Spatio-temporal evolution of life history traits related to dispersal. Brown trout (Salmo trutta L.) colonization of the sub-Antarctic Kerguelen Islands.

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Spatio-temporal evolution of life history traits related to dispersal
Brown trout (*Salmo trutta* L.) colonization of the sub-Antarctic Kerguelen Islands

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Evolution de l'anadromie chez la truite commune (*Salmo trutta* L.) dans le cadre de l'expansion des populations introduites dans les îles Kerguelen.

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Directeurs de Thèse :
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Foreword

This thesis in ecology, biology and evolution was funded with a doctoral allocation provided by the French Ministry of Higher Education and Research and granted by the doctoral school “Sciences Exactes et leurs Applications” (ED 211 – SEA, Pau). This doctoral allocation was provided through Energy Environment Solutions Project (E2S) in the “Programme Investissements d’Avenir I-Site” supported by the University of Pau and Pays de l’Adour (UPPA). This project rests upon the solid qualification of scientific structures IPREM, IPRA, MIRA, scientific laboratories INRIA, INRAE, and companies such as TOTAL, ARKEMA, TIGF, SAFRAN-Turboméca. This work also benefited from support granted by the laboratory “Ecologie Compportementale et Biologie des Populations de Poissons” (INRAE-UPPA, UMR 1224 ECOBIOP, 64310 Saint-Pée sur Nivelle), the laboratory ”Institut des Sciences Analytiques et de Physico-Chimie pour l’Environnement et les Matériaux” (CNRS-UPPA, UMR 5254 IPREM, 64000 Pau) and the University of Pau and pays de l’Adour (UPPA, ED 211 – SEA, Pau).

The different studies which are the subject of this manuscript were conducted with several collaborators: Philippe Gaudin (supervisor of the thesis), Matthias Vignon (co-supervisor of the thesis), Jean-Christophe Aymes, Jacques Labonne and Mathieu Buoro. These studies are based on analyses of data from long-term monitoring programs on salmonids in the Kerguelen Islands. It would not have been possible to work on this dataset without the precious work of program managers (counted among my collaborators), field workers, the technical support of François Guéraud, the participation of several interns under my co-supervision (Lucille Baron, Jon Levy, Gautier Magne, Paul Gouzou, Hervé Rogissart and Valentin Santanbien), as well as the technical and financial supports granted by the Polar Institute Paul Emile Victor (IPEV). All the scientific activities carried out within this three years thesis work are presented in the last appendix.

This manuscript is composed of four parts:

- The introductory part comports two chapters, the conceptual framework and the study framework.
- The methodological part comports two chapters. The Chapter 3 describes how the individual were selected in the long-term monitoring dataset. The Chapter 4 is based upon the first published article of this manuscript, and highlights the methodology used to rebuilt life-history traits of interest.
- The following part discusses the results on the evolution of life-history traits related to dispersion. It is divided into two chapters, the first on the evolution of the liability traits to migration and the second on the evolution of the reaction norm. Each of these chapters is the subject of an article in preparation.
- This manuscript ends with a general discussion.

This manuscript is written in English. To facilitate the reading of this manuscript, a discussion of each of the two central parts is carried out and the bibliographical references are given by part. A shortened French version of this manuscript is presented in a preface. In addition, appendices are given in the end of the manuscript, either written in English or French, depending on the target audience.

The present manuscript deals with the evolution of traits related to dispersal. The choice was made to focus the study on the evolution of seaward migration as a pre-requisite to dispersal, as all dispersers have been migrants. The term migration in this work refers to migratory movements from fresh waters to the sea and not all migrants will become dispersers.

The public defence was held on **January 12, 2021 at the University of Pau and Pays de l’Adour in Anglet**. The jury was composed of: Dr. Marie Nevoux, Dr. Thomas Reed, Dr. Agnes Bardonnet, Dr. Yan Ropert-Coudert, Dr. Philippe Gaudin, and Dr. Matthias Vignon. Dr. Ben L. Phillips was invited as an expert.

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Evolution de l'anadromie chez la truite commune (*Salmo trutta* L.) dans le cadre de l'expansion des populations introduites dans les îles Kerguelen

Introduction générale

Ecologie et évolution des traits d'histoire de vie

L'écologie est un domaine scientifique visant à comprendre les interactions entre les organismes (facteurs biotiques) et leurs environnements (facteurs biotiques ou abiotiques), à plusieurs niveaux : l'organisme, la population, la communauté et l'écosystème. Le terme évolution au sens large se réfère à tout changement graduel ou temporel d'un système, d'un organisme ou encore d'une population. En biologie, le terme évolution se réfère aux changements des caractères héréditaires d'une génération à une autre. Ces caractères héréditaires sont portés par les gènes, et transmis au fil des générations par la reproduction. La théorie de l'histoire de vie cherche à expliquer comment différentes forces évolutives permettent aux organismes de faire face aux changements environnementaux (Stearns, 1992). Tous les traits liés aux capacités de reproduction ou de survie sont appelés traits d'histoire de vie. Ces traits peuvent être morphologiques, physiologiques ou comportementaux. Ces caractères sont quantitatifs et en partie héréditaires (chez les oiseaux : Berthold and Terrill, 1991; chez les poissons : Carlson and Seamons, 2008; chez l'huître : Ernande et al., 2003). Ils sont donc soumis aux forces évolutives (la sélection naturelle, la mutation génique, l'homogamie positive, la dérive génétique et la migration).

Tout changement naturel ou anthropique de l'habitat des organismes (*e.g.* variation de la température, disponibilité de la nourriture, accès aux habitats pour la reproduction) peut entraîner des changements évolutifs. Face à l'évolution rapide de l'environnement, les organismes qui survivent ont deux solutions : se déplacer vers des habitats plus propices ou bien s'adapter. L'adaptation suppose la maximisation de la condition physique par l'appariement du phénotype individuel avec un trait optimal. C'est ce qu'on appelle la plasticité phénotypique (Stearns, 1989; Tufto, 2000). En d'autres termes, les caractères discrets (phénotypes) sont conditionnés par la valeur prise par un caractère donné relativement à une valeur seuil (cette valeur délimite le seuil au-dessous duquel un phénotype est exprimé et au-dessus duquel l'autre l'est) (Pulido, 2011). L'existence d'un polymorphisme contrôlé par l'environnement est appelée stratégie conditionnelle ou stratégie des caractères de seuil (Roff, 1996; Stearns, 1989). Si ces traits sont héréditaires, des réponses évolutives sont attendues (Phillis et al., 2016).

La migration, une des clés de l'évolution de l'histoire de vie

Pour beaucoup d'organismes, la migration est un phénomène essentiel pour se reproduire, se nourrir, se protéger des prédateurs et des conditions environnementales difficiles (Boyle, 2011; Marco-Rius et al., 2013a). En 2019, Ferguson et al. définissent la migration comme des « mouvements dirigés entre deux habitats distincts se produisant avec une périodicité régulière sur une base temporellement prévisible » (*Fig. 1.1*). La forme la plus fréquente de migration est la « migration partielle ». Elle se caractérise par une variation de la tendance à migrer au sein de la population (Chapman et al., 2011a). Une population partiellement migratrice est composée de non-migrants (généralement appelés résidents) et de migrants partageant ou non leur site de reproduction. Le choix pour une tactique migratoire résulte souvent d'une balance entre des coûts (risques de prédation) et des bénéfices (accessibilité/quantité de la ressource alimentaire) (Hebblewhite and Merrill, 2007; Hebblewhite and Merrill, 2011). L'étude de la migration partielle est centrale en écologie évolutive car elle est liée à l'adaptation, au maintien du polymorphisme, et même à l'évolution du comportement migratoire lui-même.

