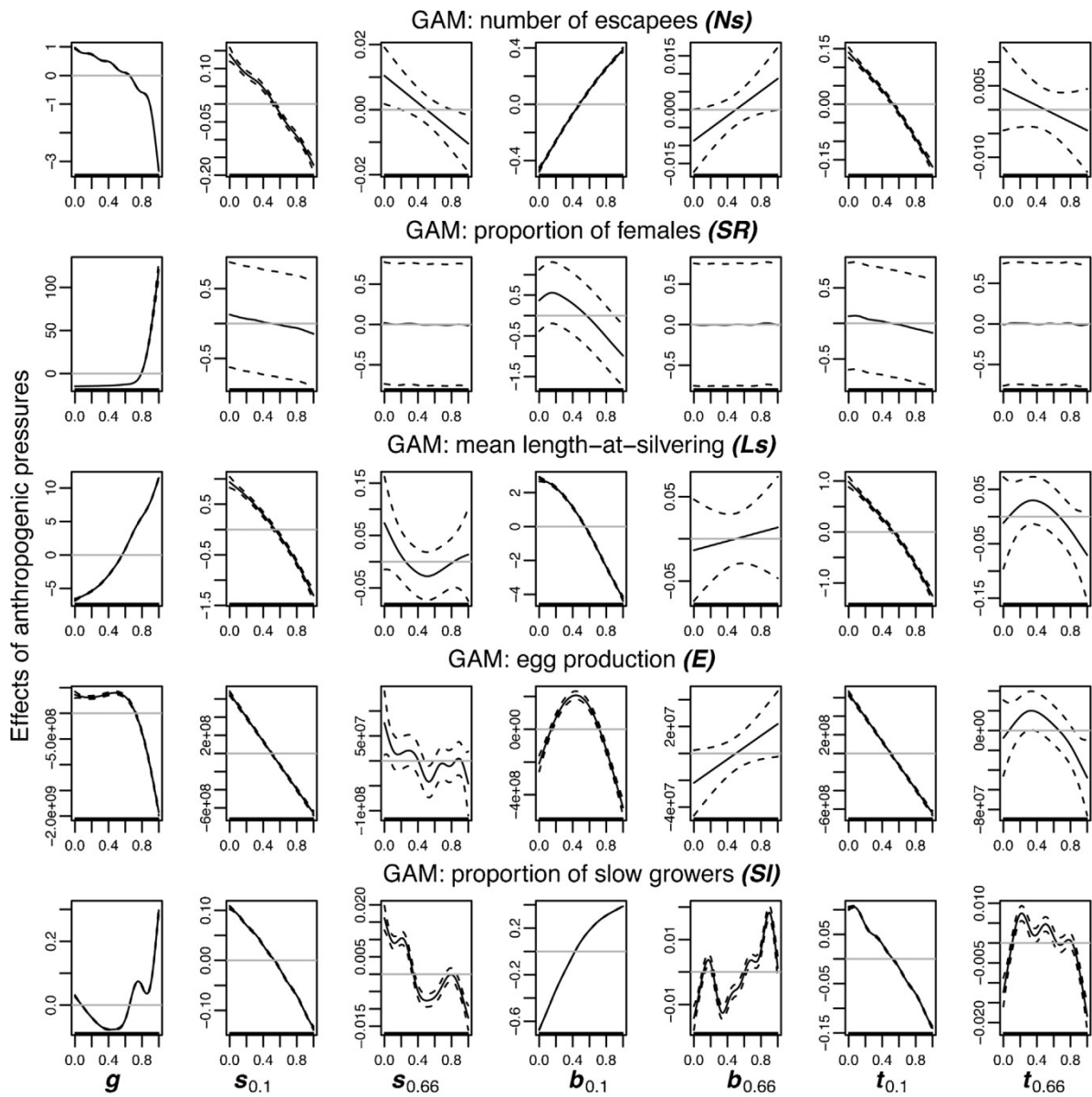
### 3.4. Results

The PRCC are summarized in table 3-1. The glass eel fishery had the most important influence; it had negative effects on the number of escapees and positive effects on the length-at-silvering and the proportion of females. Its influence was more limited on egg production (negative effects) and the proportion of slow growers (positive effects). Regarding egg production, the silver eel fishery and turbine located near the river mouth had negative effects that were similar to that of the glass eel fishery. Unsurprisingly, they also had important negative effects on the proportion of slow growers, the mean length-at-silvering and the number of escapees. Obstacles located near the river mouth had a great influence on all indicators except egg production; they had negative effects on the length-at-silvering and the proportion of females and positive effects on the number of escapees and the proportion of slow growers. The turbine and silver eel fishery located near the river source had lesser influences on the model outputs than the rest of the pressures.

	<i>Ns</i>	<i>Ls</i>	<i>SR</i>	<i>E</i>	<i>Sl</i>
<i>g</i>	-0.95	0.94	0.95	-0.49	0.22
<i>b<sub>0.1</sub></i>	0.77	-0.75	-0.57	-0.01	0.88
<i>b<sub>0.66</sub></i>	0.02	0	0.01	0.01	0.02
<i>s<sub>0.1</sub></i>	-0.39	-0.33	-0.14	-0.42	-0.35
<i>s<sub>0.66</sub></i>	-0.02	0	0.01	-0.01	-0.03
<i>t<sub>0.1</sub></i>	-0.39	-0.33	-0.12	-0.4	-0.35
<i>t<sub>0.66</sub></i>	-0.01	-0.02	-0.01	-0.01	-0.01

**Table 3-1** Partial rank correlation coefficients between output variables (columns) and pressures (rows). A positive coefficient indicates a positive correlation. *g*: glass eel fishery, *s<sub>0.66</sub>*: silver eel fishery located near the river source, *s<sub>0.1</sub>*: silver eel fishery located near the river mouth, *t<sub>0.66</sub>*: turbine located near the river source, *t<sub>0.1</sub>*: turbine located near the river mouth, *b<sub>0.66</sub>*: obstacle to upstream migration, *b<sub>0.1</sub>*: obstacle to downstream migration.

The GAM summaries are presented in table S3-1. All pressures had a negative impact on the number of escapees (*Ns*) except for obstacles located near the river mouth (*b<sub>0.1</sub>*), which had a positive impact (table 3-1 - figure 3-2). Indeed, they blocked individuals in a zone with faster growth rates, decreasing the time to length-at-silvering and increasing the survival until escapement. Interestingly, the slope of the glass eel fishery effect was more moderate for small intensities than for strong intensities (figure 3-2). At low intensities, fisheries led to a decrease in density and therefore to lower density-dependent mortality and a higher survival rate of the remaining individuals, which balanced the effect of the fishery.



**Figure 3-2.** Effects of the pressures on the five indicators estimated by the GAMs. *g*: glass eel fishery,  $s_{0.66}$  and  $s_{0.1}$ : silver eel fisheries located near the river source and the river mouth, respectively,  $t_{0.66}$  and  $t_{0.1}$ : turbines located near the river source and the river mouth, respectively,  $b_{0.66}$  and  $b_{0.1}$ : obstacles located near the river source and the river mouth, respectively.

Regarding the proportion of females (figure 3-2 - table 3-1), the glass eel fishery had the greatest impact by removing individuals. It drastically decreased the density and consequently the density-dependent mortality, favoring females, especially at high intensity (figure 3-2). The patterns were less obvious for the other pressures, except for obstacles located near the river mouth ( $b_{0.1}$ ); after a given level, an increasing blockage rate increased the density in downstream habitats, increasing the density-dependent mortality and favoring males (figure 3-2).

The effects of other pressures (turbines and the silver eel fishery) was not due to density dependence, but rather the distribution of individuals in the river catchment; there was a female-biased sex ratio in the upstream habitat, and females were consequently more impacted by mortalities directed toward downstream migrants.

Regarding the length-at-silvering (table 3-1 - figure 3-2), the results were very similar to the proportion of females since males have a constant and low length-at-silvering, while females have a variable and larger length-at-silvering. However, the effects of the silver eel fishery and the turbine located near the river mouth ( $s_{0.1}$  and  $t_{0.1}$ , respectively) were much more obvious.

Although obstacles located near the river mouth and the glass eel fishery ( $b_{0.1}$  and  $g$ , respectively) were the pressures most impacting the three first indicators, the silver eel fishery and the turbine located near the river mouth ( $s_{0.1}$  and  $t_{0.1}$ , respectively) had similar influences on egg production, and they were more important than the glass eel fishery ( $g$ ) (table 3-1). Indeed, the effect of  $g$  on the number of escapees was mitigated by the lower competition and the production of females in downstream zones of the catchment, explaining the flat effects observed for low  $g$  (figure 3-2). For obstacles located near the river mouth ( $b_{0.1}$ ), the increase in the number of escapees explained an increase in egg production when blockage was low. However, for high blockage rates, the increase in escapees (figure 3-2) was outweighed by a higher proportion of males (figure 3-2), leading to a decrease in egg production (figure 3-2). For the silver eel fishery and the turbine located near the river mouth ( $s_{0.1}$  and  $t_{0.1}$ , respectively), their impacts on both the proportion of females and the number of escapees were negative, decreasing the effect on egg production.

Finally, the silver eel fishery and the turbine located near the river mouth decreased the proportion of slow growers because those individuals tended to settle in upstream habitats and were consequently more impacted than fast growers (table 3-1 - figure 3-2). On the other hand, obstacles located near the river mouth tended to increase the proportion of slow growers; those individuals were blocked in downstream habitats where growth was faster, resulting in a better survival until length-at-silvering (as observed in the number of escapees ( $N_s$ ), figure 3-2). However, blocked individuals were “constrained” to remain in downstream habitats, resulting in a decrease in their fitness and to strong competition with fast growers. Interestingly, the glass eel fishery, which harvested slow and fast growers equally, tended to favor fast growers at low intensities and slow growers at high intensities (figure 3-2; at high intensities, the very low density-dependent mortality strongly benefited slow growers by removing fast growers, which were dominant competitors).

## **3.5. Discussion**

### **3.5.1. Assessing the impact of anthropogenic pressures: why consider other indicators than only the number of escapees?**

The collapse in temperate eel populations required immediate actions (Dekker, 2009) to decrease all sources of anthropogenic pressures. This is the spirit of the European Regulation on the European eel and of subsequent eel management plans in European Union Member States. Logically, the first criteria used to assess the impact of anthropogenic pressures are mortality rates and escapement. However, given the large phenotypic variability observed at the distribution scale (Vélez-Espino and Koops, 2009), likely due to both phenotypic plasticity (Drouineau *et al.*, 2014; Mateo *et al.*, 2017a) and the consideration of genetic polymorphism (Côté *et al.*, 2015), the number of escapees may not be sufficient, and it is worthwhile to explore the effects of anthropogenic pressures on other components. Thus, the aim of this study was to use the GenEveel model to explore the effects of different types of anthropogenic pressures on the number of escapees as well as other indicators accounting for life history traits and genetic polymorphism.

### **3.5.2. Using a theoretical model to explore the possible consequences of anthropogenic pressures**

GenEveel is a theoretical model, but is parameterized with the best biological information available in the literature. Regarding the intensity, high levels have been observed for each type of pressure. For example, the exploitation rates of glass eels were found to be very high in some catchments: 13-30% in the Adour River (France) (Prouzet, 2002), 6.2-48.7% in the Oria River (Spain) (Aranburu *et al.*, 2016), 30.8-51.8% in Nova Scotia (Jessop, 2000), 44.1-75% in Shang-Chi (Taiwan) (Tzeng, 1984) and even 78.1-99.7% in the Vilaine River (France) (Briand *et al.*, 2005). The passability for upstream migration was estimated to range between 19.8 and 49.1% for an obstacle in the Canal des Etangs (France) (Drouineau *et al.*, 2015). A similar result was obtained by Briand *et al.* (2005), who calculated an efficiency of the trapping ladder as 30% in the Vilaine catchment (France). Passability is probably even lower for obstacles not equipped with an eel ladder. Turbine impacts appear to vary considerably depending on study sites. On the Meuse River, Winter *et al.* (2007) estimated that the two hydropower plants induced an overall mortality of approximately 20-30%. In a Swedish river, Calles *et al.* (2010) found mortality rates of 40% and 60% induced by two plants. At a Polish

site, Dębowski *et al.* (2016) estimated a mortality rate of 55%. Mortality due to silver eel fisheries also varies from 22-26% in the Meuse River (Netherlands) (Winter *et al.*, 2006) to 82% mortality in the Gudena River and Randers Fjord (Denmark) (Aarestrup *et al.*, 2008) and can reach even higher levels in some Mediterranean lagoons (Amilhat *et al.*, 2008).

Given the large variability in the pressure intensities, and the fact that they vary at the distribution area scale, we used a Latin hypercube sampling design to carry out the global exploration of their effects in a theoretical catchment in GenEveel. Consequently, the exercise is clearly theoretical, and our raw results should not be used to classify the effects of anthropogenic pressures. However, they provide valuable insights on the type of effects induced by the different pressures and indicate that the significance of these effects greatly depends on the considered output indicator.

We did not consider the effects of yellow eel fisheries in this exercise for various reasons. First, the GenEveel model did not describe the growth phase precisely, so it is difficult to incorporate such mortalities. Moreover, most of the pressures occur in specific parts of the catchments (the estuary for glass eel fisheries, obstacles one after another) and at a specific times (migration), while yellow eel fisheries are more widespread and occur all along the growth phase, so comparisons of these pressures would be more uncertain.

### **3.5.3. The effect of anthropogenic pressures depends on their location within the catchment**

Among the most obvious results, the impacts of anthropogenic pressures clearly depend on their location in the river catchment, and pressures located in the very upper parts of the catchment, where densities are low, have limited impacts. Although this result is obvious, its consequence at the population scale is less obvious because anthropogenic activities are not uniformly distributed across the distribution area. For example, in Europe, some hydropower facilities can be found in downstream areas of river catchments, similar to in Scandinavia, while they are located upstream in France. Silver eel fisheries are mainly located in Scandinavia and the Mediterranean Sea (Dekker, 2003b), while glass eel fisheries are dominant in France and Spain. Since life history patterns and differences in densities are also observed at the distribution area scale, it is very difficult to draw up an overall picture of the effect of each individual pressure at the population scale.



### **3.5.4. Effect of pressures on escapement: existence of compensatory mechanisms**

Another important message is that the number of escapees and the resulting egg production are not necessarily correlated. In our simulations, glass eel fisheries and migratory obstacles had the greatest influence on the number of escapees, the sex ratio and the length-at-silvering (although the effects were different depending on pressures). Nevertheless, the silver eel fishery and turbine mortality had similar negative impacts on egg production, which were greater than that of the glass eel fishery and were more significant than those of obstacles. This is explained by compensatory mechanisms that mitigate the negative effects of glass eel fisheries and obstacles to upstream migration, while there are no such mechanisms for those of silver eel fisheries and turbine mortality. For example, the decrease in escapement induced by the glass eel fishery can be compensated by the higher production of females. For obstacles to upstream migration, the decrease in female production is compensated by the better survival of individuals and consequently an increase in escapement. In other words, the pressure inducing the highest direct mortality does not necessarily have the greatest influence on silver eel escapement. Even pressures that do not induce any direct mortality, such as migratory obstacles, can influence some demographic attributes of escapees, such as the proportion of females or length-at-silvering. For example, obstacles close to the river mouth blocked individuals during their upstream migration in downstream habitats. As a consequence, slow growers that usually tend to settle in upstream habitats are forced to settle in downstream habitats with a faster growth rate and higher mortality due to competition. In these conditions, slow growers become males with a time-minimizing strategy, while they would have turned into females with a size-maximizing strategy in upstream habitats; this is why the proportion of females decreased. Since growth is fast in downstream habitats and those individuals mature very early (at male length-at-silvering), they have a higher survival rate until silvering than they would have known in upstream habitats, leading to an increase in the proportion of slow growers. However, they would have had higher fitness as a female in upstream habitats since the loss in survival would have been compensated by high fecundity.

Interestingly, by decreasing the number of individuals that enter the river catchment, a simulation with a glass eel fishery “mimics” a simulation with a depleted population. It is interesting to note that in such a situation, a decrease in competition enables individuals to settle in downstream habitats, where growth is faster. More females are also produced because of these lower densities. As a result, egg production is less impacted than the number

of escapees. As such, the phenotypic plasticity of eels can be considered as a resilience factor in a depleted population.

### **3.5.5. Anthropogenic pressures as selective pressures**

The final output of the model is the impact of anthropogenic pressures on slow and fast growers. Most pressures, except for the glass eel fishery, tend to favor fast growers over slow growers, and as such, anthropogenic pressures can be selective pressures. The selective pressure induced by obstacles on elver migration has already been observed at the gene expression level (Podgorniak *et al.*, 2015a, 2015b, 2016). If most anthropogenic activities act as several pressures favoring fast growers, we can wonder how slow growers were preserved by natural selection. A possible explanation may be due to gender differences. Males are predominantly fast growers, while females are both slow and fast growers (Côté *et al.*, 2015; Mateo *et al.*, 2017a), but slow-growing females have a larger length-at-silvering and greater fecundity than fast-growing females (Mateo *et al.*, 2017a). In a high-abundance context, we can assume that males are fast growers, females are predominantly slow growers, and the two types are necessary. In a collapsed population, anthropogenic pressures tend to favor males and fast growers (table 3-1), and egg production can become limiting. Consequently, the few remaining slow-growing females (which are less impacted by competition and can settle in downstream habitats) can become even more important, explaining their preservation to some extent. To validate this assumption, it would be interesting to carry out a similar simulation exercise at the population scale and with multiple generations to explore the impacts of anthropogenic pressures on the two types of individuals. Moreover, this would allow us to explore the assumption of spatially varying selection proposed by Gagnaire *et al.* (2012) and Côté *et al.* (2014) by simulating the arrival of slow and fast growers in random and contrasting river catchments, where they would suffer different mortalities and would consequently be more or less adapted.

Selective pressure due to fishing activities on exploited marine stocks has been demonstrated for many fish stocks (Law, 2000; Pinsky and Palumbi, 2014). A major collapse in abundance is required to reduce the overall genetic diversity. Since current recruitment is now less than 5% of historical recruitment and, for the American eel, recruitment has ceased in Lake Ontario and Upper Saint-Lawrence (Casselman, 2003), a loss of genetic diversity is not impossible. This question of diversity at the individual level is crucial for eel conservation since it may contribute to population resilience through a storage and portfolio effect (Secor, 2015a).

The misunderstanding of the effects of anthropogenic pressures also means that we poorly understand the effects of some mitigating measures. Stocking programs have been widely used (Couillard *et al.*, 2014) and are still widely used by European countries (Brämick *et al.*, 2016; Josset *et al.*, 2016; Simon *et al.*, 2013). However, by modifying densities and moving slow or fast growers into habitats where they are not adapted, such measures can have unexpected effects on escapement. Such observations were made in Canada, where eels were stocked in the Great Lakes, and the escapees produced were more similar to escapees from their original sites than to native silver eels from the Great Lakes (Couillard *et al.*, 2014; Stacey *et al.*, 2015). Exploring this issue with GenEeel by artificially “moving” individuals after their sex and growth habitat have been determined will bring new insights into the ways stocking programs can affect the whole population.

### **3.6. Conclusion**

Our theoretical exercise provided new insights on the impact of anthropogenic pressures, both direct and indirect. Since this simulation exercise is purely theoretical and because of the spatial heterogeneity in both anthropogenic pressures and eel life history traits, it is impossible to promote any specific management measures, which should be chosen according to the local conditions. However, our results imply that managers and scientists should not only assess the quantity of escapees but also their quality. Quantifying human-induced mortalities and the effects of anthropogenic pressures on the number of escapees is a main priority, given the dramatic situation of the three temperate eel populations. However, further research to investigate the possible impacts of anthropogenic pressures on phenotypic changes in life history traits and consequently the reproductive output of the spawning stock will be required to achieve sustainable management of the species.

### **3.7. Acknowledgements**

This study was supported by the Hynes project between Irstea and EDF R&D. We would like to thank Christian Rigaud, Bruno Ernande, Martin Castonguay and Laurent Beaulaton for their participation in fruitful discussions. We acknowledge the two referees for their helpful comments.

## ***Take-home messages***

- ✓ Impacts that cause the **highest mortality do not necessarily have the greatest impact** on overall egg production:

Because of adaptive mechanisms, anthropogenic pressures can lead to modification of the population sex-ratio and the length-at-silvering. Consequently, even pressures that have killed few individuals can have drastic consequence on the overall egg production.

- ✓ **The phenotypic plasticity** could act as a **compensatory mechanism** and could be **source of resilience** for the population:

The phenotypic plasticity can mitigate the negative effects of some pressures (glass eel fishery and obstacle to upstream migrations) and it could be source of resilience for eel population, while there are no such compensatory mechanisms for other pressures (silver eel fisheries and turbine mortality).

- ✓ **Anthropogenic pressures** can be **selective pressures**:

Some pressures tend to favor fast-growing individuals against slow-growing individuals suggesting that these pressures can induce permanent selection. Given the disadvantage of slow-growing individuals, we can wonder how they were preserved by natural selection. A plausible explanation could be that most females are slow-growing individuals with high fecundity, which can become even more important in a context of populations in decline.

## ***To go further***

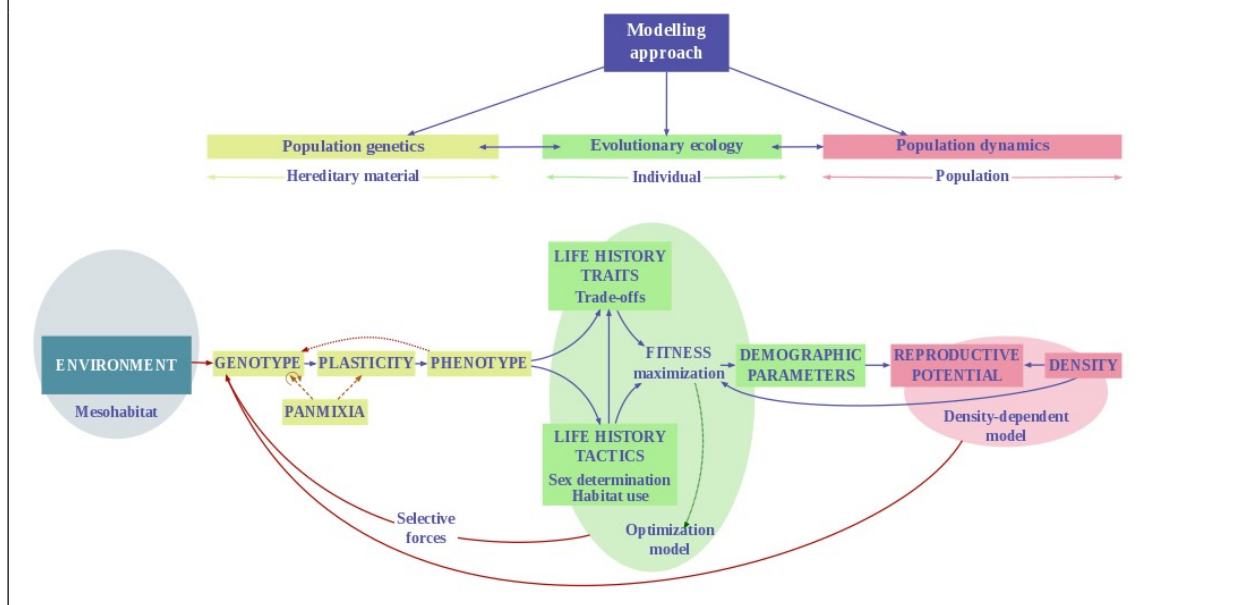
To explore the question of the preservation of slow-growing and fast-growing individuals over generations, a multi-generation model at the distribution scale is required. This would also allow us to study the situations in which adaptive phenotypic plasticity and genetic polymorphism may have been selected as a response to environmental heterogeneity. Moreover, will allow to have a more comprehensive overview of the impact of anthropogenic pressures over multiple generations.

**Chapter 4:**  
**Towards a life cycle model for eels to explore the  
emergence of adaptive mechanisms**

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## Foreword

This chapter presents the last step of this PhD. EvEel (Drouineau *et al.*, 2014) and GenEveel (Mateo *et al.*, 2017a) are based on the assumption that phenotypic plasticity is an adaptive response emerging from natural selection. This implies that phenotypic plasticity provides an evolutionary advantage greater than the related costs. The assumption is necessary to justify the use of a fitness optimization approach but has not been validated. In this context, I supervised a six-month trainee who developed MaxEel, a simple individual based model that explores in which ecological conditions, phenotypic plasticity would be selected despite its costs. In these conditions, we also explored if plasticity remained adaptive in a collapsed population. The model simulates the evolution of reaction norms and explores in which conditions these norms become plastic. It considers a panmictic population of eels whose individuals randomly colonize three river basins that are contrasted in terms of growth and survival (depending on the temperature of the environment). A numerical exploration was carried out to analyze the impact of ecological parameters on the emergence of the plastic lengths-at-silvering. To go one step further, the prototype of a demo-genetic model is described. It combines genetic polymorphism and phenotypic plasticity and is based on all precedent models. Contrary to MaxEel, this model is based on a much more realistic description of genetic inheritance process, it describes the whole life cycle and operates in the distribution area. As such, it summarizes our overall understanding of the functioning of adaptation mechanisms. Although the model is still a prototype and has not been used yet, we discuss the perspectives of use and the insights that such a model can bring to management. The following figure summarizes the positioning of this chapter within the overall PhD project.



## 4.1. Introduction

Global change refers to the modifications of ecosystems due to anthropogenic pressures (Steffen *et al.*, 2005) that threatens many species of extinction (Spurgeon, 2000; Thomas *et al.*, 2004; Steffen *et al.*, 2005; Brook *et al.*, 2008; Cahill *et al.*, 2012; Urban, 2015). The threat is not only due to the magnitude of the changes, but also due to its rate, which is occurring since the second half of the 20th century, the period called the “Great Acceleration” (Steffen *et al.*, 2005, 2015). This acceleration may outpace species adaptation capacity (Donner *et al.*, 2005; Visser, 2008; Ayllón *et al.*, 2016). The response of species with large distribution areas to global change is even more challenging due to the great range of environmental conditions and potentially many different selective pressures that these species have to deal with. In view of this, there is a need to improve our understanding of adaptive capacities of species to enhance conservation and restoration actions in the context of a changing environment.

Phenotypic plasticity and selection are among the adaptive processes that shape the response of individuals to their environment and exploitation. These processes operate at different temporal scales and have different degrees of reversibility. Plastic responses are induced within a single generation and their costs are experienced at a physiological level of individuals (DeWitt *et al.*, 1998; Schlichting and Pigliucci, 1998). On the other hand, selection implies genetic variations over several generations by selection of the more adapted genotypes but at risk of genetic diversity reduction within the population (Allendorf *et al.*, 2014; Pinsky and Palumbi, 2014). Therefore, understanding the adaptive potential of organisms requires information on plastic and genetic components, and on their relative contribution. Furthermore, phenotypic plasticity can be characterized by reaction norms that correspond to the set of phenotypes that would be produced by a single genotype across a range of environments (Schlichting and Pigliucci, 1998). The level of plasticity is measured by the slope of the genotype-specific environment-phenotype function (Pigliucci, 2005). Moreover, quantitative genetic parameters can be used to study the inheritance of varying traits and the maintenance of the genetic variability. They refer to the variance components of quantitative traits and provide information to estimate the heritability, i.e. a good predictor of the degree to which the population respond to selection (Falconer and Mackay, 1996).

Despite the number of methods to quantify phenotypic plasticity and selection, it is difficult to demonstrate adaptive evolution in the wild because of the genetic basis of most life history traits are not known (Ellegren and Sheldon, 2008) and the estimation of natural selection remains a challenging issue (Hersch and Phillips, 2004). In view of this, models are useful

tools to provide a better understanding of the mechanisms involved in life history variation, becoming a guide for empirical studies or a predictive tool to explore the consequences of human impacts on threatened species. In recent years, several approaches have been developed to study the evolution of life history traits: the most employed are optimization models, quantitative genetics models and eco-genetic models. Optimization models (Stearns and Koella, 1986; Houston and McNamara, 1992; Sasaki and de Jong, 1999) search for the optimal strategy that maximizes fitness and focus on the ecological conditions that promote the evolution of traits. However, they do not consider the underlying genetic basis. GenEveel (Mateo *et al.*, 2017a) and Eveel (Drouineau *et al.*, 2014) belong to this kind of model. Quantitative genetic models (Via and Lande, 1985, 1987; Tienderen, 1991; Gomulkiewicz and Kirkpatrick, 1992; Gavrillets and Scheiner, 1993) include genetic variance of traits and genetic correlation between traits to study the response to selection of a population. Nevertheless, these models usually neglect the environmental effects on selection. The recent development of eco-genetic models (Dunlop *et al.*, 2009) covers the genetic (the traits are inherited by the offspring from their parents and they are coded as polygenic quantitative characters) and the ecological components (including variables of individuals such as phenotypic plasticity and density dependent processes) leading to a detailed description of the life history of individuals. Andreello *et al.* (2011) developed a genetic-demographic model to explore how migrations of adults and larvae impact the genetic structure of the European eel along its continental distribution area. The results showed that low levels of mixing during different migration stages are enough to prevent genetic differentiation. They also showed that small scale temporal differences in the recruitment can arise if the spawning stock is subdivided into different reproductive groups. Nevertheless, the adaptive response of depleted population of temperate eels has not been fully investigated.

In the last few years, conservation actions have flourished for the three eel species. However, the strong spatial heterogeneity of anthropogenic pressures affecting their populations combined with the spatial variability in life history traits at the distribution area and river catchment scales raise specific challenges for management. How temperate eels deal with environmental changes as a result of human activities is further complicated by the panmixia, the passive larval drift and their large distribution that promote the emergence of phenotypic plasticity rather than local adaptation.

In the previous chapter, we have seen how optimization models were used to explore whether phenotypic plasticity (of length-at-silvering, sex-determination and habitat use) and the existence of genetically determined ecotypes (in growth) can be the result of adaptive



responses to environmental heterogeneity. We also show how, in such a situation, adaptive mechanisms can interfere with anthropogenic pressures to mitigate or worsen their effects. However, as optimization models, they postulate that phenotypic plasticity and genetic polymorphism (only for GenEveel) were selected by natural selection. This is a strong assumption since environmental conditions have changed quickly in the last decades. So, the response which used to be adapted in a context of abundant populations may not be adapted anymore in a context of depleted populations. Moreover, we have not considered costs of phenotypic plasticity that are a main constraint for the emergence of such an adaptive response (DeWitt *et al.*, 1998). Finally, we have only worked at the river catchment scale and on a single generation whereas the emergence of adaptive responses should be considered in a multigenerational scale and at the distribution scale. In this context, this chapter proposes two different steps:

- (i) A preliminary model to determine ecological conditions in which phenotypic plasticity is indeed adaptive for eel populations. Phenotypic plasticity may facilitate adaptation allowing for a single genotype to produce phenotypes that are appropriate within their habitats (Bradshaw, 1965), as shown several species (Schlichting, 1986; Sultan, 1987; Scheiner, 1993; Pigliucci, 2005). The phenotypic plasticity is favored by environmental heterogeneity (Via *et al.*, 1995) and by density-dependent mechanisms (Ernande *et al.*, 2004). To be selected, the benefit of phenotypic plasticity must be higher than the associated costs (Tienderen, 1991; DeWitt *et al.*, 1998). These costs may be subdivided into maintenance costs, i.e. the maintenance of energetic, regulator and sensorial mechanisms that induce the plastic responses, and production costs paid by a plastic individual (compared to a non-plastic individual). In view of this, Maxime Olsommer realized a research internship (under my direction and the co-supervision of Hilaire Drouineau) to explore in which ecological and density-dependent conditions the phenotypic plasticity can be selected as an adaptive response despite its costs. In such conditions, Maxime also analyzed if phenotypic plasticity remains adapted in a context of depleted populations. To this end, he developed a model named MaxEel that describes a simplistic life cycle of temperate eels.
- (ii) Building on MaxEel, a model is presented, which allows for phenotypic plasticity through plastic reaction norms of length-at-silvering and genetic polymorphism through individual intrinsic growth rates. Based on a quantitative genetic approach, the model aims to explore the emergence of ecotypes and phenotypic plasticity as a result of environmental heterogeneity. The model addresses

MaxEel's limitations by incorporating males in it to provide a better spatial resolution of river catchments and explicitly considers the genetic polymorphism. The model summarizes the understanding of eels adaptation mechanisms that we have at the end of this work. Ultimately, the model may be a relevant operating model to explore the effects of anthropogenic pressures and provide new insights for management.

## **4.2. A model to explore the conditions favoring the emergence of phenotypic plasticity and if they are still gathered in the current context of a depleted population**

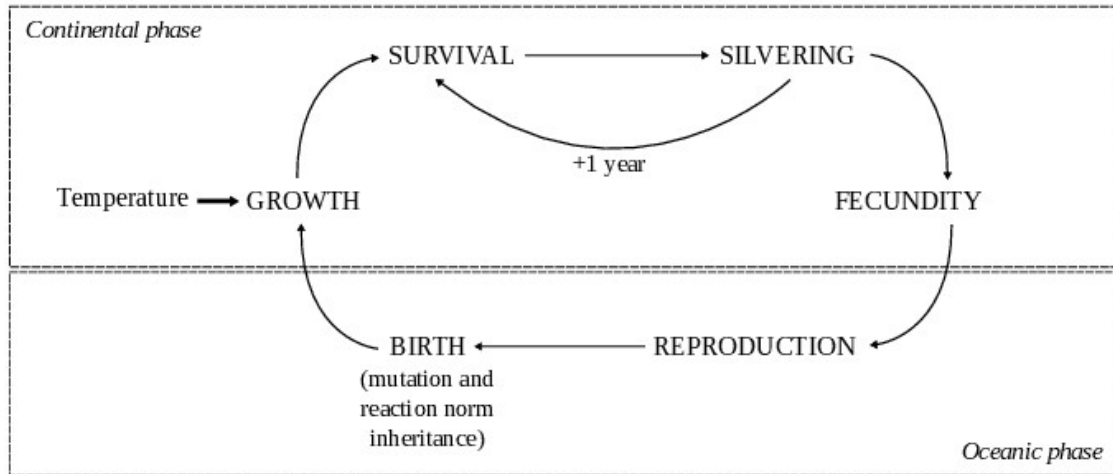
### **4.2.1. Model description**

In MaxEel, phenotypic plasticity was modelled by reaction norms, i.e. the range of phenotypes that a genotype can produce depending on environmental conditions (Dobzhansky and Spassky, 1944; Stearns and Koella, 1986). More specifically, reaction norms selected over generations were studied to explore the evolution of phenotypic plasticity.

In MaxEel, a panmictic eel population was considered in which all individuals breed together and the offspring is distributed randomly to the three virtual river basins. Each river basin was characterized by a water temperature which was used to compute natural mortality and growth rates using empirical relationships from the literature (Pauly, 1980; Dekker, 2000b; Bevacqua *et al.*, 2011). Each individual was characterized by a reaction norm (a length-at-silvering for each of the three river basins), which were more or less plastic (plasticity was measured as the variance of lengths-at-silvering). Within river basins, individuals followed a von Bertalanffy growth, suffered a density-dependent survival, and matured when reaching the length defined by its reaction norm for its river residence. Unlike GenEeel, the river basins were determined by only one cell (spatial gradient in the river was missing) for simplicity, and genetic polymorphism of growth was not incorporated. In this simple model, only females were represented.

Only individuals that survived until length-at-silvering were able to reproduce. The number of offspring was a function of (i) the length-at-silvering through an allometric relationship (Andrello *et al.*, 2011) and (ii) the costs of phenotypic plasticity (we assumed that the costs associated with a plastic reaction norm lead to a decrease of the number of offspring). Offspring inherited the reaction norms of their mothers, with possible random mutations (normal draw) around those norms. Offspring produced each time step (one year) are then

distributed randomly in one of three river basins to mimic a passive drift of larvae and therefore a non-selected growth habitat (figure 4-1).