Tous les migrants ne sont pas des dispersants (*Fig. 1.2*). La migration se rapporte uniquement aux déplacements entre les habitats alors que la dispersion se rapporte à un cycle complet allant de la décision de migrer (départ) suivie d'une phase de mouvement transitoire (migration) jusqu'à l'établissement des organismes dans une nouvelle population (reproduction) (Berthold and Terrill, 1991). Si la dispersion se produit dans une population déjà fondée, alors elle contribue à changer la fréquence des allèles dans cette population. Si la dispersion se produit dans un habitat vierge, les dispersants fondent une nouvelle population. Ce dernier cas sera mentionné sous le nom de colonisation. Les gènes qui forment la nouvelle population font l'objet d'une sélection naturelle et les gènes délétères, qui peuvent changer de fréquence, contribuent à la dépression de consanguinité (Glémin, 2005). Le sort d'un gène dans une population dépend de la structure de la population elle-même et du nombre de migrants/émigrants (flux génétique) dans la population.

Comment la migration partielle est-elle maintenue à travers le temps ?

L'instabilité environnementale influence la capacité des organismes à atteindre leur valeur sélective maximale (Kuno, 1981) et une façon de faire face aux changements est de disperser. Dans un contexte de changement global, l'instabilité peut résulter de changements des conditions météorologiques (*e.g.* températures, précipitations, débits fluviaux) ou de changements de la structure de la communauté (*e.g.* densité de la population, chaînes trophiques) (Brodersen et al., 2011). Lorsque la taille de la population augmente, la densité devrait devenir le principal facteur de dispersion (Grayson and Wilbur, 2009; Kaitala et al., 1993) en augmentant la concurrence pour l'accès à l'habitat, à la ressource alimentaire et aux partenaires sexuels (Loe et al., 2009; Nathan et al., 2008). Au contraire, dans les populations à faible densité, c'est la forte compétition entre les apparentés (kin competition) qui pousse les individus à disperser.

La dispersion peut être héréditaire. L'héritabilité peut être directe comme c'est le cas du comportement (Páez et al., 2011). Il a été démontré que les caractères phénotypiques dimorphiques sont partiellement héréditaires (Roff, 1998), comme l'âge à la migration chez certains poissons (Reed et al., 2010) ou la migration saisonnière chez les oiseaux (Pulido and Widmer, 2005). L'héritabilité peut aussi être indirecte dépendant du statut énergétique des reproducteurs ou dépendant du développement juvénile (*e.g.* variabilité dans la capacité de mouvement, compétitivité corrélée positivement à la taille ou au poids). Par exemple, la restriction alimentaire pendant certains stades de développement a un effet significatif sur les tactiques migratoires (résidence *vs.* migration), tactiques également en corrélation avec le sexe (Archer et al., 2019).

De nombreuses hypothèses sont émises pour expliquer les raisons de la dispersion. Ces hypothèses sont souvent en lien avec la compétition pour la ressource, favorisant la migration pour les plus petits individus (competitive release hypothesis ou "libération concurentielle", Yeaton and Cody, 1974) ou les plus intolérants au jeûne (limited foraging opportunity ou "limitation alimentaire", Millar and Hickling, 1990). Mais la dispersion dépend aussi des équilibres démographiques (Griswold et al., 2011; Kokko et al., 2006). Dans les deux cas, il semble que les effets de densité de population soient impliqués. La distribution spatiale et temporelle de la ressource joue aussi un rôle important dans le choix de la tactique dispersive (Ayer et al., 2018; Gross, 1987).

Quelles sont les conséquences de la migration partielle dans le processus évolutif ?

Les espèces qui colonisent de nouveaux environnements présentent souvent des changements évolutifs rapides (Westley, 2011). Il est maintenant établi que l'évolution peut agir à des échelles de temps écologiquement pertinentes (Thompson, 1998) et il s'avère qu'elle affecte considérablement la dynamique des populations. Les invasions biologiques sont à l'origine d'importantes modifications de la structure et du fonctionnement des écosystèmes (Buoro, Olden et al., 2016) et sont considérées comme la deuxième menace envers la biodiversité après la perte d'habitat (Park, 2004). Dans la plupart des cas, les invasions biologiques sont mal documentées et soumises à des facteurs externes (comme la sélection naturelle, les facteurs anthropiques, la facilitation ou la pression d'échantillonnage) qui empêchent de comprendre les phénomènes intrinsèques permettant une évaluation objective des risques (Blanchet, 2012; Labonne et al., 2013). L'évaluation de ces phénomènes permet de comprendre et de prévoir la dynamique et l'évolution des populations même si la discrimination des différents processus d'évolution sous-jacents aux invasions est difficile. Les espèces envahissantes sont sujettes à un goulot d'étranglement démographique transitoire, ainsi la dispersion peut maintenir une variation génétique pertinente, réduire la charge de mutation ou accroître l'effet de la sélection naturelle. La plasticité phénotypique adaptative est plus susceptible d'évoluer pour les espèces envahissantes parce qu'elles rencontrent divers habitats (*Fig. 1.3*). Ainsi, on s'attend à ce que les populations d'espèces envahissantes évoluent avec une plus grande plasticité que dans leur aire de répartition géographique d'origine (Richards et al., 2006).

La question de l'évolution des populations sur les fronts d'expansion a déjà été abordé de manière théorique (Burton et al., 2010) et empirique (*e.g.* Phillips, Brown, Webb et al., 2006). Sur le plan de l'expansion, la faible densité de population sur les bords de la zone d'expansion et un fort gradient de densité entraînent des processus évolutifs comme le tri spatial et la charge d'expansion (Phillips, Brown and Shine, 2010). Les événements de dispersion à longue distance peuvent réduire la diversité sur le front en affectant la fréquence des gènes le long de la route migratoire (Fayard et al., 2009). Les populations en périphérie, créées par une fraction de la population initialement introduite (les fondateurs), devraient être génétiquement différentes (effet fondateur) du fait de la sélection de flux géniques. Ce phénomène s'appelle le tri spatial. Si la stratégie de dispersion est héréditaire (Imbert, 1999), et sous l'hypothèse d'un tri spatial, la probabilité de trouver des dispersants devrait être plus forte sur les bords de la zone d'expansion plutôt qu'en son cœur.

Tout changement de conditions dans l'environnement natal, le long du trajet migratoire, ou dans l'environnement de destination, implique des changements dans la balance coûts/bénéfices de la migration. Bien que, en théorie, les caractères qui améliorent la fitness d'une population devraient se fixer, l'équilibre de la sélection peut contrebalancer et aboutir au maintien évolutif de la variation des caractères au sein de la population (Hendry et al., 2004). Si la tactique résidente est avantageuse dans certaines conditions, une tactique migratoire pourrait l'être dans d'autres, avec des adaptations compensatoires pour équilibrer les avantages et les coûts de la tactique (B. Jonsson, M. Jonsson et al., 2016). Il est donc important d'acquérir de meilleures connaissances permettant de comparer les résidents et les migrants afin de faire la lumière sur les mécanismes de la migration partielle (Chapman et al., 2011b).

Contexte de l'étude

La truite commune (Salmo trutta L.) et son introduction dans les îles sub-antarctiques de Kerguelen

Les études sur les salmonidés sont particulièrement bien adaptées pour aborder la question de la réponse évolutive dans la décision de migrer. La migration partielle illustre la diversité considérable des stratégies du cycle de vie et peut être facilement suivie par des méthodes de capture-marquage-recapture (CMR) à l'aide de la télémétrie (Davidsen et al., 2014) ou par marquage (Rifflart et al., 2006). L'utilisation des structures calcifiées est une autre façon de suivre l'historique de vie des poissons (écailles et otolithes) (Burnet, 1969; Campbell et al., 2015; Elliott and Chambers, 1996; Ombredane and Baglinière, 1992). Les structures calcifiées enregistrent des informations de l'histoire de vie des poissons telles que l'âge, la croissance, les événements de reproduction et l'environnement. Ces structures sont assez faciles à échantillonner et sont des matériels d'études préférentiels utilisés par de nombreux ichtyologues (Borgenson et al., 2014; Ottaway, 1978).