**Figure 4-1.** Conceptual diagram of eel life cycle represented in the model.

The process mentioned above is defined by the following algorithm (see table 4-1 for parameter definitions):

(1) For each catchment:

- For each individual  $i$  in catchment  $c$ :

- survive with a probability  $e^{-\left(M_c + \alpha \cdot N_c(t)\right)}$  (Bernoulli trial) – if  $i$  dies, it is discarded
- update length  $L_i(t) = L_\infty \cdot \left(1 - \exp^{-K_c \cdot A_i(t)}\right)$
- if  $L_i(t) > L_{s_i}(c)$ : individual matures
  - fecundity:  $a_1 + aL_{s_i}(c)^b$
  - cost of phenotypic plasticity:

$$C \cdot \left[ (1 - \beta) \cdot \sum_{c_1=1}^3 \left( L_{s_i}(c_1) - d_i \right)^2 + \beta \cdot \left( L_{s_i}(c) - d_i \right)^2 \right] \text{ with } d_i = (1 - \beta) \cdot \overline{L_{s_i}} + \beta \cdot \sum_{c_1=1}^3 p_{c_1} \cdot L_{s_i}(c_1)$$

- production of (fecundity – cost) with the same reaction norm as  $i$ , which are sent to the Sargasso Sea
- individual  $i$  is discarded

(2) In the Sargasso Sea:

- if  $R_{th}(i) > R$ ,  $R_{th}(i) - R$  offspring are randomly discarded
- for each offspring  $o$ :

- for each catchment  $c$ :
  - $Ls_o(c)$  mutates with probability  $p_m$  (Bernoulli trial) – if mutation occurs,  $Ls_o(c)$  is multiplied by a random number drawn from a lognormal distribution  $LN\sim(0,\sigma_m)$
- offspring  $o$  is sent to a river catchment according to a multinomial trial of probabilities  $\{p_1,p_2,p_3\}$

Entity	Parameter	Definition
Catchment $c$ (from 1 to 3)	$T_c$	Temperature in catchment $c$
	$M_c$	Natural mortality rate in catchment $c$ . Calculated using a statistical relationship between $M$ and $T$ from Bevacqua <i>et al.</i> (2011)
	$K_c$	Brody coefficient of the von Bertalanffy growth curve in catchment $c$ . Calculated using a statistical relationship between $M$ , $K$ and $T$ from Pauly (1980)
	$N_c(t)$	Number of living immature individual in catchment $c$ at time step $t$
Individual $i$	$Ls_i$	Vector of three elements representing the reaction norms, i.e. the length at which individual $i$ matures in each of the three catchments
	$L_i(t)$	Length at time $t$
	$A_i(t)$	Age at time $t$
Population	$a_i, a, b$	Parameters of the fecundity allometric relationship from Andrelo <i>et al.</i> (2011)
	$\alpha$	Intensity of natural mortality density-dependence
	$L_\infty$	Asymptotic length of the von Bertalanffy growth curve
	$p_m, \sigma_m$	Probability of mutation of the reaction norm and corresponding standard deviation
	$\beta$	Balance between maintenance and production costs for the phenotypic plasticity ( $0=$ maintenance, $1=$ production)
	$C$	Intensity of phenotypic plasticity cost (independent of the cost)
Sargasso Sea composed of offspring $o$	$R$	Maximum total number of offspring per iteration
	$R_{th}(t)$	Theoretical number of offspring that would have been produced at time $t$ in the absence of a threshold in the hockey stick stock recruitment relationship
	$\{p_1,p_2,p_3\}$	Vector containing the probabilities to drift towards catchment $c$

**Table 4-1.** Model parameters.

At the end of each simulation, reaction norms of length-at silvering of survivors were monitored. Then, we computed three indicators for each norm: its variance (of the three lengths-at-silvering), its range (difference between maximum and minimum) and the corresponding costs associated to phenotypic plasticity of the norm. The two first indicators quantified the degree of plasticity of selected norms while the third indicator quantified the costs paid by individuals for being plastic.

#### **4.2.2. Model exploration and results analysis**

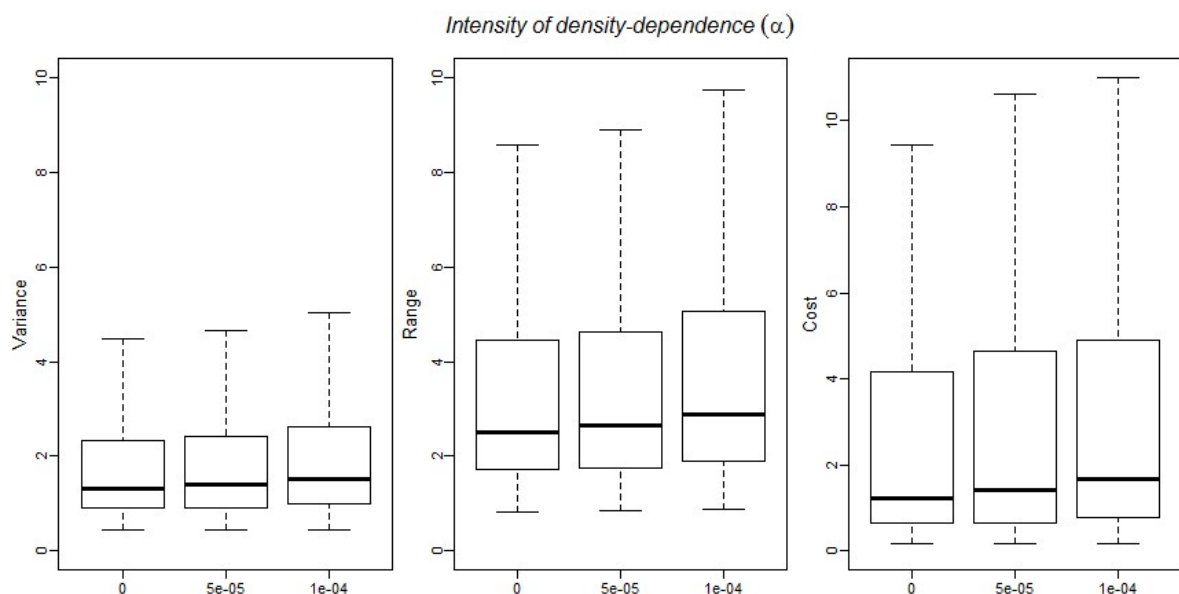
We built an experimental design to determine the impacts of (i) larvae distribution within river basins,  $D$ , (either homogeneous, biased to the most favorable habitat or biased to the less favorable habitat), (ii) the degree of heterogeneity between environments,  $\Delta T$ , (leading to contrasts in growth rate and survival probability), (iii) the intensity of density-dependence,  $\alpha$ , (different density-dependent mortalities), (iv) the intensity of plasticity costs,  $c$ , and (v) the kind of costs,  $\beta$ , (maintenance or production) of phenotypic plasticity on the emergence of plastic reaction norms. The reference value, a high and a low value around this one were set for each parameter and we built a full-simulation design consisting of all combinations of parameter values ( $3^5 = 243$ ). We carried out 10 replicates for each combination of parameters to account for model stochasticity, leading to 2430 simulations. Then a linear model was conducted for each indicator (variance and range of the three lengths-at-silvering, and costs of plasticity) and the best model was selected according to Akaike Information Criterion. The sign of the regression coefficient reveals the effect of the parameters on these indicators. We analyzed the proportion of variance explained by each parameter to compare their relative importance.

#### **4.2.3. Results and discussion**

The results of the linear models are summarized in table 4-2. The intensity of plasticity costs ( $c$ ) had the largest (negative) impact whatever the indicator. The negative effect on the variance and the range of reactions norms confirmed that strong cost reduce the degree of plasticity that emerges from natural selection (DeWitt *et al.*, 1998). Also, with no intensity of costs, plasticity increased. This is obvious but unreal in nature. The production of a plastic response requires the development of sensing mechanisms to collect information about the environment and it is costly in terms of energy to produce the phenotype that matches the environment (Tienderen, 1991; Fusco and Minelli, 2010). When the intensity of the costs increased, plasticity decreased and reaction norms tended to a constant phenotype,

independent of the environment (Ernande *et al.*, 2004). When the intensity of costs is at the highest, there are no costs because individuals are not plastic anymore.

The second most influencing parameter was density dependence intensity ( $\alpha$ ) (table 4-2), Consistently with (Ernande *et al.*, 2004), the positive effect on all indicators confirmed that density-dependence favors the emergence of plasticity (figure 4-2). This point is especially important in a context of depleted population as, density-dependent mortality is reduced and has a minor influence on the population dynamics. In these scenarios without density-dependence, the phenotypic plasticity was still present but very much decreased (the reaction norms are much less variable). Therefore, this suggests that plasticity can still have an evolutionary advantage even in a depleted population. Nevertheless, the degree of plasticity selected in a context of high abundance may be too high in this new context, because of unnecessary costs. This would not be a maladaptation but a suboptimal situation. Furthermore, the intensity of density dependence showed interactions with other parameters, e.g. the distribution of larvae ( $D$ ), confirming that in some ecological situations the selected reaction norm in a high population context could be more distant than the optimal reaction norm for a depleted population.



**Figure 4-2.** Variations in variance and range of reaction norms and the costs paid to be plastic across the three values of the density dependence intensity ( $\alpha$ ).

The third most important parameter was the kind of costs ( $\beta$ ) (table 4-2.). Norms are more plastic when costs are dominated by production costs ( $\beta = 1$ ) than when they are dominated by maintenance costs ( $\beta = 0$ ). This is because when maintenance cost predominates, individuals tend to “specialize” for the more favorable basin or for the basin in which they are

the most likely to grow, to avoid paying a cost for a phenotype they will rarely produce. This result is consistent with previous findings from (Ernande *et al.*, 2004). The kind of costs had similar effects on the costs of plasticity.

The distribution of larvae and the degree of heterogeneity between river catchments had fewer impacts on the degree of plasticity and no effect on the costs of a plastic response (table 4-2). Moreover, coefficients were small compared to interactions coefficients which meant that the distribution could not be interpreted alone but through its interaction with density-dependence and plasticity costs.

When the river catchments were more contrasted in terms of temperature ( $\Delta T = 5$ ), the variance and the range of reaction norms increased, showing that plasticity facilitates adaptation (Pigliucci, 2005). Finally, some interactions between parameters can modulate the adaptive value of the plastic response. For example, a negative interaction was observed between the environmental heterogeneity ( $\Delta T$ ) and the intensity of costs ( $c$ ) for the variance and the range of length-at-silvering (table 4-2), which decreased the degree of plasticity. When the river catchments were more contrasted ( $\Delta T = 5$ ), the reaction norms of length were more variable and the costs to be plastic increased also due to high plasticity, showing the trade-off between the advantage and costs of being plastic.

### **4.3. A demo-genetic modelling proposal to explore the emergence of adaptive mechanisms**

#### **4.3.1. Model description**

The model description follows the ODD (Overview, Design concepts, Details) protocol to describe individual-based models (Grimm *et al.*, 2006, 2010). Through this section, an index  $i$  denotes an individual,  $x$  a habitat,  $c$  a river catchment,  $s$  a gender and  $t$  a time-step.

##### **4.3.1.1. Overview**

###### **4.3.1.1.1. Purpose**

The aim of the model was to determine in which ecological conditions phenotypic plasticity and genetic polymorphism (i) could be selected by evolution and (ii) could be maintained in the current context of depleted populations. The ecological conditions to explore were: the temperature gradient between river catchments (as a latitudinal cline to represent the spatial distribution of eels), spatial variability within river catchments (i.e. upstream-downstream

Parameter	Modality	VARIANCE		RANGE		COSTS	
		Estimate	Explained variance	Estimate	Explained variance	Estimate	Explained variance
<i>c</i>	0	0.000		0.000		0.000	
	0.5	-0.914	59.342	-0.907	59.359	0.000	9.075
	1	-1.219		-1.213		-0.447	
<i>a</i>	0	0.000		0.000		0	
	$5.0 \times 10^{-5}$	0.106	0.572	0.130	0.575	0.144	2.025
	$1.0 \times 10^{-4}$	0.183		0.156		0.191	
<i>β</i>	0	0.000		0.000		0.000	
	0.5	0.023	0.413	0.024	0.413	0.005	0.246
	1	0.096		0.096		0.079	
<i>D</i>	best habitat	0.000		0.000			
	homogeneous	-0.161	0.379	-0.161	0.377		
	worst habitat	-0.003		-0.004			
<i>ΔT</i>	0.5	0.000		0.000			
	2	0.065	0.248	0.065	0.243		
	5	0.209		0.207			
<i>c: D</i>	0.5: homogenous	0.173		0.172			
	1: homogeneous	0.159	0.535	0.157	0.533		
	0.5: worst habitat	0.114		0.112			
	1: worst habitat	0.243		0.241			
<i>a: D</i>	$5.0 \times 10^{-5}$ : homogenous	0.012		0.014			
	$1.0 \times 10^{-4}$ : homogeneous	-0.078	0.352	-0.075	0.345		
	$5.0 \times 10^{-5}$ : worst habitat	-0.171		-0.168			
	$1.0 \times 10^{-4}$ : worst habitat	-0.118		-0.114			
<i>c: ΔT</i>	0.5: 5	-0.211		-0.209			
	1: 5	-0.187	0.516	-0.185	0.509		
	0.5: 2	-0.071		-0.068			
	1: 2	0.031		0.029			
<i>c: a</i>	0.5: $5.0 \times 10^{-5}$			-0.013			
	1: $5.0 \times 10^{-5}$			-0.067	0.149	-0.099	0.387
	0.5: $1.0 \times 10^{-4}$			0.007			
	1: $1.0 \times 10^{-4}$			0.070		0.124	

**Table 4-2.** Summary of linear models with estimated for each model parameter and the explained variance. P-values were not presented because significance tests are not recommended when analyzing simulation model results (White *et al.*, 2014)



gradient) and demographic parameters, such as the population abundance. To analyze the evolutionary emergence of phenotypic plasticity, we also explore the effect of its costs since they are expected to act as major constraints for the selective advantage of this mechanism.

#### 4.3.1.1.2. State variables and scales

*Temporal scales:* the model has a yearly time step. The model is run until spatial patterns (see section *Design concepts*) are stable (assessed through a Mann-Kendall trend tests) over 100 years.

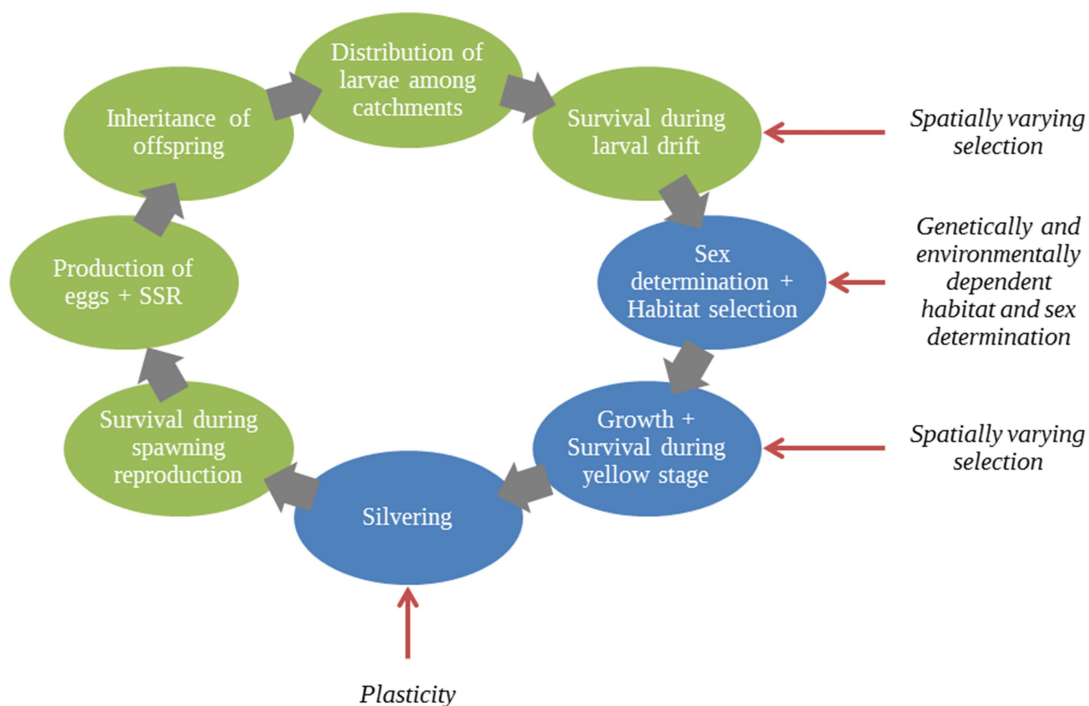
*Entities and spatial scales:* The environment is composed of an oceanic and a continental compartment. Reproduction, genetic inheritance, dispersion and larvae survival take place in the oceanic compartment. The continental phase is split into three river catchments with different temperatures reflecting a latitudinal cline. Each river catchment is represented by two “habitats” of similar size: a first habitat represents brackish or salt water environment and a second habitat represents fresh water environment. Juvenile survival, growth and silvering occur throughout this phase. Each individual  $i$  is initially characterized by several parameters (table 4-4). Three types of parameters are considered to be coded genetically and consequently partially inherited by the offspring. For each of these types of parameters, the “genetic value” corresponds to the value which is indeed genetically coded and can be inherited, and is noted with an index  $g$ . A stochastic value is associated to each genetic value and accounts for a non-directed and non-heritable environmental noise (same notation without the index  $g$ ).

These parameters correspond to the standard set of traits that are recommended to investigate life history evolution (Dunlop *et al.*, 2009). The first type of genetically coded parameters corresponds to the intrinsic growth rate ( $k(i)$  and  $k_g(i)$ ). It should be noted that  $k(i)$  also directly constrains an intrinsic mortality rate  $m(i)$ . The second type of parameters plays a role in the sex-determination process ( $f(i)$  and  $f_g(i)$ ). Finally, the third type of parameters correspond to the intercept ( $ls\mu(i)$  and  $ls\mu_g(i)$ ) and the slope ( $lsa(i)$  and  $lsa_g(i)$ ) of the length-at-silvering reaction norms. At the end of each generation, each individual is described by a gender, a habitat location (in the river catchments), and a length-at-silvering.

The population entity groups parameters common to all individuals, such as parameters of the stock-recruitment relationships, parameters of the larval drift, parameters that govern the inheritance process, and parameters that govern the influence of environment on biological processes.

#### 4.3.1.1.3. Process overview and scheduling

The model covers the whole life-cycle of the temperate eels. It is structured in different processes; offspring produced in each reproduction are distributed randomly among river catchments and suffered mortality during larval drift. This mortality depends on larvae intrinsic characteristics, the drift duration and water temperature. The differential mortality which depends on genetic characteristics of individuals and the characteristics of environment opens the door to spatially-variable selection operating as early as in the larval drift. When they enter in inland waters, individuals “select” their growth habitat (brackish or freshwater position in the river) and determine a sex (female or male) by maximizing their expected fitness. Then, they grow and die during the continental stage with a growth and a mortality that depend on individuals’ characteristics, habitat condition and density-dependence. When they reach a length-at-silvering, defined by an environment dependent reaction-norm, they migrate into the spawning areas to reproduce. Offspring inherit part of their parents attributes and the cycle starts again.



**Figure 4-3.** Succession of processes. Blue circles stand for processes that take place within continental catchments whereas green circles stand for processes occurring in the marine environment (called Sargasso Sea for simplicity).

## 4.3.1.2. Design concepts

### 4.3.1.2.1. Basic principles

This individual-based model combines an eco-genetic structure (Dunlop *et al.*, 2009), based on the premise that many genes and the environment act and interact to determine traits (Falconer and Mackay, 1996; Lynch and Walsh, 1998). The model design allows exploring the emergence of genetic polymorphism (eco-genetic structure) and adaptive phenotypic plasticity (optimization model).

### 4.3.1.2.2. Emergence

The pattern-oriented modelling approach (Grimm and Railsback, 2012) is used to compare predicted spatial patterns with those observed in real-world. Nine emergent population spatial patterns are analyzed from the literature:

- Among river catchments:
  - (Oi) male-biased sex ratio in the southern part of the distribution area and female-biased sex ratio in the northern part,
  - (Oii) male-biased sex ratio in an environment with high density,
  - (Oiii) faster growth in southern latitudes,
  - (Oiv) larger females in the northern part.
- Within river catchments:
  - (Ov) higher density downstream than upstream,
  - (Ovi) higher length-at-silvering upstream than downstream,
  - (Ovii) male-biased sex ratio downstream and female-biased sex ratio upstream,
  - (Oviii) the phenotypic response led to faster growth rate downstream than upstream.

A last (no spatial) pattern is defined regarding the population distribution in terms of growth:

- (Oix) males have strong genetic values of growth rate while females have a wider range of genetic values of growth rate.

### 4.3.1.2.3. Adaptation

At the individual scale, the selection of habitat within river basin is assumed to be adaptive. Length-at-silvering, sex-determination reaction norms and natural growth rate are also subject to natural selection to potentially address environmental heterogeneity (figure 4-3).

#### **4.3.1.2.4. Prediction**

Individuals could predict expected fitness during the sex and habitat determination process.

#### **4.3.1.2.5. Sensing**

Individuals are assumed to sense the number of individuals and environmental conditions affecting their fitness.

#### **4.3.1.2.6. Interaction**

Interactions occurred through reproduction and density-dependent mortality.

#### **4.3.1.2.7. Stochasticity**

Stochasticity occurred at different levels. At the initialisation of the simulation, values of heritable traits are drawn from uniform distributions in order to reflect heterogeneity among individuals. Stochasticity is also used to distribute larvae into the river catchments. At each time step, each individual has a given probability of dying that depends on environmental conditions and densities of individuals. Finally, the recruitment function in reproduction is also based on stochastic events because parents are drawn randomly according to the probability of reaching the length-at-silvering. The inheritance transmission to each offspring is also stochastic.

#### **4.3.1.2.8. Observations**

Nine patterns are computed at the end of the simulation (table 4-3). They corresponded to those available in the literature: simulated patterns Si, Siv, Sv, and Sviii, according to observed patterns Oi, Ovi, Ov and Oviii, are validated when a negative trend is observed from north to south, and downstream to upstream; whereas patterns Sii, Siii, Svi, and Svii corresponds to observed patterns Oii, Oiii, Ovi and Ovii and are consistent with literature when a positive trend is observed from north to south and downstream to upstream. The last pattern (ix) is validated when a bimodal distribution by gender appears in the whole population distribution.

Observed patterns	Simulation outputs	Reference
<b>Among river catchments:</b>		
<b>Oi.</b> Male-biased sex ratio in the southern part of the distribution area and female-biased sex ratio in the northern part	<b>Si.</b> Proportion of females per river catchments	(Helfman <i>et al.</i> , 1984, 1987)
<b>Oii.</b> Male-biased sex ratio in an environment with high density	<b>Sii.</b> Number of individuals per river catchment	(Tesch, 2003)
<b>Oiii.</b> Faster growth in southern latitudes	<b>Siii.</b> Phenotypic response of mean realized growth rate per river catchment	(Hansen and Eversole, 1984; Oliveira, 1999)
<b>Oiv.</b> Larger females in the northern part	<b>Siv.</b> Mean length-at-silvering per river catchment	(Vollestad, 1992; Oliveira, 1999) (Oliveira, 1999)
<b>Within river catchments:</b>		
<b>Ov.</b> Higher density downstream than upstream	<b>Sv.</b> Number of individuals per cell in the river catchments	(Tesch, 2003)
<b>Ovi.</b> Higher length-at-silvering upstream than downstream	<b>Svi.</b> Mean length-at-silvering per cell in the river catchments	(Helfman <i>et al.</i> , 1987; Vélez-Espino and Koops, 2010)
<b>Ovii.</b> Male-biased sex ratio downstream and female-biased sex ratio upstream	<b>Svii.</b> Proportion of females per cells in each river catchment	(Oliveira and McCleave, 2000)
<b>Oviii.</b> The phenotypic response led to faster growth rate downstream than upstream	<b>Sviii.</b> phenotypic response of mean realized growth rate per cells in each river catchment	(Thibault <i>et al.</i> , 2007b)
<b>Regarding population distribution in terms of growth:</b>		
<b>Oix.</b> Male growth distribution is mainly fast while females have a large variation in growth	<b>Six.</b> Number of individuals by gender	(Côté <i>et al.</i> , 2015)

**Table 4-3.** Description of the observed patterns (O) and those calculated in outputs from model (S).

### 4.3.1.3. Details

#### 4.3.1.3.1. Initialization

At the beginning of the simulation, three river catchments were empty.  $N$  individuals are created and their genetic values are randomly picked in uniform distributions. They have not yet entered the river catchment.

#### 4.3.1.3.2. Input data

A reference simulation is used to test the model. Values of parameters were selected from literature (table 4-4). The model outputs were identified based on spatial patterns defined in *Observations*.

Entities	Parameters	Notation	Value	Reference
<b>Individuals</b>	Intrinsic growth rate	$k_g(i)$	Equation 11	
	Intrinsic growth rate with undirected effect of environment	$k(i)$	Equation 12	
	Genetic value of fertility	$f_g(i)$	Equation 11	
	Fertility with undirected effect of environment	$f(i)$	Equation 12	
	Genetic value of intercept of female length-at-silvering reaction norm	$ls\mu_g(i)$	Equation 11	
	Intercept of female length-at-silvering reaction norm with undirected effect of environment	$ls\mu(i)$	Equation 12	
	Genetic value of slope of female length-at-silvering reaction norm	$lsa_g(i)$		
	Slope of female length-at-silvering reaction norm with undirected effect of environment	$lsa(i)$	Equation 11	
	Intrinsic natural mortality rate with undirected effect of environment	$m(i)$	Equation 12	
	Gender	$S(i)$	Fitness maximization ( <i>Sex-determination and habitat selection</i> )	
	Length-at-silvering	$Ls(i)$	Equation 9	(Andrello <i>et al.</i> , 2011)
	Effective growth rate due to the directed effect of environment $x$	$K(i,x)$	Equation 7	(Drouineau <i>et al.</i> , 2014)
	Effective natural mortality due to the effective effect of environment at time $t$ , without density dependence and with density-dependence	$M(i,x)$ and $M(i,x,t)$	Equation 6	(Bonhommeau <i>et al.</i> , 2009)
<b>Population</b>	Parameters from the length – fecundity allometric relationship	$a, a_1$ and $b$	8846, 1.387, 3.2	(Melià <i>et al.</i> , 2006b; Andrello <i>et al.</i> , 2011)
	Length of glass eel	$L_g$	7.5 cm	(Desaunay and Guerault, 1997; Dekker, 1998; Desaunay <i>et al.</i> , 2012)
	Asymptotic length	$L_\infty$	76.2 cm	(De Leo and Gatto, 1995)
	Temperature of reference used	$T_{ref}$	11.4°C	(Mitchell et

	to scale intrinsic growth and mortality rates			Jones 2005)
	Intensity of density-dependence	$\beta$	0,00005	(Drouineau <i>et al.</i> , 2014)
	Males length-at-silvering	$L_{sm}$	40.5 cm	(Vollestad, 1992)
	Intensity of phenotypic plasticity costs	$c$	0.5	
	Relative weights of production costs	$\omega$	0.5	(Ernande and Dieckmann, 2004)
<b>Sargasso sea</b>	Probability that a larvae reach catchment c	$p_c$	0.33, 0.33, 0.33	
	Duration of larval drift to reach catchment c	$d_c$	21 months + 6 months	(Bonhommeau <i>et al.</i> , 2009)
	Probability to achieve the spawning migration	$\eta$	0.3	(Bonhommeau <i>et al.</i> , 2009)
	Maximum number of offspring	$R_{max}$	$0.777 \times 10^6$	(Andrello <i>et al.</i> , 2011)
	Genetic variances of inherited traits	$\sigma_{k_g}^2, \sigma_{f_g}^2, \sigma_{ls\mu_g}^2, \sigma_{ls\alpha_g}^2$	0.06	(Dunlop <i>et al.</i> , 2009; Enberg <i>et al.</i> , 2009)
	Environmental variances of inherited traits	$\sigma_{k^2}, \sigma_{f^2}, \sigma_{ls\mu^2}, \sigma_{ls\alpha^2}$	0.20, ?, 8.3, 0.11	(Enberg <i>et al.</i> , 2009)
	Heritability of inherited traits	$h_{k^2}, h_{f^2}, h_{ls\mu^2}, h_{ls\alpha^2}$	0.2	(Lynch and Walsh, 1998)
<b>River catchment</b>	Temperature in river catchment c	$T_c$	5, 15, 25	(Drouineau <i>et al.</i> , 2014)
	Contrast of growth rate between brackish (1 <sup>st</sup> cell of a catchment) and freshwater (2 <sup>nd</sup> cell of a catchment) habitats	$v_x$	1, 0.5	(Cairns <i>et al.</i> , 2009)
	Number of individuals in habitat x at time t	$N(x,t)$		result of habitat selection and mortality during the growth stage

**Table 4-4.** Parameter description with initial reference value.

#### 4.3.1.3.3. Submodels

The model design consists of the following submodels:

*Fitness:* Following Mateo *et al.* (2017a), fitness is sex-specific since eels have different life history strategies. Female fitness is assumed to be a trade-off between length-at-silvering, a proxy of fecundity, and survival since females are thought to follow a size maximizing strategy (Davey and Jellyman, 2005). Therefore, female fitness is defined by the probability

of surviving until length-at-silvering and fecundity. Fecundity is calculated using an allometric relationship, if individual  $i$  is a female, then

$$(1) \text{ fecundity}(i) = \left( a_1 + a \cdot L_s(i, x)^b \right)$$

$a_1$ ,  $a$  and  $b$  are the parameters to relate individual fecundity and female length-at-silvering  $L_{sf}$  (Melià *et al.*, 2006b; Andrello *et al.*, 2011). Then, the fitness (Drouineau *et al.*, 2014) of the individual  $i$  is

$$(2) \Pi_f(i, x, t) = \text{fecundity}(L_s(i, x)) \cdot \left[ \frac{L_\infty - L_g}{L_\infty - L_s(i, x)} \right]^{\frac{-M(i, x, t)}{K(i, x)}}$$

With  $\Pi_f(i, x, t)$  the individual female fitness in habitat  $x$ ,  $L_\infty$  the asymptotic length,  $L_g$  is the length at recruitment, and  $\frac{-M(i, x, t)}{K(i, x)}$  is the ratio of natural mortality to growth rate.

On the other hand, males adopt a time minimizing strategy, in which fitness does not depend on size but only in the probability to survive to a length that ensure successful migration (Helfman *et al.*, 1987). Consequently, male fitness is defined as the probability of surviving until a length-at-silvering multiplied by the male fertility  $f(i)$ , as an expectation of eggs to rescale male fitness relatively to female fitness (Mateo *et al.*, 2017a):

$$(3) \Pi_m(i, x) = f(i) \cdot \left[ \frac{L_\infty - L_g}{L_\infty - L_s(i, x)} \right]^{\frac{-M(i, x, t)}{K(i, x)}}$$

*Larvae dispersion and survival:* During the oceanic journey, the number of larvae distributed from the spawning area to the river catchments followed a multinomial probability. Bonhommeau *et al.* (2009) estimated a survival rate of larval drift based on a steady-state hypothesis in which two eggs per female should survive and reproduce successfully. On it, mortality rate of  $M_{drift} = 3.8 \text{ year}^{-1}$  was estimated in 21 months of larval drift and a continental mortality rate of  $M_{ref} = 0.14 \text{ year}^{-1}$  was estimated for individuals. Using the relationship, we computed a probability to survive the larval drift as a function of its duration until reach each river basin ( $d_c$ ) and of the intrinsic mortality rate of the individual  $i$ :

$$(4) \alpha(i, c) = e^{-M_{drift} \frac{m_i}{M_{ref}} \cdot d_c}$$



*Juvenile survival and growth:*

- *Scaling of natural mortality and growth rates:*

Each individual is characterized by an intrinsic growth rate. Nevertheless, we have to define how the environment modulates this intrinsic growth rate and how the intrinsic mortality rate can be defined based on the intrinsic growth rate.

We assumed that the intrinsic growth rate corresponds to the growth rate that would occur at a reference temperature  $T_{ref}$ . Using a statistical relationship from Pauly (1980), we can compute a corresponding intrinsic natural mortality rate at  $T_{ref}$ :

$$(5) \ln(m(i)) = -0.0066 - 0.279 \log_{10}(L_{\infty}) + 0.6543 \log_{10}(k(i)) + 0.4634 \log_{10}(T_{ref})$$

It is now necessary to find a way to scale natural mortality and growth rates for different temperatures. Bevacqua *et al.* (2011) proposed a formula that scales natural mortality to temperature as a function of a reference temperature and a mortality reference. So, we assumed that in any habitat  $x$  of catchment  $c$ , non-density dependent mortality rate is of individual  $i$  is:

$$(6) M(i,x) = m(i) \cdot e^{\frac{E}{\kappa} \cdot \frac{T_c - T_{ref}}{T_c \cdot T_{ref}}}$$

Where  $e^{\frac{E}{\kappa} \cdot \frac{T_c - T_{ref}}{T_c \cdot T_{ref}}}$  is the Boltzmann-Arrhenius factor with  $E$  the activation energy,  $K$  the Boltzmann constant,  $T_c$  the temperature in catchment  $c$  and  $T_{ref}$  the temperature at a reference mass used in MaxEel (the reference temperature is estimated in Rautjärvi Lake, in Evo, Finland, which has three river basins. CRU TS 2.1 data set is used (CRU TS pour *Climate Resarch Units Time-series*) (Mitchell and Jones, 2005)).

We then compute back a growth rate, using again the Pauly relationship:

$$(7) K(i,x) = \left( \frac{\ln(10)}{0.6543} \cdot \log_{10}(M(i,x)) + 0.0066 + 0.279 \log_{10}(L_{\infty}) - 0.4634 \log_{10}(T_c) \right) \cdot v_x$$

With  $v_x = 1$  in downstream habitat (1<sup>st</sup> cell of a catchment), and  $v_x = 0.5$  in upstream habitat (2<sup>nd</sup> cell of a catchment) since growth is faster in brackish environment than in freshwater habitats as observed by (Cairns *et al.*, 2009a).

- *Survival during the continental stage:*

At each time step until silvering, an individual  $i$  in habitat  $x$  has a probability to survive equals to  $e^{-M(i,x,t)}$ , with  $M(i,x,t) = M(i,x) + \beta \cdot N(x,t)$  assuming a density-dependent mortality and  $N(x,t)$  the number of individuals in habitat  $x$  at time  $t$ .

- *Growth during the continental stage:*

Growth was represented by a von Bertalanffy function (De Leo and Gatto, 1995):

$$(8) L(i,x,t) = L(i,x,t-1) + (L_\infty - L(i,x,t-1)) \cdot [1 - e^{-K(i,x)}]$$

Where  $L(t, i, x)$  was the length at time  $t$  and  $L_\infty$  and  $K(i, x)$  are the von Bertalanffy parameters for individual  $i$  in position  $x$  of the river catchment. Growth continues until individual reaches the length-at-silvering or till its death.

*Sex-determination and habitat selection:* once upon arrival in a catchment  $c$ , each individual  $i$  turns into male or female and select a habitat (first of second cell of the catchment) according to the following norm: the potential fitness is computed in each habitat and for each gender (equations 2, 3); the individual determines the gender and migrates to the habitat of maximum potential fitness. The fitness computation corresponds to the maximization of expected fitness given current conditions of densities in each habitat.

*Silvering:* Silvering corresponds to the beginning of the maturation process and of the seaward migration towards the spawning area. It occurs at a variable length known as length-at-silvering. This process is modelled using reaction norms of length-at-silvering for females and at a constant length for males.