Beaucoup de travaux ont déjà été menés sur les principaux moteurs écologiques de la migration partielle chez les salmonidés. La température (Pulido, 2011), l'accessibilité de la ressource alimentaire (Archer et al., 2019; Wysujack et al., 2009) et la qualité des aliments en eaux douces (Marco-Rius et al., 2013a; Olsson et al., 2006) jouent un rôle dans la décision de migrer. Parmi les vertébrés, les décisions migratoires peuvent être héréditaires, mais le rôle de l'épigénétique demeure flou (B. Jonsson and N. Jonsson, 2019). La génétique semble avoir un rôle dans la migration, en agissant sur le développement et la smoltification qui est le processus d'adaptation à la future vie en mer (printemps) par l'induction de changements physiologiques, comportementaux et morphologiques) (Arawomo, 1981; Bagliniere, 1979; Cuinat and Heland, 1979; Heland, 1980; Nichols et al., 2008; Roussel and Bardonnet, 2002). Le choix de la tactique repose sur un caractère seuil (Roff, 1996), la taille individuelle par exemple est un caractère seuil de la smoltification (Buoro, Gimenez et al., 2012) ainsi que la taille à l'âge (Carlson and Seamons, 2008).

Dodson et al. (2013) soutiennent que la taille corporelle des salmonidés est le signal le plus utilisé (et le plus adéquat) à la migration, puisque le succès de celle-ci dépend de l'énergie individuelle acquise, stockée et utilisée (Acolas et al., 2012; Bohlin et al., 1996; Forseth et al., 1999; B. Jonsson, M. Jonsson et al., 2016; Olsson et al., 2006; Rosenfeld et al., 2015). Mécanisme ultime, une plus grande taille a été associée à une meilleure condition physique (Pettersson et al., 1996; Thompson and Beauchamp, 2016), ce qui permet notamment d'accroître la survie en mer et le succès reproducteur (Goodwin et al., 2016). Mais la migration se réalise souvent au prix d'une augmentation de la mortalité (stress physiologique, risque de prédation (B. Jonsson and N. Jonsson, 2004), parasites . . .). La migration est souvent biaisée vers un des deux sexes et souvent favorisée pour les femelles (Ayer et al., 2018; Rundio et al., 2012). Une plus grande taille pour les femelles permet une plus grande fertilité (nombre et taille des œufs (Carlson and Seamons, 2008)). La taille des œufs a, quant à elle, une influence sur la survie et la croissance, et semble expliquer la plupart des variations populationnelle phénotypique, principalement par un effet maternel (Thorn and Morbey, 2018). La tendance migratoire de la progéniture est souvent corrélée au comportement migratoire des parents (Debowski and Dobosz, 2016).

La truite commune (*Salmo trutta* L.) est un salmonidé anadrome facultatif, où la forme anadrome (migrante) désigne l'individu qui migre en mer en dehors de la période de reproduction. Comme les migrants et les résidents présentent des différences morphologiques importantes, il a longtemps été pensé qu'il y s'agissait de deux espèces distinctes. Les importantes variations génétiques, écologiques, morphologiques et du cycle biologique de l'espèce ont donné lieu à un débat de longue date sur ses origines évolutives (McKeown et al., 2010). Le développement de techniques génétiques et les expériences de lâcher en conditions naturelles ont prouvé que les résidents et les migrants appartenaient à la même espèce et que les deux formes différaient par l'expression génétique (Nevoux et al., 2019). Chez la truite commune, les migrants et les résidents se reproduisent de façon sympatrique pendant l'hiver (*Fig. 2.1*). C'est ce que l'on appelle la « migration partielle hors reproduction » (Chapman et coll., 2011a). Une grande partie des migrants sont des « homers », c'est-à-dire qu'ils sont fidèles à leur site de naissance pour se reproduire (Ferguson et al., 2019). Le comportement de fidélité repose sur des indices olfactifs ainsi que sur la migration en groupe, et la température ressentie au stade embryonnaire (B. Jonsson and N. Jonsson, 2009). Les autres sont appelés « strayers », parce qu'ils se dispersent dans un nouvel habitat de reproduction.

Originaire d'Europe, la truite commune a été introduite dans une multitude d'endroits à travers le monde (Budy et al., 2013; Sindermann et al., 1992), où elle est souvent décrite comme envahissante (Honda et al., 2012; Young et al., 2010) (*Fig. 2.2*). La migration océanique, phénomène spectaculaire et omniprésent, permet la colonisation de nouveaux systèmes (Honda et al., 2012) puisque la reproduction se fait toujours en eau douce (Goodwin et al., 2016). La large répartition de la truite commune dans des bassins versants non connectés suggère que la migration s'est produite pendant les périodes glaciaires où la température de la mer était plus basse. La migration océanique, décidée en été-automne, s'accompagne d'un processus de smoltification (Arawomo, 1981; Bagliniere, 1979; Cuinat and Heland, 1979; Heland, 1980; Roussel and Bardonnet, 2002). Une diminution du nombre de truites migrantes a été observée en Europe, que ce soit pour la migration océanique dans le nord-ouest de l'Europe (Ferguson et al., 2019) ou la migration lacustre-fluviale (*e.g.*, en Finlande Syrjänen et al., 2017). Cela suggère un potentiel pour les changements génétiques en réponse à des changements de fitness sous l'effet de la sélection naturelle.

L'invasion et l'évolution des salmonidés ont toujours été des questions d'intérêts. Dans un contexte de changement climatique, de nombreux habitats autrefois hostiles deviennent propices à la colonisation. Les conditions environnementales ont notamment fortement changé pour les écosystèmes estuariens et marins qui représentent 70% de la surface terrestre (Cohen, 1997; Dulvy et al., 2003; Vié et al., 2009). L'impact des changements climatiques devrait être plus important aux pôles que dans les latitudes médianes (Hampe and Petit, 2005; Lebouvier et al., 2011; Pitman et al., 2020; Turner and Overland, 2009). En ce qui concerne les eaux douces, la fonte des glaces pourrait accélérer l'érosion des zones côtières et diminuer leur salinité, augmenter le nombre de cours d'eau accessibles et leur débit. La truite commune, comme la plupart des salmonidés, est un candidat viable pour coloniser ces habitats nouvellement ouverts (Klemetsen et al., 2003).

Situé à la convergence des eaux des océans Indien et Austral (69°30'E-49°30), l'archipel des îles Kerguelen, d'une superficie de 7 215 km^2, appartient aux territoires australs et antarctiques français (TAAF). Il était à l'origine exempt de poissons d'eau douce. Pour «améliorer» ces territoires vierges pour les personnels y travaillant : militaires et civils, dont des scientifiques, des introductions volontaires de poissons ont été effectuées au cours des années 50. Les îles Kerguelen offrent la possibilité d'étudier les modalités d'introduction tout en s'affranchissant des effets anthropiques. Dans un contexte de changement climatique, comprendre la dispersion des espèces et les processus de colonisation dans les îles Kerguelen est d'un intérêt majeur pour acquérir des informations sur la dynamique de population afin de gérer durablement les îles qui font aujourd'hui partie intégrante d'une Réserve Naturelle Nationale (RNN). Financé par l'Institut polaire français Paul Emile Victor, un programme de suivi à long terme a été entrepris pour comprendre l'évolution des espèces de salmonidés et leur capacité à se propager dans de nouveaux systèmes d'eaux douces. La surveillance à long terme de la migration chez les poissons permet d'étudier l'évolution des caractéristiques du cycle de vie liées à la dispersion et leur potentiel d'évolution rapide (Dodson et al., 2013; Hutchings, 2011). L'historique complet de l'introduction de salmonidés dans les îles Kerguelen est consigné par Lecomte et al. (2013). Les travaux présentés dans cette dissertation sont principalement fondés sur des données recueillies dans sept populations de truites commune des îles Kerguelen, données collectées dans le cadre d'un suivi à long terme de 1954 à aujourd'hui.

Dans ce projet de doctorat, j'ai étudié l'évolution des traits de l'histoire de la vie liés à la dispersion chez la truite commune introduite dans les îles Kerguelen, à travers l'étude spécifique de l'évolution de la migration marine. Mes objectifs spécifiques étaient (1) de traiter un grand nombre de données collectées, (2) de déterminer une méthodologie appropriée pour reconstruire les traits d'histoire de vie liés à la dispersion en utilisant les écailles des poissons, (3) d'étudier l'implication de la croissance en eau douce comme moteur de la migration, (4) de déterminer si le taux de croissance et la taille corporelle des poissons ont évolué dans le temps (depuis la colonisation) et dans l'espace (zone d'expansion) et (5) d'étudier si la valeur seuil à la première migration évolue dans le temps et dans l'espace, avec un intérêt particulier à croiser les deux dernières parties pour démêler le rôle des forces évolutives et de la plasticité phénotypique sur l'élution de la migration partielle.