For females, the reaction norm describes how length-at-silvering varies according to environmental conditions. Since individual fitness varies as a function of growth rate (which depends on intrinsic growth rate and on temperature) and mortality rate (which depends on temperature, density-dependence and intrinsic growth rate), we assume that females length-at-silvering is a linear function of the ratio  $M(i,x,t)/K(i,x)$ . So an individual  $i$  silvers at time  $t$  if:

$$(9) \begin{cases} L(i,x,t) \geq L_{s_m} & \text{if } i \text{ is a male} \\ L(i,x,t) \geq l_s \mu(i) + l_s \alpha(i) \cdot \left( \frac{M(i,x,t)}{K(i,x)} - \frac{m(i)}{k(i)} \right) & \text{if } i \text{ is a female} \end{cases}$$

the right part of the female equation corresponds to a line. We choose by convention an intercept  $ls\mu(i)$  which would correspond to the length-at-silvering at  $T_{ref}$  in brackish water (at  $T_{ref}$ ,  $M(i,x,t)=m(i)$  and  $K(i,x)=k(i)$  according to equations 5 and 6) in an empty habitat.

*Adult migration:* Following Bonhommeau *et al.* (2009), we assumed that each individual has a probability  $\eta=0.3$  to achieve the reproduction migration successfully.

*Reproduction:*

- *Number of offspring and cost of phenotypic plasticity:*

The number of offspring produced by a female is theoretically equal to its fecundity. However, their plasticity implies both maintenance costs (i.e. costs to maintain all the sensory and regulatory systems) and production costs (i.e. expenses to produce a given phenotype) (Ernande and Dieckmann, 2004), that should be accounted. Since phenotypic cost corresponds to an energetic expense, this energy is no longer available to produce offspring. Therefore, we assumed that phenotypic plasticity costs decrease the number of offspring. We do not account any costs for males: this is probably a simplifying assumption but we consider that they lose their plasticity in very early stages (during sex-determination) and do not have necessarily to produce and maintain dedicated sensory and regulatory systems.

Following Ernande and Dieckmann (2004), the cost of phenotypic plasticity,  $C(i)$  is defined by the product of a constant intensity of cost ( $c$ ) (expressed in terms of ovocytes), and the sum of maintenance and production components that depend on the difference between the expressed reaction norm of an individual and a reaction norm without plasticity, i.e. cost-free reaction norm ( $Ls$ ):

$$(10) C(i,x) = c \cdot \left[ (1-\omega) \cdot ls\alpha^2 + \omega \left( \frac{Ls(i)-ls\mu}{ls\mu} \right)^2 \right]$$

$ls\alpha^2$  is the slope of the reaction norms, therefore it measures the intensity of the potential phenotypic plasticity and corresponds to maintenance costs. The second term measures the effective difference of length-at-silvering and the length-at-silvering that would occur at  $T_{ref}$ . Therefore it measures a production cost. Parameter  $\omega$  makes the balance between production and maintenance costs.

Then each female produces a number of offspring equals to its *fecundity*( $Ls(i)$ ) -  $C(i,x)$  rounded to the nearest integer. If the total number of offspring (sum over all silver females) is

greater than  $R_{max}$ , we sample  $R_{max}$  offspring (without replacement) to mimic a hockey-stick stock-recruitment relationship.

- *Genetic code and transmission (or genetic inheritance):*

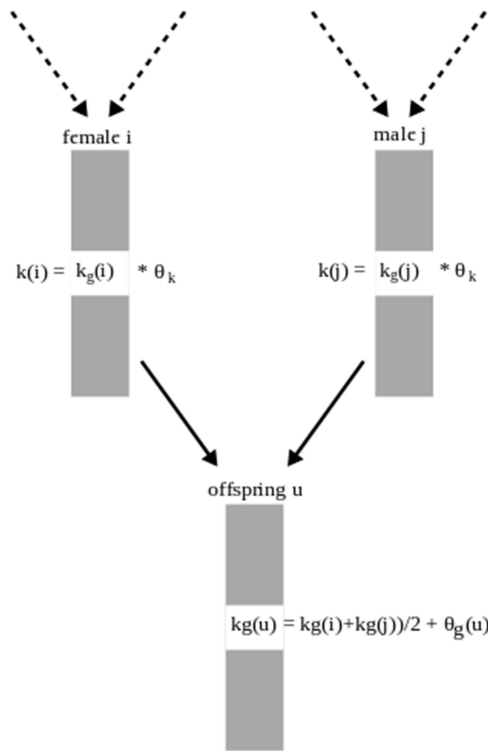
Four traits have a genetic basis and consequently, can be partially transmitted to offspring: intrinsic growth rate  $k(i)$ , fertility  $f(i)$ , slope  $lsa(i)$  and intercept  $ls\mu(i)$  of the female length-at-silvering reaction norm. Each offspring inherits traits from its mother and from a “father” randomly sampled within the pool of males.

We followed the approach of (Dunlop *et al.*, 2009) to model the transmission of heritable traits. Trait inheritance is based on quantitative genetics theory: most of life-history traits are considered as polygenic quantitative characters (i.e. determined by many loci). An offspring inherits the genetic value from its parents: in a codominance system for a given trait, the genetic value of the offspring is the average of its parents’ genetic values plus a random noise to account for a noise due to other loci of minor importance (figure 4.4). For example, for the intrinsic growth rate, an offspring  $u$  of a father  $i$  and a mother  $j$  receives:

$$(11) k_g(u) = \frac{k_g(i) + k_g(j)}{2} + \theta_{k_g}(u) \quad \text{with } \theta_{k_g}(u) \sim \text{Normal}\left(0, \sigma_{k_g}\right)$$

Then, the intrinsic growth rate is calculated by adding a random noise to account for undirected effect of environment:

$$(12) k(u) = k_g(u) \times \theta_k(u) \quad \text{with } \theta_k(u) \sim \text{Normal}(1, \sigma_k)$$



**Figure 4-4.** Transmission of genetic value of growth trait ( $k_g$ ) from parents ( $i, j$ ) to its offspring ( $u$ ).

The phenotypic variance of a trait is decomposed into additive genetic and environmental variance:

$$(13) \sigma_{Pk}^2 = \sigma_{k_g}^2 + \sigma_k^2$$

The corresponding narrow-sense heritability<sup>1</sup>  $h_k^2$  is defined by the ratio of these additive genetic and phenotypic variances (explaining how much of the phenotypic variance is explained by the additive genetic variance).

$$(14) h_k^2 = \sigma_{k_g}^2 / \sigma_{Pk}^2$$

Based on the (Carlson and Seamons, 2008), the heritability is fixed to 0.2 for life history traits associated with fitness in natural populations, so if we set the genetic variance, the environmental variance can be derived.

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<sup>1</sup> Making difference between “broad-sense heritability”, which achieves the proportion of phenotypic variation due to genetic variation that may include effects of dominance and epistasis, and “narrow-sense heritability” that explains only the proportion of genetic variation due to additive genetic values (Wray et al., 2008).

## **4.4. Discussion**

### **4.4.1. MaxEel: towards a demo-genetic model**

Vollestad (1992) highlighted geographic variations in length-at-silvering of the European eel due to phenotypic plasticity. Building on this observation, this exercise explored the conditions that would favor adaptive phenotypic plasticity. The results showed that adaptive phenotypic plasticity is optimal with extreme ecological conditions: i.e. highest density-dependence intensity, more larvae distributed into the worst habitat, and strongest thermal contrast among river basins. This is consistent with results of (Ernande and Dieckmann, 2004) who showed that plasticity is especially adapted when environments are more extremes in terms of intrinsic carrying capacity. Regarding plasticity costs, these results also illustrated the trade-off between fitness gains that arise from phenotypic plasticity and associated maintenance and production costs.

As mentioned earlier, the results showed that strong density-dependent mortality favors phenotypic plasticity. In this exercise, phenotypic plasticity was still selected in a situation without density-dependence but with a limited magnitude. In a context of a depleted population, density-dependant mortality decreases. Therefore, the results suggest that the plasticity is not necessarily a maladaptation in a context of depleted population, but that its magnitude is not maximal anymore. In other words, the plasticity selected in conditions with high abundance is too strong when the number of individuals decreases as it, generates excessive costs. However, density plays an important role in others traits and, the costs and trade-offs of phenotypic plasticity are not well known, which impairs our ability to derive the cost/benefit ratio. Nevertheless, the magnitude of phenotypic plasticity may not be optimal in the current conditions, it may be adaptive again if the population recovers, and is an asset to adapt to the rapid changes caused by global change.

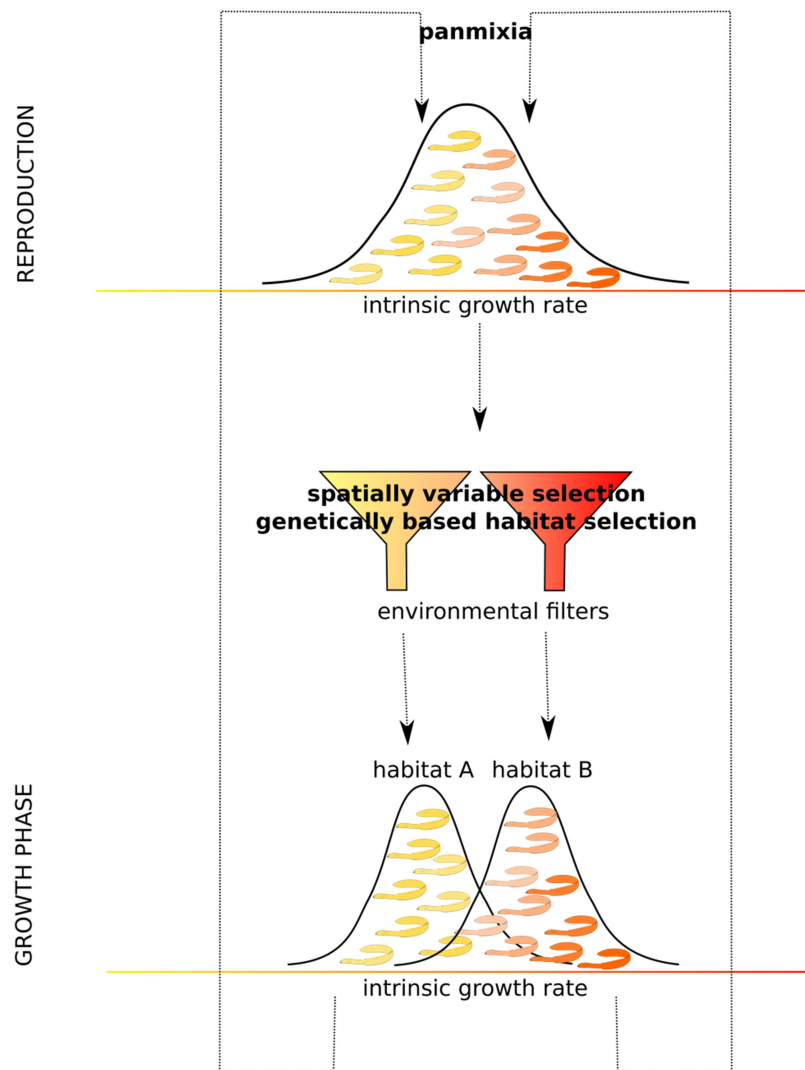
### **4.4.2. Our demo-genetic model: a work in progress**

In this chapter, we presented a demo-genetic life cycle model for eels. This is clearly a work in progress: the model has not been implemented yet. So, we were not able to explore it to derive first results. Consequently, our ODD should be seen as a first prototype of the model, which will most likely be modified when first results will be available. However, it is important to present this prototype in this chapter for various reasons. First, the model summarizes all our understanding on the functioning of the eel population, especially on its

adaptation to environmental heterogeneity. It is based on our understanding of adaptation obtained with GenEveel, which combines it with population dynamics at the distribution scale and puts it into an evolutionary perspective by completing the life cycle and allowing multi-generations simulations. Second, presenting the model allows us to present all the perspective of our work, especially by discussing how the model may be used to explore different questions about the effect of anthropogenic pressures, population resilience, or conservation measures.

#### **4.4.2.1. Could ecotypes arise from a quantitative genetic model?**

In the new model, we included a genetic basis for growth. Similarly to MaxEel, the aim is to explore the conditions that favor the emergence of phenotypic plasticity and genetic polymorphism. Because of the inheritance system and the panmixia, we expect that the distribution of growth rate would be normal at the beginning of the simulations, and evolving over generations but remaining symmetric. However, the spatially structured environments defined in the model can act as spatially variable selective pressures. Thus, the duration of larval drift affects the larval survival differently depending on the intrinsic mortality rates of the individuals, the temperature of river catchments lead to different growth and mortality rates among individuals, salinity differences modify the gradient of growth rate within the river and biotic interactions such as resources competition leads to density-dependent mortalities. The expected results would be that specific values of traits would be favored in specific habitats. Since phenotypes have partly a genetic basis, we can expect an association between intrinsic growth rates and habitats. In such association, environmental conditions would act as filters that separate individuals into genetically homogenous clusters, generating ecotypes (figure 4-5). It would be interesting to check whether the model mimics the results of Côté *et al.* (2015) and Pavey *et al.* (2015). In them, genetic differences correlated with the environments lead to clusters of growth depending on sex, i.e. fast growing males and more variable female growth depending on environments (Côté *et al.*, 2015). Additionally, we would be able to check the emergence of ecotypes proposed by Pavey *et al.* (2015) in which individuals reared in freshwater tend to grow slowly and become females, compared with those of brackish waters. In any case, validating these patterns of geographic variation in growth, depending on sex, would confirm that spatially varying selection and genetically dependent habitat selection are plausible to explain observed ecotypes, and complementary to the phenotypic plasticity known for this species.



**Figure 4-5.** Schematic representation of how spatially variable selection and genetically based habitat selection could act in each generation resulting in genetic differences among habitat, i.e. ecotypes.

#### **4.4.2.2. Do the anthropogenic pressures induce selection for length-at-silvering or ecotypes?**

The first use of the model would be to update results from chapter three which intends to explore the effects of anthropogenic pressures on eel population and their consequences on adaptive response of plastic traits. Many studies have revealed changes in life history traits, such as growth rates, age and size at maturity, and reproductive effort in harvested populations, which demonstrates that the strong and size-selective mortalities imposed by fisheries induce evolution in these traits (Edeline, 2007; Swain *et al.*, 2007; Enberg *et al.*, 2012). Since all life stages of eel are exploited, it would be interesting to compare the effects of glass eels, yellow eels and silver eels fisheries. Glass-eels are generally located in downstream catchments and thus do not discriminate specific traits. In the other hand, yellow



eels fisheries effects probably depend on their location within the catchments while silver eels fisheries tends to select large silver eels. Bevacqua *et al.* (2012) have already studied yellow and silver eel fisheries using field data. They showed that fast growing yellow eels are removed because are preferentially targeted by fishermen. However, they suggested that fisheries induced evolution is difficult to confirm in the European eel, due to panmixia. It would be interesting to account for these fisheries in our model to compare with these results. Bevacqua *et al.* (2012) did not observe significant induced selection due to silver eel fisheries. Nevertheless, the sampling methods did not allow to have a real post-fishery sample and there were mostly males in the sampling sites (Mediterranean lagoons) limiting length-at-silvering contrasts. However, the largest individuals are probably more harvested than small silver eels in most silver eel fisheries. Such a selection would decrease the benefit of large length-at-silvering and may lead to a maladaptation or a homogenization of phenotype, decreasing diversity and losing plasticity. These type of questions are relevant for fisheries and also for all anthropogenic pressures. The model can be used to explore which anthropogenic pressures are more likely to reduce the species genetic and phenotypic diversity and the consequences on species resilience.

#### **4.4.2.3. Are adaptive mechanisms sources of portfolio and storage effects?**

The capacity of eels to settle in a wide range of habitats can be viewed as a portfolio effect because the diversity of habitats smooths out environmental variations in each single habitat (Secor, 2015a). Using a model, (ICES, 2009) measured the portfolio effect in eel population and showed that the use of fresh and saltwater habitats have a great influence on the population dynamics and stability. It would be interesting to revisit this exercise with our model, to check whether the use of multiple river basins and multiple habitats within each basin increase the resilience of the population against environmental variations. Carrying out this exercise at the species distribution scale would contribute to study the effect of climatic change at large scale and to provide spatial scale insights to develop appropriate management and conservation actions.

The storage effect refers a situation in complex life cycle in which a long and relatively stable stage buffers rapid variations of survival in a short stage (Secor, 2015a). For eels, the growth stage, especially in upstream habitat can be source of storage effect by buffering variations in recruitment (ICES, 2009). In view of this, we can use our model to study how the population responds to periods of unfavorable recruitments if upstream habitats are available and in if

these upstream habitats are absent or not. We expect that unfavorable conditions would be buffered by the overlapping generations, which depend on the diversity of maturation rates. In our model, these maturation rates are related to growth during the continental phase, growth being under the joint influence of genetic and environmental conditions.

#### **4.4.2.4. How does the diversity loss affect eel population?**

Storage and portfolio effects are based on individual diversity that allows diversity of growth habitat use. Diversity is crucial for temperate eels to ensure population persistence, stability and resilience (Secor, 2015b). In view of this, it would be interesting to explore how a decrease in diversity, for example as a result of anthropogenic pressures, affects the population. For example, we would like to explore the consequences of a reduction of genetic diversity. In such a case, if habitats remain heterogeneous, we expect that phenotypic plasticity would become even more important. However, some associations between genotypes and sex-determination or length-at-silvering, result in a reduction of genetic diversity that would produce a modification of the population sex-ratio and of the population length-at-silvering, and consequently on the overall fecundity. It would likely reduce the storage and portfolio effects and thus reduce the population resilience and stability.

The model can also be used to explore the effect of habitat homogenization, which can be the result of human induced ecosystem fragmentation or habitat destruction. In such situation, we expect a reduction of genetic diversity and of plasticity and that individual would progressively become more and more adapted to the habitat, but at risk of extinction if environmental conditions change.

#### **4.4.2.5. Future applications: ecological and evolutionary consequences of restocking**

In view of worldwide eel decline, restocking or translocation of early eel life from high to low recruitment areas has been proposed as a conservation measure for eel populations conservation (Dekker and Beaulaton, 2016). Nevertheless, the efficiency of these programs remains unclear. For example, a large restocking program in the Saint-Lawrence River have yielded unexpected outcomes. It has resulted in the production of small silver eels in the lake Ontario which used to produce only very large silver eels (Verreault *et al.*, 2010). More generally, stocked eels tended to display life history traits comparable to those observed in

their capture site than traits of the areas in which they were stocked (Stacey *et al.*, 2015). This is probably because the adaptive mechanisms to environmental heterogeneity were not considered at all in the restocking programs. In this context, our demo-genetic model provides a useful tool to explore the consequences of this practice. Several questions could be addressed: (i) what are the consequences of moving individuals towards unsuitable habitats in terms of abundance and of life history traits? (ii) Should restocking program target specific types of individuals? (iii) Is it possible to propose restocking strategies that do not modify life history traits? These questions can be explored by simulating the transfer of a fix amount of individuals from a basin to a given habitat. This exercise will disrupt the genotype dependent habitat selection within river basin and the spatially variable selection that occurs during the larval drift in cases of restocking between distinct river basins.

## ***Take-home messages***

- ✓ In which **conditions** evolutionary benefits of **phenotypic plasticity surpass related costs?**

The intensity of costs had the strongest effect on the emergence of phenotypic plasticity. The intensity of the density dependence was the second factor favoring plasticity. Reaction norms were more plastic with production costs than maintenance costs. The degree of heterogeneity between river basins and the distribution of the larvae had less important effects on the adaptive value of phenotypic plasticity, but by their own, but can have significant influence through interactions.

- ✓ **The suboptimal situation of adaptive phenotypic plasticity in the context of depleted population:**

In absence of density dependence, such as in depleted population, phenotypic plasticity is still present, but very much attenuated. This shows that plasticity still has an evolutionary advantage, but is not an optimal situation.

- ✓ **The demo-genetic model a promising operating model:**

The model could not be used throughout this thesis. However, the model summarizes the knowledge of the functioning of the eel population acquired in this thesis. It is based on the understanding of the adaptation obtained in GenEveel, combined with the population dynamics at the distribution scale, providing an evolutionary perspective.

## ***To go further***

The prototype of the demo-genetic model represents a tool with many applications: assess the influence of global change in eel populations, display how the conservation of genetic diversity and the range of habitats are crucial for the species viability, search conservation strategies such as restocking programs and explore the anthropogenic pressures as selective pressures for life history traits of eels.

**Chapter 5:**  
**Discussion and perspectives**

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## **5.1. The major contributions of this thesis**

Despite the great interest for temperate eels and the vast scientific literature dealing with particular aspects and population dynamics of these species, the progress about how eels cope with environmental heterogeneity have been developed in recent years. Many studies have documented correlations between one specific life-history trait and environmental gradients, such as length-at-silvering, sex ratio, and effects of density on growth. Recently, other experimental studies highlighted about the genetic basis of geographic variation of life history traits such as growth and the correlation between environmental conditions and gene expression. However, few studies have analyzed all these observations simultaneously, in order to find a common adaptive meaning.

This PhD brings together all the available knowledge about life history of eels that comes from different research fields, in order to analyze vital features of eel during the continental phase. Using models, we gave a meaning to all these disparate observations. We were able to propose an overall scheme of the mechanisms involved in the adaptation to environmental heterogeneity and to provide new insights to management.

More specifically in chapter two, we explored how genetic polymorphism in intrinsic growth rate might result in and how phenotypic plasticity can cause adaptations to environmental heterogeneity. This chapter provides new insights on the discrepancy of life strategies between males and females, suggesting that it could be caused by genetic differences in growth. Moreover, this work shows how density and environmental factors determine ecological patterns.

Building on this, chapter three assesses the direct and indirect impact of several anthropogenic pressures on eel escapement. Since the model is not calibrated on real data, it is impossible to derive obvious management recommendations with this work. However results clearly show that the impact of management pressures can have unpredictable consequences on escapement because of the complex system of adaptation of the species. In view of this, it suggests that management should not focus only on mortality rates but also consider the consequences of anthropogenic activities on the diversity of eel traits and habitat selection.

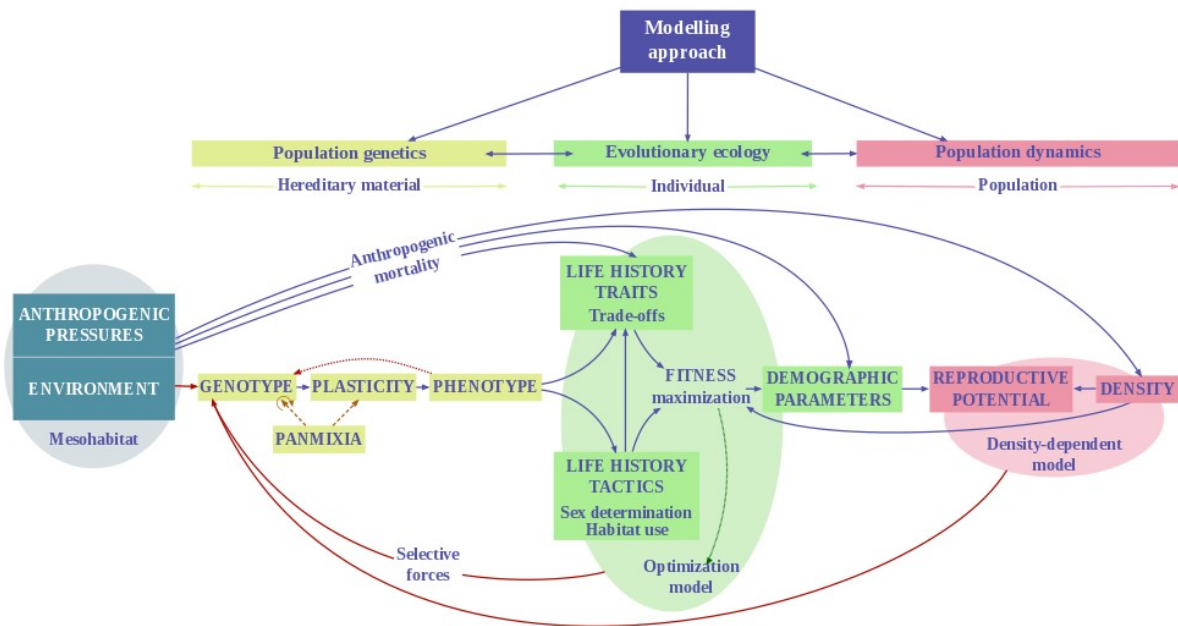
## **5.2. Perspectives: Applications of demo-genetic model**

Building on previous results, chapter four proposes a model that goes one step further and summarizes our current understanding of this enigmatic species. By predicting the effects of

anthropogenic pressures on eels, such model is a relevant tool to assess the influence of global change on eel populations and inform management and conservation policies. This model is also useful to illustrate how the preservation of both genetic and habitat diversity is crucial for the viability of the species. It is a good candidate to be an operating model to explore the relevance of management strategies. The latter perspective includes restocking that is one of the main management measure used to restore eel populations (Wickström and Sjöberg, 2014; Dekker and Beaulaton, 2016). The practice consists in translocating individuals of early life stages from natural habitats with high abundance to others, more or less distant habitats where survival is expected to be better. Stacey *et al.* (2015) compared American eels stocked into the St. Lawrence River basin originating from donor areas 200km far away, with those of natural recruits. Their results showed that stocked females experienced faster growth and were significantly larger than the natural recruits, and similar results were obtained on older ages of European eels in Lithuania (Lin *et al.*, 2007). An explanation could be that environmentally induced plasticity on its own is not enough to explain the observed differences in life history traits and demographic attributes, and that those differences may also arise from different genes expression (Stacey *et al.*, 2015). This could be the case if natural selection operates early, as the larval drift, through differential mortality for slow and fast-growing individuals. This would lead to early spatially variable selection and a “non-equivalence” of glass eels among river basins. In view of the lack of knowledge about these consequences on population dynamics, the relevance of restocking is strongly questioned and it should be applied with caution (Stacey *et al.*, 2015). The examples mentioned before demonstrate why it is crucial to consider adaptive mechanisms to assess restocking as measure, and more generally, in the management of eel populations. The model that we propose can be a valuable exploration tool, especially when it will be calibrated with real data.

The model can also be used to explore the risk of human induced selection of life history traits. Many studies have used similar models to explore fishing-induced changes on traits (Dunlop *et al.*, 2007; Wang and Höök, 2009; Eikeset *et al.*, 2016). Their results have shown possible altered growth rates, earlier maturation at smaller size and high reproductive effort in harvested populations, which demonstrates that the strong and size-selective mortalities imposed by fishing induce evolution in life history traits. In accordance to the different anthropogenic pressures that impact temperate eels, it would be interesting to adapt the model for some of them, as we did in chapter two. Further research of the role of anthropogenic pressures as selective pressures will allow to analyze whether slow-growing individuals are still preserved by natural and artificial selection (figure 5-1). Based on (Reed *et al.*, 2011;

Ayllón *et al.*, 2016), the evolution of life-history traits and population abundance under a range of climate change scenarios can be also explored, assuming a continuous linear increase in temperature through time.



**Figure 5-1.** Scheme of the thesis outline.

The calibration phase to fit the model on real data represents a challenging task if the aim is to use these models as tools to support decision-making and implement management. Modifications of the model may be necessary to achieve a successful calibration. For example, the model assumes that fishes are omniscient (perfect knowledge of the entire river catchment) and omnipotent (they are able to migrate to any part of the catchment without any delay). This is clearly untrue and probably additional assumptions will be required to fit field data. However, before modifying the model, the first step would be to collect enough data on available habitats and life history traits. Regarding habitats, it would be needed data on the amount of available habitats (freshwater and brackish) and on temperature within habitats. Regarding life-history traits, densities per habitats are available because of electrofishing data. However, data on sex ratio and length-at-silvering are not as widely available. Perhaps, recent findings on genetic basis for head shape, possibly correlated to intrinsic growth rates (De Meyer *et al.*, 2017), would facilitate data collection since it is more easily measurable than sex or genotype. A second step would be to choose an appropriate spatial scale. If working at the European scale, it would be necessary to simplify the river basin scale. A possible solution would be to define a few geographic zones in which it is assumed that environmental and biologic features are similar. Each zone would correspond to a unique basin that would be subdivided into two habitats (brackish and freshwater). For example, it would be possible to



use the zones defined in the GEREM model (Bornarel *et al.*, in press): Bay of Biscay, Iberian coast, Mediterranean Sea, North Sea, British Isles and English/Bristol Channel. These zones were defined because of similar oceanographic features and similar glass-eel recruitments trends. GEREM would provide time-series of recruitments that can be used to calibrate the larval drift and, more specifically, the distribution of recruitment among zones. Fitting the model at the European scale is an ambitious task and probably not realistic in the short term. A more reasonable solution would be to apply the model we presented in chapter three (GenEveel) on a single river basin. The Garonne-Dordogne river basin would be a relevant basin to work on because all anthropogenic pressures are present on it and datasets are largely available. Though less ambitious, such an exercise would already be relevant to management since river catchments constitute independent units during the continental stage and management measures are often prioritized at this spatial scale.

### **5.3. Preserving eel diversity: need for a change of paradigm in conservation?**

Eels' adaptation capacity is based on the combination of genetic diversity and phenotypic plasticity that are source of life history traits diversity and allow eels to use diverse habitats. As such, eels are also interesting examples of how diversity might contribute to population resilience and stability. The environmental conditions during the oceanic phase have been a major driver of contemporary population dynamic and they have probably contributed to shape the evolution of eels (Kettle *et al.*, 2008; Munk *et al.*, 2010; Baltazar-Soares, 2014). However, the large variability of habitat use during the continental phase should not be neglected. Eels that settle in freshwater habitats tend to become females, grow slowly and mature older than in others habitats, leading to slow but smoother population dynamics. Conversely, eels in brackish habitats tend to grow faster and mature earlier, leading to fast but more erratic population dynamics. Therefore, the great variation of responses to environmental conditions during the continental phase suggests that management and conservation measures should focus on the wide range of habitats; from brackish and saltwater habitats where the number of recruits is more important and the dynamics fast to freshwater habitats where dynamics is slower but can counterbalance fast oscillations of oceanic and brackish habitats conditions (Secor, 2015a). Furthermore, age diversity and spatial structure improve population resilience to environmental and anthropogenic pressures. The diversity in age structure of silver eels that emigrate from different continental growth conditions and the overlapping generations is source of the storage effect, while the

multiplicity of growth habitats is source of a portfolio effect (ICES, 2009; Secor, 2015a). Consequently, the use of diverse habitats is required for eel populations. Therefore, the protection of the genetic diversity and all mechanisms involved in phenotypic diversity are crucial for eels.

In view of that, management strategies must consider the amount of change that these species can absorb, i.e. identify the population resilience, and anticipate the changes in environmental and anthropogenic conditions that impair this resilience (West *et al.*, 2009). For that, ecological modelling studies are useful tools to explore the genetic and the plastic life history adaptations to new environments. It can also be used to explore, scenarios on management consequences that supporting environmental decision-making.

#### **5.4. Why temperate eels represent a model to study adaptation in the current context of global change?**

Most species are threatened by the unprecedented rate of change induced by global change. In this context, is needed to enhance our knowledge on the capacity of species to adaptation and on their adaptation speed to guide management strategies and conservation policies. In recent years, many studies have addressed this subject, focusing on evolutionary mechanisms, and the advantages of selection versus phenotypic plasticity on the rate of adaptation. This work contributes to this debate using eels as an example. But, why eels are illustrative model to explore such question?

Temperate eels are interesting species from an ecological and evolutionary point of view. Panmixia and passive larval drift are the two major constraints to adapt in heterogeneous environments. Meanwhile, a large diversity in life history traits such as growth and length-at-silvering, and in life history strategies such as migratory behaviour, has been observed. This is the result of the amazing adaptation capacity of eels that is based on the combination of adaptive phenotypic plasticity and genetic ecotypes that are shuffled at each generation. This original combination makes eels a very good example to study the relative advantages of phenotypic plasticity and genetic evolution in a context of global change. Because of its complex life-cycle, eels are good candidates to study whether panmixia and large distribution arears hinder species adaptation to global and climate change. In addition, because of the strong density dependence and the current decline of the population, eels also raise question about the maladaptation of phenotypic plasticity in depleted populations.

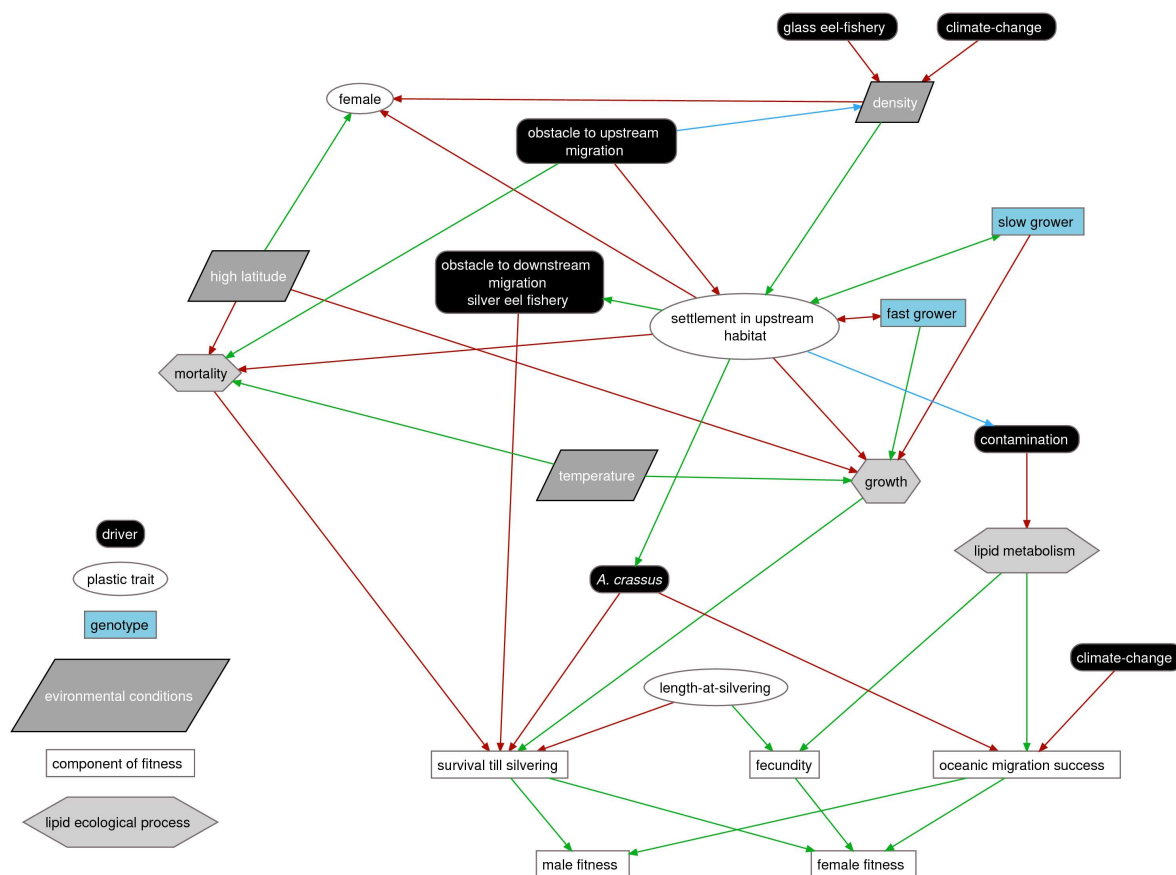
These species are a perfect candidate to research the effects of the global change components and their synergies. We have seen in the introduction that there are five main components of global change: (i) global warming and modifications of oceanic conditions, (ii) fragmentation of ecosystem and habitat loss, (iii) over-exploitation of natural resources, (iv) biodiversity modifications and biological invasions and (iv) contamination and increase of nutrient loads. Since the radiation of the genus *Anguilla*, about 20 million years ago (Lin *et al.*, 2001), temperate eels have shown an incredible adaptation capacity: they survived to glacial periods and continental drift (which separated the spawning ground from growth habitats in continental waters), occupy a wide variety of habitats (saltwater, brackish water and freshwater) and have adapted to them even without choosing the habitat they will grow on (due to the passive larval drift). Why then in the brief period of 30 years eel populations have declined dramatically? Five main causes have been proposed, and each cause corresponds to one of the components of global change:

1. Climate change and oceanic modifications affect eel populations in two ways: a decrease in prey quantity and quality for leptocephali larvae in the spawning grounds hindering the larval survival (Bonhommeau *et al.*, 2008; Miller *et al.*, 2016), and the negative effects on the larval transport of the Japanese eels (Kim *et al.*, 2007; Zenimoto *et al.*, 2009).
2. Because of fragmentation and habitat loss mostly due to dam construction that has been intensified between the 1950s and the 1970s (World Commission on Dams, 2000), European eel has lost 50-80% of its habitat (Feunteun, 2002) while for the American eel, the Saint-Lawrence habitat has been reduced to 40-50% (Verreault *et al.*, 2004). Furthermore, hydroelectric turbines from dams induce mortality in silver eels when they migrate downstream to leave continental waters.
3. Fisheries harvest all life stages of eels. The demand for European glass eels for Asian aquaculture exploded in the 1970s and lead to a rapid increase in export price – about €500 per kg (Ringuet *et al.*, 2002; Briand *et al.*, 2007) – and therefore a rapid increase in fishing effort and landings. As a consequence, amazing exploitation rates were estimated at different river basins (Aprahamian *et al.*, 2007; Briand *et al.*, 2015; Drouineau *et al.*, 2016). For example, in the Vilaine River (France) 95% of the glass eel recruitment used to be harvested (Briand *et al.*, 2005). Such example shows how glass eels fisheries have drastically changed since the second half of the 20<sup>th</sup> century.
4. The natural parasite of Japanese glass eels, *Anguillicoides crassus*, was introduced in Europe. The parasite affects European eels and has colonized most continental water habitats during the 1970s-1980s. It was also introduced in Northern America and has

quickly spread in the United States and Canada (Barse and Secor, 1999; Hein *et al.*, 2014). This parasite alters the swim bladder of the fish that impairs the capacity of eels to complete the spawning migration (Kirk, 2003).