De l'utilisation des écailles à la détermination d'une méthodologie pour reconstruire les traits d'histoire de vie

La sélection des individus dans une large base de données

Dans le **Chapitre 3**, je décris l'impressionnante quantité de données disponibles, acquises grâce au suivi à long-terme mené dans les îles Kerguelen depuis les années 50 (Lecomte et al., 2013). A ce jour, on dénombre plus de 151000 lignes d'informations dans la base de données dédiée aux introductions volontaires de poissons qui ont été réalisées. Le travail dans ce manuscrit repose sur une version antérieure de la base de données, qui comportaient 81184 lignes correspondant à environ 70000 poissons, dont 74% sont des truites communes. En effet, plusieurs lignes de données peuvent représenter le même poisson car des expériences de suivi par marquage-recapture (CMR) ont été réalisées. Parmi les salmonidés introduits, la truite commune est l'espèce qui s'est le mieux adapté. Introduite dans 10 rivières, on la dénombre dans 32 nouvelles rivières en 2013. Ce succès de dispersion dans de nouveaux systèmes repose à la fois sur les multiples efforts d'introductions mais probablement également sur la diversité des souches génétiques introduites (Ayllon et al., 2006; Labonne et al., 2013). Au cours du suivi à long-terme, de nombreuses informations telle que la taille (mm), le poids (g), le phénotype (résident ou migrant), le sexe (si possible) sont collectées sur les poissons capturés lors des pêches (électriques principalement, mais aussi à la ligne ponctuellement). Des prélèvements biologiques sont réalisés, notamment le prélèvement d'écailles, mais aussi d'otolithes (pièces calcifiées de l'oreille interne), de contenus stomacaux ou bien de tissus (*e.g.* nageoires). Les pièces calcifiées servent de traceurs de l'histoire de vie des poissons. A l'image de la lecture des cernes d'arbres (dendrochronologie), les écailles permettent d'accéder à de nombreuses informations sur l'histoire de vie des poissons, telles que leur âge (Burnet, 1969; Erickson, 1983), leur croissance) ou encore leur milieu de vie (Boughamou et al., 2014; Fabre and Saint-Paul, 1998; Ogle, 2013) (*Fig 4.1*).

Avec toutes ces informations à disposition, il a été nécessaire de faire des choix pour étudier l'évolution des traits d'histoire de vie des poissons. Tout d'abord, j'ai déterminé un cadre spatio-temporel pseudo-répliqué pour mon étude, en sélectionnant des rivières selon des caractéristiques de date à la colonisation et de localisation sur le front d'expansion (*Table 3.4*). J'ai choisi d'étudier 7 rivières, sur lesquelles on dispose de 16771 poissons dont les écailles ont été prélevées. Malgré la sélection de 7 rivières, ils reste donc beaucoup de données individuelles à traiter et il faut décider quels poissons seront analysés dans cette étude. Afin d'obtenir un ensemble de données équilibré et de sélectionner des poissons appartenant à des cohortes similaires (année de naissance), j'ai réalisé une analyse d'inférence de l'âge probable des poissons connaissant leur taille à la capture. Sur les 28968 données scalimétriques de la base de données (toutes rivières confondues), 6775 poissons ont déjà été âgé. Ils nous permettent d'établir une relation taille à la capture-âge. J'ai considéré 2 modèles d'inférence, un basé sur la distribution réelle des fréquences de taille, l'autre utilisant des distributions gaussiennes. J'ai appliqué ces modèles au jeu de données, en déclinant la relation taille à la capture-âge par phénotype à la capture (*Figs. 3.9, 3.10*). Au final, après comparaison des deux modèles, le meilleur modèle pour réassigner un âge est le modèle de distribution de fréquence. La base de données étudiées comporte finalement 5713 échantillons, pour 4750 poissons sur les 7 rivières sélectionnées pour ce manuscrit. Avec un erreur d'ageage prédite à 27%, on a finalement obtenu 48% d'erreur en comparant la prédiction du modèle avec l'âge réel déterminé par la lecture des écailles (*Tab. 3.7*).

L'utilisation des écailles pour reconstruire les traits d'histoire de vie. Définition d'une méthodologie de laboratoire

L'utilisation des écailles en écologie halieutique est très répandue. Les écailles permettent notamment de reconstruire l'âge des individus, par la lecture des anneaux qui se déposent de manière périodique (journalière, mensuelle, annuelle) sur la structure (Ibáñez et al., 2008; Thomas et al., 2019). Ces anneaux concentriques nommés circuli, sont déposés de manière plus espacés lors de période de croissance plus forte des poissons et leur dépôt se fait sur une zone moins étendue en période de ralentissement de croissance. La zone de resserrement forme un annulus. Ce ralentissement de croissance annuel permet de déterminer l'âge des poissons. Les mesures d'éloignement entre deux annuli permettent de déterminer le taux d'accroissement annuel. Les écailles sont donc aussi des marqueurs de la croissance des poissons (Casselman, 1990; Kipling, 1962; Marco-Rius et al., 2013b; Pierce et al., 1996). Cependant les écailles sont des structures calcifiées externes et sont donc aussi source d'erreur quant à la détermination des traits d'histoire de vie (Bereiter-Hahn and Zylberberg, 1993; Kacem et al., 2013) (*Fig. 4.2*). A cause de ces erreurs, les études ichtyologiques basées sur la lecture des écailles utilisent souvent plusieurs écailles (Haraldstad et al., 2016), mais au sein d'une même espèce la méthodologie est variable d'un auteur à un autre. De plus, les études préliminaires sur l'exactitude (accuracy) et les biais introduits par la méthodologie choisie sont assez rare (Campana, 2001). Face à la diversité de méthodologie existante, j'ai été confrontée aux problèmes suivants : « Comment reconstruire les traits d'histoire de vie avec une méthode dont je maitrise les biais ? ». J'ai donc décomposé hiérarchiquement les sources de variance qui peuvent affecter la détermination de l'âge et de la croissance des poissons, en considérant les effets imbriqués individuels (poissons), lecteur et écailles. Ce chapitre est l'objet de mon premier article publié dans le cadre de cette thèse[1]. J'y démontre l'intérêt de réaliser une telle pré-analyse pour permettre de mesurer les sources de variance et leur impact sur la reconstruction des traits de vie. Notamment, la plus grande variabilité vient de l'effet individuel quel que soit le trait reconstruit (âge ou taille de l'écaille). Mais, les traits en lien avec la migration semblent plus difficiles à reconstruire (moins répétables), d'autant plus en ce qui concerne l'âge des poissons à la migration (*Table 4.6*). Ce travail me permet de définir la méthodologie à utiliser, en considérant plusieurs écailles pour lire l'âge des poissons et en ne réalisant les mesures de croissance que sur une de ces écailles.

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[1] Aulus Giacosa L., Aymes J-C., Gaudin P., Vignon M. Hierarchical variance decomposition of fish scale growth and age to investigate the relative contributions of readers and scales. Marine and Freshwater Research, CSIRO Publishing, 2019, 70 (12), pp.1828-1837. 10.1071/MF19059.

Finalement, cette partie méthodologique nous a permis de déterminer le jeu de données final avec lequel les analyses de l'évolution des traits ont été réalisées. Le but de cette étude étant de modéliser l'évolution de la croissance, de la taille et de l'âge, il nous a fallu reconstruire les tailles somatiques des poissons en passant par un modèle de rétro-calcul. Nous avons choisi le modèle de Fraser-Lee que nous avons modélisé dans un cadre statistique bayésien. Ce modèle nous as permis de traiter l'évolution de la croissance et de la taille à l'âge. Cependant, malgré les biais introduits dans cette étude (sélection des individus, sélection des écailles, reconstruction de la taille à l'âge), nous avons pu utiliser un jeu de données unique de suivi à long-terme pour répondre à nos questions d'intérêt.