5. Eels are especially impacted by contamination. Their high trophic position makes them subject to biomagnification of many compounds in trophic networks. Moreover, they are especially subject to bioaccumulation because of their high lipid storage that is required to achieve the spawning migration (they do not feed during the journey). This leads to an alter lipid metabolism that can impair migration success and pollutants can potentially be transferred to the offspring (Geeraerts and Belpaire, 2010).

Consequently, by working on eels, is possible to explore the effect of each component of the global change in species and its potential role as selective pressures, altering life history traits and ecotypes in different ways (figure 5-2). Furthermore, it is also possible to analyze the synergies between components and how they interfere with species adaptation capacities. Typically, the demo-genetic model proposed in this thesis can be used to explore such questions.



**Figure 5-2.** Adaptation mechanisms to environmental heterogeneity. A red arrow means “unfavorable”, a green arrow means “favorable”. A blue arrow means a relationship which is either favorable” or “unfavorable” depending on situations. (Drouineau *et al.*, submitted).

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# Appendix

## Supplementary chapter 2

**Table S2.1.** Results of the 256 combinations. The signs +/- refer to the modalities of the parameters groups. The last five columns represent the spatial patterns. An ascendant arrows stands for positive Mann-Kendall tau value (increasing trend from downstream to upstream). Conversely, a descendant arrow stands for a negative Mann-Kendall tau value.

	$N$	$fertility,$ $L_{sm}$	$K_{fast}(i, I),$ $M_{fast}(i, I)$	$K_{slow}(i, I),$ $M_{slow}(i, I)$	$propK$	$a$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
1	-	-	-	+	+	+	+	+	-	-	+	+	↘	↗	↗	↘	↘
2	+	-	-	+	-	+	+	+	-	+	+	+	↘	↗	↗	↘	↘
3	+	-	-	+	+	-	+	+	-	+	+	-	↘	↗	↗	↘	↘
4	-	-	-	+	-	-	+	+	-	-	+	-	↘	↗	↗	↘	↘
5	+	-	+	+	+	-	-	+	-	-	+	-	↘	↗	↗	↘	↘
6	+	-	-	+	-	-	-	+	-	+	-	-	↘	↗	↗	↘	↘
7	-	-	-	+	-	+	+	-	+	+	+	+	↘	↗	↗	↘	↘
8	-	-	+	+	-	-	-	+	-	+	+	-	↘	↗	↗	↘	↘
9	-	-	+	+	+	+	-	+	-	+	+	+	↘	↗	↗	↘	↘
10	-	-	+	+	-	+	+	+	-	+	-	+	↘	↗	↗	↘	↘
11	+	-	+	+	-	+	-	+	-	-	+	+	↘	↗	↗	↘	↘
12	-	-	-	+	-	+	-	+	-	-	-	+	↘	↗	↗	↘	↘
13	+	-	+	+	-	-	+	+	-	-	-	-	↘	↗	↗	↘	↘
14	-	-	-	+	-	-	-	-	+	+	-	-	↘	↗	↘	↘	↘
15	+	+	+	-	-	-	+	+	-	-	+	-	↘	↗	↘	↘	↘
16	+	-	-	-	-	+	+	-	+	+	-	-	↘	↗	↘	↘	↘
17	-	-	-	-	+	-	+	+	-	+	-	+	↘	↗	↘	↘	↘
18	+	+	+	+	+	-	-	+	+	+	-	-	↘	↗	↘	↘	↘
19	+	-	-	-	-	-	-	-	+	+	+	+	↘	↗	↘	↘	↘
20	-	+	+	+	+	-	+	+	+	-	+	-	↘	↗	↘	↘	↘
21	+	-	-	-	-	-	+	+	-	-	-	+	↘	↗	↘	↘	↘



	$N$	fertility, $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
22	+	-	-	+	-	-	+	-	+	-	+	-	↘	↗	↘	↘	↘
23	-	-	-	-	-	-	+	-	+	-	-	+	↘	↗	↘	↘	↘
24	+	-	+	-	+	-	+	+	-	+	+	+	↘	↗	↘	↘	↘
25	+	+	-	+	-	-	-	+	+	-	+	-	↘	↗	↘	↘	↘
26	+	-	+	-	-	-	+	+	+	+	-	-	↘	↗	↘	↘	↘
27	-	-	+	-	-	-	+	+	-	-	+	+	↘	↗	↘	↘	↘
28	-	-	-	+	+	-	+	-	+	+	+	-	↘	↗	↘	↘	↘
29	+	+	+	-	+	-	-	+	-	-	-	-	↘	↗	↘	↘	↘
30	-	-	+	-	-	-	-	+	+	-	+	-	↘	↗	↘	↘	↘
31	+	-	+	-	-	+	-	-	+	-	-	-	↘	↗	↘	↘	↘
32	-	+	-	-	+	-	+	+	+	-	+	+	↘	↗	↘	↘	↘
33	+	+	+	+	+	-	-	-	+	-	+	+	↘	↗	↘	↘	↘
34	+	-	+	+	+	+	-	-	+	+	+	+	↘	↗	↘	↘	↘
35	+	+	-	+	+	-	+	+	+	-	-	-	↘	↗	↘	↘	↘
36	-	+	+	-	+	-	-	+	+	+	+	+	↘	↗	↘	↘	↘
37	-	-	-	+	+	-	+	+	+	-	-	+	↘	↗	↘	↘	↘
38	-	+	+	-	-	-	+	+	+	+	-	+	↘	↗	↘	↘	↘
39	-	+	-	+	-	-	+	+	+	+	-	-	↘	↗	↘	↘	↘
40	-	+	-	-	-	-	-	+	+	-	-	+	↘	↗	↘	↘	↘
41	+	+	+	-	+	-	+	-	+	+	+	-	↘	↗	↘	↘	↘
42	-	+	-	+	+	-	-	+	+	+	+	-	↘	↗	↘	↘	↘
43	+	-	+	+	-	-	-	+	+	-	-	+	↘	↗	↘	↘	↘
44	-	-	+	-	-	+	+	-	+	+	+	-	↘	↗	↘	↘	↘
45	+	-	+	+	-	-	-	-	+	+	+	-	↘	↗	↘	↘	↘
46	+	-	+	+	+	-	+	+	+	-	+	+	↘	↗	↘	↘	↘
47	-	-	-	+	-	-	-	+	+	-	+	+	↘	↗	↘	↘	↘
48	-	-	+	+	+	-	+	+	-	+	-	-	↘	↗	↘	↘	↘
49	+	-	-	+	+	-	-	+	+	+	+	+	↘	↗	↘	↘	↘
50	+	+	-	-	-	+	-	+	+	+	-	-	↘	↗	↘	↘	↘
51	+	-	-	-	-	-	+	+	-	-	-	+	↘	↗	↘	↘	↘
52	-	-	+	+	+	-	-	+	+	+	-	+	↘	↗	↘	↘	↘
53	-	-	-	-	+	-	-	-	+	-	+	+	↘	↗	↘	↘	↘

	$N$	fertility, $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
54	-	+	-	-	+	-	+	-	+	+	-	-	↘	↗	↘	↘	↘
55	-	-	-	-	+	-	-	+	+	+	-	-	↘	↗	↘	↘	↘
56	-	+	+	-	-	-	+	-	+	-	-	-	↘	↗	↘	↘	↘
57	-	+	+	-	-	-	+	-	+	-	+	-	↘	↗	↘	↘	↘
58	-	-	-	-	-	+	-	-	+	-	+	-	↘	↗	↘	↘	↘
59	+	+	+	-	-	-	-	-	+	+	-	-	↘	↗	↘	↘	↘
60	-	+	-	-	-	-	+	+	-	-	-	-	↘	↗	↘	↘	↘
61	-	+	+	-	+	-	-	-	+	-	-	-	↘	↗	↘	↘	↘
62	+	-	+	-	+	-	-	-	+	-	-	+	↘	↗	↘	↘	↘
63	+	-	+	-	-	-	+	-	+	-	+	+	↘	↗	↘	↘	↘
64	+	-	-	-	+	-	+	-	+	+	-	+	↘	↗	↘	↘	↘
65	-	-	-	-	+	+	+	-	+	-	-	-	↘	↗	↘	↘	↘
66	+	-	-	+	-	-	+	+	+	+	-	+	↘	↗	↘	↘	↘
67	-	-	+	-	+	-	-	+	-	-	-	+	↘	↗	↘	↘	↘
68	-	-	-	+	+	-	-	+	-	-	-	-	↘	↗	↘	↘	↘
69	-	-	+	-	+	-	+	+	+	-	-	-	↘	↗	↘	↘	↘
70	-	-	+	-	+	-	+	-	+	+	+	+	↘	↗	↘	↘	↘
71	+	-	-	-	+	-	+	+	+	-	+	-	↘	↗	↘	↘	↘
72	-	-	+	-	-	-	-	-	+	+	-	+	↘	↗	↘	↘	↘
73	-	-	-	-	-	-	+	+	+	+	+	-	↘	↗	↘	↘	↘
74	+	+	-	-	+	-	-	-	+	-	+	-	↘	↗	↘	↘	↘
75	+	-	-	-	+	-	-	+	-	-	+	+	↘	↗	↘	↘	↘
75	-	-	+	+	-	-	+	-	+	-	-	-	↘	↗	↘	↘	↘
76	-	+	-	-	-	-	-	-	+	+	+	-	↘	↗	↘	↘	↘
78	+	-	-	-	+	+	-	-	+	+	+	-	↘	↗	↘	↘	↘
79	+	+	+	-	+	-	+	+	+	-	-	+	↘	↗	↘	↘	↘
80	-	-	+	-	+	+	-	-	+	+	-	-	↘	↗	↘	↘	↘
81	-	-	+	+	+	-	-	-	+	-	+	-	↘	↗	↘	↘	↘
82	-	-	+	+	+	-	-	+	+	+	-	+	↘	↗	↘	↘	↘
83	+	-	+	+	+	-	+	-	+	+	-	-	↘	↗	↘	↘	↘
84	+	-	+	-	-	-	-	+	-	+	-	+	↘	↗	↘	↘	↘
85	+	-	-	+	+	-	-	-	+	-	-	-	↘	↗	↘	↘	↘

	$N$	fertility, $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
86	-	+	+	+	-	-	-	+	+	-	-	-	↘	↗	↘	↘	↘
87	+	+	-	-	-	-	+	+	+	+	+	+	↘	↗	↘	↘	↘
88	+	-	+	-	+	-	-	+	+	+	+	-	↘	↗	↘	↘	↘
89	+	+	+	+	-	+	-	-	+	-	+	-	↘	↗	↘	↘	↘
90	-	-	-	-	-	-	-	+	-	+	+	+	↘	↗	↘	↘	↘
91	-	+	+	-	+	-	+	+	-	+	+	-	↘	↗	↘	↘	↘
92	+	+	-	-	-	-	+	-	+	-	-	-	↘	↗	↘	↘	↘
93	-	-	+	+	-	-	+	+	+	+	+	+	↘	↗	↘	↘	↘
94	+	+	-	-	+	-	-	+	+	+	-	+	↘	↗	↘	↘	↘
95	+	+	-	-	+	-	+	+	-	+	-	-	↘	↗	↘	↘	↘
96	+	+	-	-	-	-	-	+	-	+	+	-	↘	↗	↘	↘	↘
97	+	-	+	-	+	+	+	-	+	-	+	-	↘	↗	↘	↘	↘
98	+	+	-	+	+	-	-	+	-	-	-	+	↘	↗	↘	↘	↘
99	-	+	-	-	+	-	-	+	-	-	+	-	↘	↗	↘	↘	↘
100	+	-	-	-	-	-	-	+	+	-	-	-	↘	↗	↘	↘	↘
101	+	+	+	+	-	-	+	+	+	+	+	-	↘	↗	↘	↘	↘
102	+	-	-	+	+	+	-	+	-	+	-	+	↘	↘	↘	↘	↘
103	-	+	-	-	+	+	+	+	-	-	-	+	↘	↘	↘	↘	↘
104	+	+	+	-	-	+	+	-	+	+	+	+	↘	↘	↘	↘	↘
105	-	+	+	+	+	+	-	-	+	+	+	-	↘	↘	↘	↘	↘
106	-	+	-	+	+	-	-	-	+	-	-	+	↘	↘	↘	↘	↘
107	-	+	-	-	+	+	-	-	+	+	+	+	↘	↘	↘	↘	↘
108	+	+	-	+	-	-	+	+	-	-	+	+	↘	↘	↘	↘	↘
109	+	+	+	+	+	-	+	+	-	+	-	+	↘	↘	↘	↘	↘
110	+	+	-	+	-	-	-	-	+	+	-	+	↘	↘	↘	↘	↘
111	-	+	+	+	-	-	-	-	+	+	+	+	↘	↘	↘	↘	↘
112	+	+	+	+	+	+	-	+	-	+	+	-	↘	↘	↘	↘	↘
113	+	-	-	-	-	+	-	+	-	-	+	-	↘	↘	↘	↘	↘
114	+	+	-	+	+	-	+	-	+	+	+	+	↘	↘	↘	↘	↘
115	-	+	-	+	+	+	+	-	+	-	+	-	↘	↘	↘	↘	↘
116	+	+	-	+	-	+	+	-	+	+	+	-	↘	↘	↘	↘	↘
117	-	-	+	-	-	+	-	+	-	-	-	-	↘	↘	↘	↘	↘

	$N$	fertility, $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
118	+	-	-	-	+	+	+	+	-	-	-	-	↘	↘	↘	↘	↘
119	+	-	-	+	+	+	+	-	+	-	+	+	↘	↘	↘	↘	↘
120	-	-	-	-	+	+	-	+	-	+	+	-	↘	↘	↘	↘	↘
121	-	+	-	+	-	-	+	-	+	-	+	+	↘	↘	↘	↘	↘
122	-	+	+	-	+	+	-	+	-	+	-	+	↘	↘	↘	↘	↘
123	+	+	-	-	+	+	+	-	+	-	-	+	↘	↘	↘	↘	↘
124	-	+	-	-	-	+	-	+	-	-	+	+	↘	↘	↘	↘	↘
125	+	+	+	-	+	+	+	+	-	-	+	+	↘	↘	↘	↘	↘
126	-	+	-	+	-	+	-	-	+	-	-	-	↘	↘	↘	↘	↘
127	+	+	-	+	-	+	-	+	-	-	-	-	↘	↘	↘	↘	↘
128	-	+	+	+	+	-	-	+	-	-	+	+	↘	↘	↘	↘	↘
129	+	-	+	-	-	+	+	+	-	+	+	-	↘	↘	↘	↘	↘
130	-	+	-	+	+	-	+	+	-	+	+	+	↘	↘	↘	↘	↘
131	-	+	+	-	-	+	-	-	+	-	-	+	↘	↘	↘	↘	↘
132	-	-	+	+	+	+	+	-	+	-	-	+	↘	↘	↘	↘	↘
133	-	-	-	-	-	+	+	+	-	+	-	-	↘	↘	↘	↘	↘
134	-	+	+	-	-	+	+	+	-	+	+	+	↘	↘	↘	↘	↘
135	+	+	+	-	-	-	-	+	+	-	+	+	↘	↘	↘	↘	↘
136	+	+	+	+	-	-	+	-	+	-	-	+	↘	↘	↘	↘	↘
137	-	-	+	+	-	+	-	-	+	-	+	+	↘	↘	↘	↘	↘
138	+	+	-	+	+	+	-	-	+	+	-	-	↘	↘	↘	↘	↘
139	-	+	+	-	+	+	+	-	+	-	+	+	↘	↘	↘	↘	↘
140	-	+	-	+	-	-	-	+	-	+	-	+	↘	↘	↘	↘	↘
141	+	-	-	+	-	+	-	-	+	-	-	+	↘	↘	↘	↘	↘
142	+	+	-	-	-	+	-	-	+	-	+	+	↘	↘	↘	↘	↘
143	-	+	-	+	+	+	-	+	-	+	-	-	↘	↘	↘	↘	↘
144	+	+	-	+	+	-	+	-	+	+	+	+	↘	↘	↘	↘	↘
145	+	+	-	-	-	+	+	+	-	+	-	+	↘	↘	↘	↘	↘
146	-	+	+	+	-	+	-	+	-	-	+	-	↘	↘	↘	↘	↘
147	+	+	+	-	+	+	-	-	+	+	-	+	↘	↘	↘	↘	↘
148	-	+	-	-	-	+	+	-	+	+	-	+	↘	↘	↘	↘	↘
149	+	-	+	+	+	+	+	+	-	-	-	+	↘	↘	↘	↘	↘