L'évolution des traits d'histoire de vie en lien avec la migration partielle

Evolution de la croissance et de la taille à l'âge le long d'un front de colonisation

La croissance individuelle ainsi que la taille à l'âge sont des traits d'histoire de vie impliqués dans les déterminants de la *fitness* (reproduction et survie). Ces deux traits ont bien souvent été démontrés comme indirectement impliqués dans les décisions migratoires individuelles (Dodson et al., 2013; Gillanders et al., 2015; Nevoux et al., 2019). Sous certaines hypothèses, ce serait les individus avec la plus forte croissance qui auraient une propension plus forte à migrer, mais d'autres hypothèses démontrent le contraire. Que la décision migratoire dépende du taux de croissance ou bien de la taille à l'âge, on s'attend à ce que ces traits évoluent dans des populations en expansion pour plusieurs raisons. Tout d'abord, dans ces populations, on s'attend à ce que les effets démographiques soient contrastés entre les populations au cœur de la zone en comparaison avec celles situées sur les bords (Chuang and Peterson, 2016). Un exemple notable est la densité qui diminue le long de ce front de colonisation. Des contrastes environnementaux peuvent également être attendus, et donc entraîner des adaptations aux conditions locales. Enfin, les populations en expansion sont fondées par une fraction des migrants qui sont les dispersants. En théorie, on s'attend donc à des effets fondateurs impliqués dans la différentiation des populations (flux géniques) (Phillips and Perkins, 2017; Wagner et al., 2017). Je me suis donc intéressée à l'évolution de la croissance et de la taille à l'âge au cours du temps dans le contexte de l'expansion de la truite commune aux îles Kerguelen.

Vers une décroissance et une diminution de la taille à l'âge

Dans un premier temps, j'ai modélisé l'évolution de la croissance en eau douce en me basant sur le modèle de Von Bertalanffy (vBGF) dans un cadre statistique bayésien. Je montre que le taux de croissance et la taille à l'âge diminuent au fil du temps depuis la colonisation, principalement sous l'effet de la densité. La diminution du taux de croissance est forte et rapide lors des 5 premières années pot-colonisation, puis semble décroitre de moins en moins vite (*Fig. 5.4*). Les deux phénotypes (futures tactiques migratoires) sont affectés de la même manière par ce processus démographique temporel (*Fig. 5.5*). La diminution de ce taux de croissance affecte de manière significative l'estimation de la taille aux âges de 1 et 2 ans. Aux âges supérieurs, l'estimation des différences de tailles devient forte mais aussi beaucoup plus variable (*Fig. 5.6*). Le taux de croissance des individus pendant la phase d'eau douce semble lié à la propension migratoire des individus, les poissons à croissance plus rapide ayant plus de chances de devenir de futurs migrants. Rappelons que parmi ces migrants, certains peuvent être des dispersants. Contrairement aux attendus, la croissance des individus ne semble pas différer significativement en fonction des populations étudiées (localisations).

Dans une seconde étude, en préparation pour publication, j'ai adopté une approche complémentaire sur l'évolution de la taille à l'âge. J'ai pour cela, utilisé mon jeu de données scalimétriques (comprenant des individus appartenant à plusieurs classes d'âges) et un extrait de la base de données à long-terme ne comprenant que les individus capturés à un an. Ces jeux de données ne contiennent donc pas les mêmes informations en terme de survie. J'ai utilisé une approche de *random forest* pour déterminer l'implication des variables sur la taille à l'âge en eau douce : temps (temps écoulé depuis la colonisation), cohorte (année de naissance), rivière et type de colonisation (introduction volontaire ou colonisation naturelle). Pour l'âge d'un an, j'ai utilisé les deux jeux de données précédemment décrits. Pour les âges 2 à 6, seul le jeu de données scalimétriques a été utilisé. Dans cette étude je montre que les variables influant sur la taille à l'âge sont le temps (comme indicateur de la densité) et la cohorte (comme indicateur des variations environnementales à travers le temps). L'effet conjoint de ces variables montre une évolution vers de plus petites tailles à l'âge au travers du temps, mais aussi au travers de l'espace. Les individus sur les marges de la zone d'expansion semblent souffrir d'effets négatifs plus forts de densité-dépendance sur la taille à l'âge (*Fig. 5.8* et *Fig. 5.9*). Contre toute attente, la relaxe de la densité sur les marges ne semble pas être en faveur des individus les plus grands (Imre et al., 2005) (*Fig. 5.10*).

La diminuton de la taille seuil à la migration, réponse plastique

Les tactiques migratoires alternatives, comme la migration partielle chez les salmonidés, sont considérées comme des tactiques seuils à cause de leur caractère polygénique (Dodson et al., 2013). Cependant, chez les salmonidés, la décision de migrer est souvent conditionnée par la croissance des individus et leur taille à l'âge (traits déterminants). Les interactions environnementales et génétiques peuvent entraîner l'expression de plusieurs phénotypes, c'est ce qu'on appelle une norme de réaction rendant possible l'évolution des traits (Pulido, 2011). J'ai donc utilisé ce cadre théorique pour étudier l'évolution de la valeur seuil à la migration afin de déterminer comment la migration partielle évoluerait dans le contexte de population en expansion dans les îles Kerguelen. Si la valeur seuil du trait pour la décision de migrer est stable, on s'attend à ce que toute évolution de la taille à l'âge (trait déterminant, « liability »), conduise à un changement de l'âge de la migration. Une migration plus précoce devrait avoir lieu lorsque les capacités de croissance augmentent et le contraire lorsque la croissance ralentit. Cependant, si la taille est stable on peut également s'attendre à une évolution de l'âge de la migration si la valeur seuil évolue (Phillis et al., 2016). Dans cette étude, en préparation pour publication, je démontre que la pente de la norme de réaction évolue de manière significative dans les populations au cœur de la zone d'expansion (plasticité phénotypique), là où elle n'évolue pas ou peu sur les marges, peut être sous l'effet de canalisations environnementales *Fig. 6.3*. Le seuil de taille minimal à la première migration est toujours au-dessus de 200 mm (pour des âges à la migration entre 2 ans et 4 ans). Les individus devenant de plus en plus petits à l'âge, on observe que la propension à migrer diminue pour les individus les plus jeunes (2 ans). Dans les populations au cœur de la zone d'expansion, le déterminant de la migration (taille) évolue vers de plus petites valeurs mais le seuil à la migration aussi, ce qui semble favoriser le maintien de la tactique migratoire. Au contraire, sur les populations les plus en marge de la zone d'expansion, on n'observe pas de pattern commun généralisable. On observe même une augmentation du seuil à la migration pour une des rivières (Acœna), entrainant des délais dans le premier âge à la migration *Fig. 6.4*. Le long du front de colonisation, on observe donc de forts contrastes environnementaux, suggérant un rôle important de l'adaptation locale, mais aussi d'autres forces évolutives en action.

L'évolution simultanée du taux de croissance, de la taille à l'âge et de la norme de réaction (interactions génotype x environnement) nous permet de conclure que l'âge à la première migration sera retardé à mesure que les populations s'établissent (principalement sous l'effet temporel de l'augmentation de la densité) mais aussi à mesure que les populations se rapprochent des bords de la zone d'expansion (*Fig. 6.5*). Les variations temporelles mais aussi spatiales jouent un rôle central dans l'expression des polymorphismes des traits en lien avec le cycle de vie (Chapman et al., 2011b). Les populations d'origine différentes peuvent varier de façon marquée dans leur histoire de vie, soit en raison de leur origine phylogéographique (McKeown et al., 2010), soit en raison de conditions environnementales variables telles que la disponibilité de la nourriture ou la température (B. Jonsson and N. Jonsson, 2019; B. Jonsson and Ruud-Hansen, 1985). La diversité des rivières présentée dans ce manuscrit, dans leurs caractéristiques d'habitat, peut expliquer la diversité spatiale des tactiques migratoires (âge et taille lors de la première migration) et souligne l'importance de l'adaptation locale. Une autre partie de cette diversité repose sur des hypothèses génétiques. On pense que les mélanges génétiques et les introductions multiples accélèrent la capacité d'expansion des populations (Wagner et al., 2017). L'interaction antagoniste de la pression de propagule et de la colonisation des îles Kerguelen, entraîne une phase initiale d'invasion rapide, suivie d'une forte diminution du taux d'invasion (Labonne et al., 2013). La structure génétique des populations d'eau douce est aussi probablement façonnée par les conditions rencontrées dans le milieu marin (qui favorisent ou non la tactique migratoire), puisque la dispersion en mer est à l'origine du flux génique (Quéméré et al., 2016). La base génétique de la migration reste un sujet de recherche à explorer.

Vers une diminution de la capacité dispersive?

Le but de ce travail de recherche était d'étudier les traits liés à la capacité de dispersion. J'ai abordé la question à travers l'angle de la migration, prérequis à toute dispersion. Grâce à un jeu de données unique en son genre, j'ai pu étudier des traits de vie dans un cadre spatio-temporel déterminé afin de confronter l'évolution de la migration sur le front de colonisation dans les îles Kerguelen avec les attendus théoriques. J'ai pu mettre en lumière que l'expansion des populations aux îles Kerguelen ne semblent pas favoriser les individus les plus grands sur les marges de la zone d'expansion, et qu'au contraire il semblerait que les individus y soient plus petits. Cette diminution de la taille à l'âge, accompagnée d'une faible plasticité du seuil à la migration semble vouloir dire que la dispersion est moins favorisée sur les marges que dans les populations au cœur de la zone d'expansion. Avec la mise à jour de la base de données qui compte aujourd'hui plus de 151000 données, de nombreuses pistes vont pouvoir être explorées pour comprendre si effectivement la dispersion est moins favorable sur les marges de la zone d'expansion. De plus si l'âge au moment de la migration, la croissance en eau douce et la taille sont des conditions préalables à l'étude de la migration, de nombreux autres traits restent à étudier, tels que la reproduction (âge au moment de la reproduction, nombre de reproductions) ou la mortalité. Cette étude s'est concentrée sur la phase d'eau douce avant la migration. Mais la dispersion implique un transit par le milieu marin, lui-même soumis à des changements. La migration étant un équilibre individuel entre des coûts et des avantages rencontrés dans ces deux environnements, toute évolution de l'un ou de l'autre entraînera l'évolution de la migration elle-même et donc de la dispersion.

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Part I

General introduction

1

Conceptual framework

1.1 Ecology and evolution of life-history traits

Ecology is a scientific field aimed at understanding the interactions between organisms (biotic factors) and their environments (biotic or abiotic factors). Four nested hierarchical levels are studied in ecology: the organism, the population (a group of organisms belonging to the same species, living in the same environment, at the same time), the community (an organization of several populations) and the ecosystem (the community studied with its abiotic factors taken into account). In a general context, the term evolution refers to any gradual and temporal change that may affect a system (*e.g.* the climate, the composition of the ocean or the atmosphere), an organism (*e.g.* growth, weight, morphology, behaviour), or a population (*e.g.* density).

More specifically, in biology, the term evolution refers to any change in heritable characteristics noticed from one generation to another. Genes are the support of those heritable characteristics. They are transmitted to the next generation via reproduction. The expression of one or several genes allows the observation of measurable traits, which are distinct variants of a character state (*e.g.* the sex of an organism is a character state and can take the value “female” or “male”). The temporal evolution of transmitted traits can occur under five main evolutionary forces that affect allele frequencies in populations. Natural selection was originally described by Charles Darwin jointly with Russel Wallace (Darwin, 1859) and is the adaptative advantage or disadvantage that is given to an individual’s fitness under particular environmental conditions. The term fitness describes how good is an organism in term of reproduction (number of offspring in the next generation) and survival. Natural selection hypothesis stands that (1) morphological, physiological and behavioural traits vary among organisms in a population, (2) those traits confers different fitness to the individuals and (3) traits are heritable (transmitted from generation to generation) (Berthold and Pulido, 1994; McLennan et al., 2017; Roff, 1998). Mutation occurring at the genetic level plays a role in traits variance and can either create or delete alleles at the population level. Assortative mating acts on genotype frequency and is the process in which individuals with similar phenotypes mate with one another more frequently than would be expected under a random mating pattern. Genetic drift plays its role at reproduction and corresponds to the random change in allele frequencies owing to stochastic variation in birth or death rates. Finally, gene flow, assuming individual movements among populations, affects the redistribution of alleles within populations since individuals carry genes (Thomas et al., 2010).

Life history theory seeks to explain how different evolutionary forces compel organisms to face with environmental changes (Stearns, 1992). Any traits related to reproductive or survival abilities are called life-history traits (**Box 1**). Morphological, physiological, or behavioural traits can have implications on fitness (**Box 2**). Because life-history traits are quantitative and partly heritable (in birds : Berthold and Terrill, 1991, in fish : Carlson and Seamons, 2008, in the oyster : Ernande et al., 2003), they are open to evolutionary changes. Any natural/anthropogenic alteration of the organisms’ habitat (*e.g.*

environmental variation in temperature, food availability, access to habitats for reproduction) can lead to evolutionary changes.

Box 1: Life-history traits

Sexual and natural selections favour traits that improve an organism chance of survival and reproductive success. In every species, there are trade-offs between survival and traits, such as frequency of reproduction and number of offspring produced. The traits that affect an organism schedule of reproduction and survival make up its life history. Life-history traits of a species include the growth rate, age at first reproduction, number and size of offspring, reproductive lifespan and patterns of ageing. Life history optimization problems are typically modelled by using the Euler-Lotka equation (Stearns, 1992).

$$1 = \int_{\alpha}^{\omega} e^{-rx} l_x m_x dx$$

where α is the age at first reproduction, ω the age at last reproduction, l_x the probability of surviving from birth to age class x, m_x the expected number of offspring in age class x, and r the population growth rate. The equation sums the probabilities of survival and reproduction over the entire lifetime of the individuals in the population and can then be solved for r.

Box 2: Example of traits that have implications on fitness

Morphological traits

Some morphological traits such as ornaments in organisms can be secondary sexual character selected under mate choice. A higher probability to reproduce is commonly observed across taxa for the most ornamented morphs (in birds: Hunt et al., 1999; Møller, 1992, in fishes: Houde, 1987, in insects: Ellers and Boggs, 2003). Morphological traits also influence the ability of organisms to survive. For example, in plants, the structure of roots has implication for water uptake (Hernández et al., 2010). Body size is another morphological trait that can be inherited and have implications on survival. Bigger being often better, with higher competitiveness (Garnett, 1981) or better condition status (Johnsson et al., 1999).

Physiological traits

Traits related to the energetics status of individuals within a population are often good predictors of the migratory status, where migration affects indirectly the ability to survive and reproduce. In blue tits, the basal metabolic rate is lower for migrants than residents (Nilsson et al., 2006). In the brown trout, the gill Na,K-ATPase activity differs between residents and migrants, and the energetic status for migrants before migration is often lower than for residents (Boel et al., 2014).

Behavioural traits

The behaviour of individuals within population can condition their ability to survive and reproduce. Traits related to competitiveness have implications on mating competition, on progeny or territory defence... In salmonids, it is not uncommon to find a sneaking strategy where the smallest males skip one one-year migration to invest their energy into reproduction thus competing bigger fish (Weir et al., 2016). The migration itself is also an individual behaviour affecting the fitness components.

Faced with rapid environment change, surviving organisms either move towards suitable habitats or adapt. Adaptation implies fitness maximization through the match of the individual phenotype with an optimum trait. This is called adaptative phenotypic plasticity (Stearns, 1989a; Tufto, 2000) and this process involves individual-level responses. Plasticity can occur for continuous traits or discrete traits, such as phenotype. For the latter, they are conditioned by a liability trait relatively to some threshold value (where one phenotype is expressed below the threshold value of the liability trait and the other one above) (Pulido, 2011). The existence of polymorphism controlled by the environment is called a conditional strategy or threshold traits strategy (Roff, 1996; Stearns, 1989b). At the population level, if those traits are heritable, adaptative genetic responses (evolution) are expected (Phillis et al., 2016). However, how fast will be this evolution? The rate of evolution whether gradual or punctuated [measured in “darwin” (d) or haldanes] can greatly vary depending on the considered ecological timescale (generation-to-generation or period over many generations) (Gingerich, 2019). The trait evolvability is the ability of a trait to adapt not merely due to novel genetic diversity but rather evolve under natural selection.