	$N$	fertility, $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
150	-	-	-	+	+	+	-	-	+	+	-	+	↘	↘	↘	↘	↘
151	+	+	+	+	-	-	-	+	-	+	+	+	↘	↘	↘	↘	↘
152	+	-	+	-	+	+	-	+	-	+	-	-	↘	↘	↘	↘	↘
153	-	+	+	+	-	-	+	+	-	-	-	+	↘	↘	↘	↘	↘
154	-	+	+	+	-	+	+	-	+	+	-	-	↘	↘	↘	↘	↘
155	+	+	-	+	+	+	+	+	-	-	+	-	↘	↘	↘	↘	↘
156	+	+	+	-	-	+	-	+	-	-	-	+	↘	↘	↘	↘	↘
157	-	+	+	+	+	-	+	-	+	+	-	+	↘	↘	↘	↘	↘
158	+	+	+	+	+	+	+	-	+	-	-	-	↘	↘	↘	↘	↘
159	+	+	+	+	-	+	+	+	-	+	-	-	↘	↘	↘	↘	↘
160	+	+	-	-	+	+	-	+	-	+	+	+	↘	↘	↘	↘	↘
161	-	+	-	+	-	+	+	+	-	+	+	-	↘	↗	↘	↘	↘
162	-	-	-	+	+	+	-	+	+	-	+	-	↘	↗	-	↘	↘
163	-	-	+	-	-	+	+	+	+	-	-	+	↘	↗	-	↘	↘
164	-	+	-	+	+	+	+	+	+	+	-	+	↘	↗	-	↘	↘
165	-	+	+	-	+	+	+	+	+	+	-	-	↘	↗	-	↘	↘
166	-	+	+	+	-	+	+	+	+	-	+	+	↘	↗	-	↘	↘
167	-	-	-	-	+	+	+	+	+	+	+	+	↘	↗	-	↘	↘
168	+	+	+	-	+	+	-	+	+	-	+	-	↘	↗	-	↘	↘
169	+	-	+	+	+	+	-	+	+	-	-	-	↘	↗	-	↘	↘
170	-	+	-	-	+	+	-	+	+	-	-	-	↘	↗	-	↘	↘
171	-	+	+	+	+	+	-	+	+	-	-	+	↘	↗	-	↘	↘
172	-	-	+	+	-	+	-	+	+	+	-	-	↘	↗	-	↘	↘
173	+	+	-	-	+	+	+	+	+	+	+	-	↘	↗	-	↘	↘
174	+	-	-	+	-	+	-	+	+	+	+	-	↘	↗	-	↘	↘
175	+	+	+	-	-	+	+	+	+	-	-	-	↘	↗	-	↘	↘
176	-	-	-	+	-	+	+	+	+	-	-	-	↘	↗	-	↘	↘
177	+	-	-	-	-	+	+	+	+	-	+	+	↘	↗	-	↘	↘
178	-	+	-	+	-	+	-	+	+	+	+	+	↘	↗	-	↘	↘
179	-	-	+	-	+	+	-	+	+	-	+	+	↘	↗	-	↘	↘
180	+	+	+	+	+	+	+	+	+	+	+	+	↘	↗	-	↘	↘
181	+	+	-	+	-	+	+	+	+	-	-	+	↘	↗	-	↘	↘

	$N$	fertility, $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
182	+	+	-	+	+	+	-	+	+	-	+	+	↘	↗	-	↘	↘
183	+	-	-	+	+	+	+	+	+	+	-	-	↘	↗	-	↘	↘
184	+	-	+	-	-	+	-	+	+	+	+	+	↘	↗	-	↘	↘
185	-	-	-	-	-	+	-	+	+	+	-	+	↘	↗	-	↘	↘
186	+	-	-	-	+	+	-	+	+	-	-	+	↘	↗	-	↘	↘
187	-	-	+	+	+	+	+	+	+	+	+	-	↘	↗	-	↘	↘
188	+	-	+	+	-	+	+	+	+	-	+	-	↘	↗	-	↘	↘
189	+	-	+	-	+	+	+	+	+	+	-	+	↘	↗	-	↘	↘
190	-	+	-	-	-	+	+	+	+	-	+	-	↘	↗	-	↘	↘
191	-	+	+	-	-	+	-	+	+	+	+	-	↘		-	↘	↘
192	+	+	-	-	-	+	+	-	-	-	+	-	↘	-	-	↘	↘
193	-	-	+	+	-	+	+	-	-	-	+	-	↘	-	-	↘	↘
194	+	+	-	+	+	-	-	-	-	+	+	-	↘	-	-	↘	↘
195	+	+	+	-	+	-	-	-	-	+	+	+	↘	-	-	↘	↘
196	-	-	-	+	+	+	+	-	-	+	-	-	↘	-	-	↘	↘
197	-	+	+	+	+	-	-	-	-	+	-	-	↘	-	-	↘	↘
198	-	-	-	+	+	-	-	-	-	+	+	+	↘	-	-	↘	↘
199	+	-	+	-	+	-	+	-	-	-	-	-	↘	-	-	↘	↘
200	-	+	+	-	-	+	+	-	-	-	-	-	↘	-	-	↘	↘
201	+	+	+	-	-	-	+	-	-	+	-	+	↘	-	-	↘	↘
202	-	-	+	+	+	+	-	-	-	-	-	-	↘	-	-	↘	↘
203	-	+	-	-	-	-	+	-	-	+	+	+	↘	-	-	↘	↘
204	+	+	-	+	-	+	-	-	-	+	+	+	↘	-	-	↘	↘
205	-	+	+	+	-	-	+	-	-	+	+	-	↘	-	-	↘	↘
206	-	-	-	-	+	+	-	-	-	-	-	+	↘	-	-	↘	↘
207	+	-	+	+	-	-	+	-	-	+	+	+	↘	-	-	↘	↘
208	-	-	+	-	+	+	+	-	-	+	-	+	↘	-	-	↘	↘
209	-	+	+	+	+	+	+	-	-	+	+	+	↘	-	-	↘	↘
210	-	+	-	+	+	+	-	-	-	-	+	+	↘	-	-	↘	↘
211	+	-	-	-	+	+	+	-	-	+	+	+	↘	-	-	↘	↘
212	-	-	-	-	-	+	+	-	-	-	+	+	↘	-	-	↘	↘
213	-	-	+	-	-	+	-	-	-	+	+	+	↘	-	-	↘	↘

$N$	fertility, $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	Abundance	Mean length at silvering	Sex ratio	Ratio of fast growers	Mean realized growth rate
214	+	+	-	-	-	-	-	-	-	-	+	↘	-	-	↘	↘
215	-	-	-	-	-	-	-	-	-	-	-	↘	-	-	↘	↘
216	+	+	+	+	+	-	-	-	-	-	+	↘	-	-	↘	↘
217	-	+	+	-	+	+	-	-	-	+	-	↘	-	-	↘	↘
218	-	+	+	-	-	-	-	-	-	+	+	↘	-	-	↘	↘
219	-	+	-	-	+	-	-	-	+	-	+	↘	-	-	↘	↘
220	-	+	+	-	+	+	-	-	-	-	+	↘	-	-	↘	↘
221	-	-	+	+	-	-	-	-	-	-	+	↘	-	-	↘	↘
223	+	-	-	+	+	+	-	-	-	+	-	↘	-	-	↘	↘
224	+	+	-	+	+	+	-	-	+	-	+	↘	-	-	↘	↘
225	-	-	+	-	-	+	-	-	+	-	-	↘	-	-	↘	↘
227	+	-	-	-	-	+	-	-	-	+	+	↘	-	-	↘	↘
228	+	+	+	-	-	+	-	-	-	+	-	↘	-	-	↘	↘
229	+	+	+	-	+	+	+	-	-	+	-	↘	-	-	↘	↘
230	+	+	-	-	+	-	+	-	-	-	+	↘	-	-	↘	↘
231	-	+	+	+	-	+	-	-	-	+	-	↘	-	-	↘	↘
232	+	-	-	-	+	-	-	-	-	+	-	↘	-	-	↘	↘
233	-	-	-	+	-	+	-	-	-	+	+	↘	-	-	↘	↘
234	+	-	+	-	+	+	-	-	-	-	+	↘	-	-	↘	↘
235	+	+	-	+	-	-	+	-	-	+	-	↘	-	-	↘	↘
236	+	+	-	-	+	+	-	-	-	-	-	↘	-	-	↘	↘
237	-	+	-	+	+	-	+	-	-	-	-	↘	-	-	↘	↘
238	-	-	+	-	+	-	-	-	-	+	+	↘	-	-	↘	↘
239	+	-	-	+	-	-	-	-	-	+	+	↘	-	-	↘	↘
240	-	+	-	-	-	+	-	-	-	+	-	↘	-	-	↘	↘
241	+	+	+	+	+	-	+	-	-	-	+	↘	-	-	↘	↘
242	-	-	-	-	+	-	+	-	-	-	+	↘	-	-	↘	↘
243	+	-	+	+	-	+	-	-	-	+	-	↘	-	-	↘	↘
244	-	+	-	+	-	-	-	-	-	-	+	↘	-	-	↘	↘
245	+	-	+	-	-	+	+	-	-	-	+	↘	-	-	↘	↘
246	+	-	-	-	-	-	+	-	-	+	+	↘	-	-	↘	↘

	$N$	$fertility,$ $L_{sm}$	$K_{fast}(i, l),$ $M_{fast}(i, l)$	$K_{slow}(i, l),$ $M_{slow}(i, l)$	$propK$	$\alpha$	$n$	$b$	$L_{\infty}$	$L_g$	$r_K,$ $r_M$	$\gamma_K,$ $\gamma_M$	<b>Abundance</b>	<b>Mean length</b> <b>at silvering</b>	<b>Sex ratio</b>	<b>Ratio of fast</b> <b>growers</b>	<b>Mean realized</b> <b>growth rate</b>
<b>247</b>	+	-	+	+	+	-	-	-	-	+	-	+	↘	-	-	↘	↘
<b>248</b>	-	-	+	+	+	-	+	-	-	-	+	+	↘	-	-	↘	↘
<b>249</b>	+	-	+	+	+	+	+	-	-	+	+	-	↘	-	-	↘	↘
<b>250</b>	+	+	+	+	-	-	-	-	-	-	-	-	↘	-	-	↘	↘
<b>251</b>	+	-	-	+	-	+	+	-	-	-	-	-	↘	-	-	↘	↘
<b>252</b>	-	+	-	-	+	+	+	-	-	+	+	-	↘	-	-	↘	↘
<b>253</b>	+	-	-	+	+	-	+	-	-	-	-	+	↘	-	-	↘	↘
<b>254</b>	+	+	+	+	-	+	+	-	-	-	+	+	↘	-	-	↘	↘
<b>255</b>	+	-	+	-	-	-	-	-	-	-	+	-	↘	-	-	↘	↘
<b>256</b>	-	+	-	+	-	+	+	-	-	-	-	+	↘	-	-	↘	↘



## Supplementary chapter 3

**Table S3.1.** Summary of the GAM model. edf corresponds to the estimated degrees of freedom for each model parameter. F corresponds to the Fisher statistics when the Gaussian family is used and Chis.sq to the  $\chi^2$  statistics when the binomial family is used. P-values are not presented (although all are smaller than 0.05) because significance tests are not recommended when analyzing simulation model results (White *et al.*, 2014).

	<i>Ns</i>		<i>Ls</i>		<i>SR</i>		<i>E</i>		<i>Sl</i>	
	edf	F	edf	F	edf	Chi.sq	edf	F	edf	Chi.sq
<i>s(g)</i>	9	18517.8	8.6	14036.4	9.0	3849436.9	6.6	1257.1	9.0	23175.6
<i>s(s<sub>0.1</sub>)</i>	5.0	266.2	3.3	451.8	8.8	56266.4	1.0	3906.1	8.7	52527.1
<i>s(s<sub>0.66</sub>)</i>	1.0	7.7	2.2	1.6	8.8	485.7	6.8	2.1	8.1	592.6
<i>s(b<sub>0.1</sub>)</i>	3.4	3066.9	5.2	3311.3	9.0	2598861.4	4.0	194.8	8.7	1001753.5
<i>s(b<sub>0.66</sub>)</i>	1.0	5.3	1.0	0.3	8.7	515.9	1.0	4.3	8.9	783.7
<i>s(t<sub>0.1</sub>)</i>	2.5	545.4	2.9	497.5	8.9	56169.5	1.0	3727.6	8.9	54605.7
<i>s(t<sub>0.66</sub>)</i>	1.0	1.3	2.0	2.0	8.9	541.1	2.5	3.3	8.0	357.9

## **Adaptive responses of temperate eels to environmental heterogeneity: evolutionary mechanisms, threats due to global change and implications for conservation**

The worldwide decline of temperate eels is due to a synergistic combination of several anthropogenic pressures. However, eels display very specific life-cycles and amazing adaptation capacities that impair our ability to assess the relative effects of each pressure. Temperate eels are three catadromous species with large spatially distribution area during their continental growth stage. Their panmixia and the passive larval drifts impair the possibility of local adaptation; however life history spatial patterns are correlated with environmental gradients at both river catchment and distribution area scales. This PhD aims (i) to explore whether these life history spatial patterns may result from two adaptive responses: genetic polymorphism and adaptive phenotypic plasticity, and (ii) to revisit the effect of different components of global change in consideration to these adaptive responses. In this context, GenEveel, an individual-based optimization model was developed. The model postulates that genetic-dependent habitat selection and phenotypic plasticity are mechanisms to address environmental heterogeneity. With such assumptions, the model was able to mimic observed spatial patterns in length-at-silvering, sex ratio and distribution of ecotypes. Moreover, different types of anthropogenic pressures (glass eel fishery, silver eel fishery, obstacles to upstream migration, and mortality due to hydropower facilities) were integrated in the model. Then, the model was used to assess their impacts on the number of escapees and their attributes: sex ratio, repartition between genotypes, mean length-at-silvering, and overall egg production. The results showed that the pressure that induces the highest direct mortality has not necessarily the greatest influence on the spawning biomass and does not necessarily exert the strongest selective pressure on the ecotypes. This demonstrates that phenotypic plasticity can be a source of resilience for the population and mitigates the effect of some but not all the pressures. It also suggests that management should not only focus on numbers and direct mortality but on the preservation of diversity within populations. Finally, a demo-genetic model is described summarizing our understanding of eel populations. Such model can be used in the future to explore the ecological conditions in which genetic polymorphism and phenotypic plasticity have been selected through generations and provide new insights for the conservation of endangered eel species.

*Keywords:* *Anguilla* spp., adaptive mechanisms, global change, anthropogenic pressures, life history theory, modelling

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## **Réponses adaptatives des anguilles tempérées à l'hétérogénéité environnementale : mécanismes évolutifs, menaces liées au changement global et conséquences pour la conservation**

Le déclin mondial des anguilles tempérées est lié aux effets synergiques de multiples pressions anthropiques. Cependant, la complexité du cycle de vie des anguilles et leurs incroyables capacités d'adaptation font qu'il est très difficile de connaître le poids relatif de chacune des pressions. Les anguilles tempérées sont trois espèces catadromes qui ont de très grandes aires de répartition pendant leurs phases de croissance continentales. Leurs panmixies et les longues dérives larvaires passives sont des freins aux adaptations locales, cependant on observe des patrons spatiaux de traits d'histoire de vie corrélés aux gradients environnementaux, à l'échelle du bassin versant et de son aire de répartition. Ce doctorat vise à (i) démontrer si ces patrons spatiaux d'histoire de vie sont le résultat de deux réponses adaptatives : le polymorphisme génétique et la plasticité phénotypique adaptative, et (ii) à réévaluer l'effet des différentes composantes du changement global en prenant en compte ces réponses adaptatives. Dans ce cadre, GenEveel, un modèle d'optimisation individu-centré a été développé. Ce modèle postule que la sélection de l'habitat dépendant du génotype et la plasticité phénotypique sont deux mécanismes permettant de faire face à l'hétérogénéité environnementale. Avec de telles hypothèses, le modèle permet de reproduire les patrons spatiaux observés concernant la longueur à l'argenture, le sexe-ratio et la distribution des écotypes. Par la suite, différents types des pressions anthropiques - les pêcheries de civelles et d'anguilles argentées, les obstacles à la migration de montaison et les mortalités dues aux turbines hydroélectriques - ont été intégrés dans le modèle. L'objectif a été d'évaluer leurs impacts sur l'échappement, à la fois en nombre, mais aussi sur différents attributs comme le sexe-ratio, la répartition entre génotypes, la longueur à l'argenture moyenne, et la production globale d'œufs. Les résultats montrent que la pression qui induit la plus forte mortalité directe n'a pas forcément la plus forte influence sur la biomasse féconde et n'exerce pas nécessairement la pression sélective la plus forte sur les écotypes. Le modèle met aussi en évidence que la plasticité phénotypique peut être source de résilience pour la population et qu'elle atténue l'effet de certaines pressions, mais pas de toutes. Cela suggère également que la gestion ne doit pas seulement se concentrer sur les nombres de survivants et les mortalités directes, mais aussi sur la protection de la diversité au sein des populations. Finalement, un modèle démo-génétique est décrit pour résumer notre compréhension des populations d'anguilles. Un tel modèle pourra être utilisé à l'avenir pour explorer les conditions écologiques dans lesquelles le polymorphisme génétique et la plasticité phénotypique ont été sélectionnés à travers des générations et fournir de nouvelles recommandations pour la conservation des espèces d'anguilles en voie d'extinction.

*Mots clés* : *Anguilla* spp., mécanismes adaptatifs, changement global, pressions anthropiques, théorie d'histoire de vie, modélisation

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