1.2 Migration one key to life history and dispersal evolution

For many organisms, migration is essential to breed, feed, seek refuge from predators, and avoid harsh environmental conditions (Boyle, 2011; Marco-Rius et al., 2013). In 2019, Ferguson et al. defines migration as “directed movements between two distinct habitats occurring with regular periodicity on a temporally predictable basis”. Individuals and environment conditions influence individual movements, the two components interacting with each other (*Fig. 1.1*). The most frequent form of migration is “partial migration”. The “partial migration” term comes from the ornithological literature (Chapman et al., 2011a) and is characterized by within-population variation in the tendency to migrate, such as just a fraction of the population migrates. A partial migratory population consists of non-migrants (usually terms as resident) and migrants sharing their breeding or non-breeding site. Partial migration often leads to polymorphisms (Boyle, 2011; Wysujack et al., 2009). Choosing migration is often a balance between foraging advantages and increased predation risks (Hebblewhite and Merrill, 2007; Hebblewhite and Merrill, 2011). The study of partial migration is important because it is related to adaptation, maintenance of polymorphism, and even evolution of the migrating behaviour itself. Partial migration is the result of an evolutionarily stable state (ESS), that could be a conditional strategy (CS). A CS is when the migratory status depends upon an intrinsic state of the individual (age, sex) or an intrinsic state affected by external conditions physical condition or even gene expression.

Nevertheless, it is essential to notice the differences between migration and dispersal. Not all migrants are dispersers (*Fig. 1.2*). Where migration only refers to movements between habitats, dispersal refers to an entire cycle from the decision to migrate (departure) followed by transience (migration) to finally end in the settlement of the organisms in a new population (Berthold and Terrill, 1991). Therefore, if migration evolves, we can simply hypothesize that dispersal will as well. Dispersal may happen in a previously founded population, then it contributes to change the allele frequency in the population where dispersers reproduce. If dispersal happens in an empty habitat, then, dispersers found a new population if the reproduction occurs. We will refer to the last case as “colonization”. Some genes forming the new population are under natural selection; sub-lethal and lethal genes, that may change in frequencies, contribute to the inbreeding depression (Glémin, 2005). The fate of a gene in a population depends upon the structure of the population itself and the number of migrants/emigrants (gene flux) in the population.

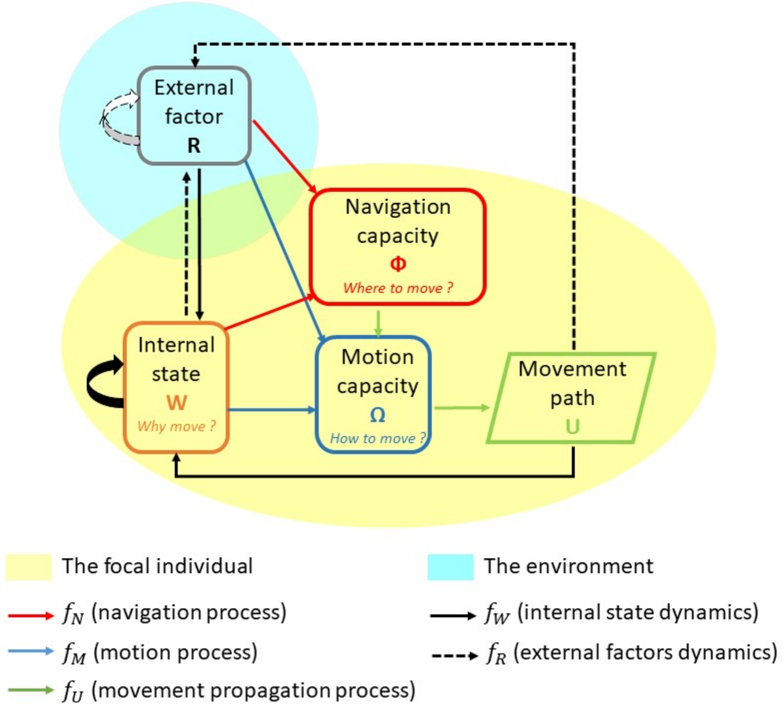

Figure **1.1**: A general conceptual framework for movement ecology. Adapted from Nathan et al. (2008).

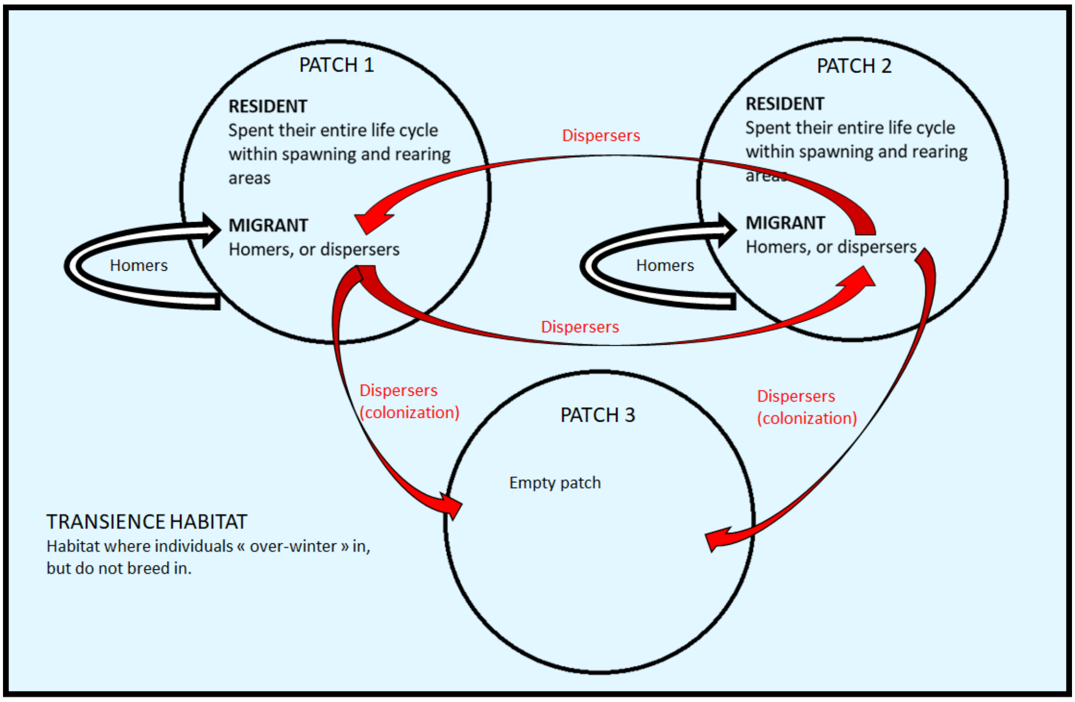

Figure **1.2**: Simple schematic of life history variation in partial migratory species. *Homers are faithfull migrant to their breeding ground. Dispersers migrate (transience) and settle in another patch, either already occupied or empty (colonization, if reproduction occurs).*

1.3 How partial migration is maintained over evolutionary times

Migration depends on habitat suitability and evolution (Ronce et al., 2000). The fate of species out of their native range is either adaptation or disappearance. If introduced in an unsuitable environment, individuals might need to **disperse, which implies migration and reproduction, to optimize their fitness**. Thus, in newly colonized habitat, individual dispersal propensity is expected to evolve. Both proximate and ultimate processes are involved in the migratory choice. Proximate mechanisms act on short timescales by direct changes in the environment, they are therefore involved in plasticity, while ultimate mechanisms act over longer periods by genetic changes. Although plasticity can also evolve, and hence be impacted over longer timeframes by ultimate processes. The decision to migrate is dually controlled by an environmental/genetic threshold that determines whether an individual may migrate or not (Chapman et al., 2011b). However, disentangling the effects of proximate and ultimate mechanisms underlying partial migration is complex. A better understanding of the mechanisms underlying migration will serve to improve our knowledge on its ecological and evolutionary consequences.

Environmental instability may affect the ability of organisms to reach their optimum in terms of reproduction and survival (Kuno, 1981). One way to face it is to disperse. As the rate of disturbances increases, the dispersal ability increases. Dispersers may reach climate refuges (Morelli et al., 2016) or new habitats that become favourable arising from climate change. Those habitats give new colonization opportunities for dispersing species (Lawler, 2009). The Arctic and Antarctic regions will soon turn into suitable ecological niches for new species. In a context of global change, the instability may arise from a change in meteorological conditions (*e.g.* temperatures, precipitation, river flow rates) or from a change in the community structure (*e.g.* population density, trophic chains) (Brodersen et al., 2011). Temperature is known as an environmental factor governing numerous developmental and life stages (*e.g.* plant development (Bollero et al., 1996), migration strategy (Alonso et al., 2009; Nilsson et al., 2006; Skov et al., 2010), and seasonal timing of life cycle events (Cagnacci et al., 2011; Gienapp et al., 2014; Reed et al., 2010)). Diverse other environmental conditions may affect the individual's behaviour such as rainfall (Boyle, 2011), fires and vegetation biomass (Naidoo et al., 2012). When population size increases, density is expected to become the main driving force of dispersal (Grayson and Wilbur, 2009; Kaitala et al., 1993), acting on the competition for habitats, resources or reproduction (Loe et al., 2009; Nathan et al., 2008). On the contrary, when the population size is small, kin competition is the selective force driving the evolution of dispersal (Ronce et al., 2000). Under the hypothesis of non-saturated habitat under competition, a decrease in the dispersal ability is observable when the survival of migrants is lower than residents' survival. If migrants have a lower fecundity than residents (number of offspring produced in a site), the dominance of the resident strategy is expected in such case.

At the individual level, dispersal may be heritable. The heritability may be direct such as the heritability of behaviour (Páez et al., 2011). Phenotypically dimorphic traits have been demonstrated to be partly heritable (Roff, 1998), such as the age at migration in some fishes or the seasonal migration in birds (Pulido and Widmer, 2005). The heritability may also be indirect depending on the energetic status of breeders or during the development of juveniles (*e.g.* variation in movement capacity or competitive ability linked to some traits such as body size or weight). For example, the food restriction at a certain developmental stage has a significant effect on the migratory tactics, also correlated to sexes (Archer, Hutton, Harman, O'Grady et al., 2019). In term of behaviour, dispersal may happen before the first breeding attempt (natal dispersal) or between two consecutive breeding attempts (breeding dispersal)

(Harts et al., 2016). In the case of natal dispersal, stable and fragmented habitats may create dispersers as a bet-hedging strategy (Clobert et al., 2012). For example, the seeds dimorphism in achenes leads to different strategies of dispersal through space and time. The peripheral seeds have higher dormancy and lower dispersal abilities than the seeds from the centre of the capitulum. This bet-hedging strategy reduces the impact of spatio-temporal changes on the reproductive ability of the species (Imbert, 1999). In term of development, body size is often a good proxy of the decision to disperse (Alerstam et al., 2003; Gyllenberg et al., 2008; Jahn et al., 2010). Divergence in body size between individuals may arise either from phenotypic plasticity and/or genetic variation (Rogell et al., 2013).

Different hypothesized factors act as drivers of dispersal. First, the competitive release hypothesis, where larger individuals outcompete the smallest, and hence the smaller subordinates disperse to achieve their needs (Yeaton and Cody, 1974). When the density increase, there should be an increase in the number of migrants. This can be true in populations where predation risks is low, on the contrary, when it is high, individuals may benefit more from living together and protecting the population as a group of residents (Chapman et al., 2011b). Second, the arrival time hypothesis, simply summarized by first arrived first served. Individuals with high phenotypic quality often arrive first on sites, this is the prior residency effect (Kokko et al., 2006). Furthermore, the dynamic of one tactic seems to depend upon the overall population demography (Griswold et al., 2011). Kokko (2011) has even shown that rules of territory acquisition matters, with either residents or migrants becoming predominant in population just under the arrival time hypothesis. Thus, partial migration could be also explained by a demographic balancing at the population-level (Hebblewhite and Merrill, 2011). Under this hypothesis, smaller individuals are expected to be less competitive in territory acquisition. This theory is prone to be sex-dependent, where males often larger than females are prone to residency and territory defence. Thirdly, the fasting endurance hypothesis (Millar and Hickling, 1990), is based upon the individual physiological differences in survival. Now it is more frequent to talk about the 'limited foraging opportunity' hypothesis, where individuals who do not tolerate the change in food intake may migrate (Boyle, 2011). Of course, spatial and temporal distributions of food may be unequal and can play a role in partial migration. The 'increasing food availability hypothesis' is also suggested by Gross (1987). Migration thus occurs when the food balance is different between habitat of departure and arrival (Ayer et al., 2018).

1.4 What are the consequences of partial migration in the evolutionary process?

Species that invade newly colonized environments often exhibit rapid evolutionary changes (Westley, 2011). It is now clear that evolution may act at ecologically relevant timescales (Thompson, 1998), and it turns out that it affects dramatically population dynamics. Biological invasions are the source of important modifications in the structure and functioning of ecosystems (Buoro, Olden et al., 2016) and are recorded as the second- threat against biodiversity after habitat loss (Park, 2004). In most of the cases, biological invasions are poorly documented and submitted to external drivers (*e.g.* natural selection, anthropogenic factors, facilitation, sampling pressure) that prevent from understanding intrinsic phenomena so as to provide an objective risk assessment (Blanchet, 2012; Labonne et al., 2013). The evaluation of those phenomena allows understanding and predicting population dynamics and evolution even if the discrimination of the different processes of evolution behind invasive success are difficult or even impossible to assess. Invasive species encompass transient demographic bottleneck because dispersal may maintain relevant genetic variation, reduces mutation load, or increases the effect of natural selection (Colautti et al., 2017). Adaptive phenotypic plasticity is more likely to evolve for invasive species because they encounter various habitat (*Fig. 1.3*).

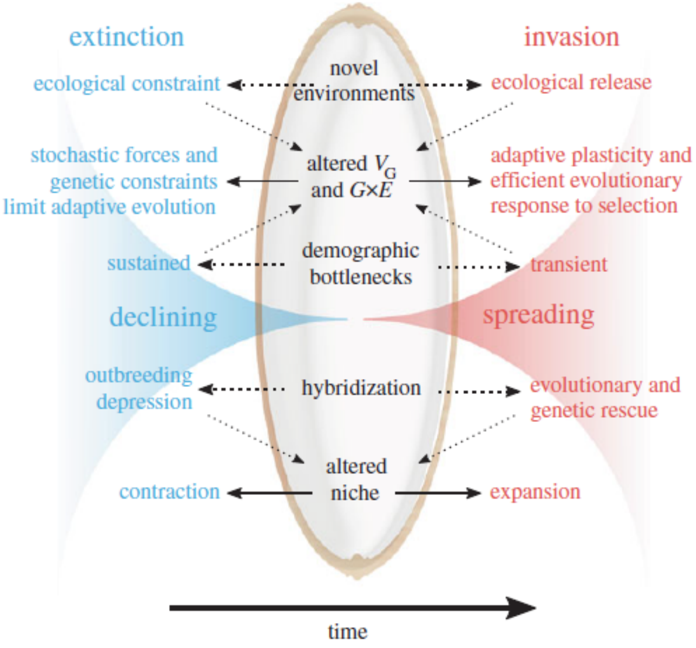

Figure **1.3**: Extinctions and invasions conceptualized 'Through the Looking Glass' of evolutionary ecology. Taken from Colautti et al. (2017).

In addition, populations of invasive species are expected to evolve greater plasticity in their invasive range compared to populations within the native range (Richards et al., 2006). According to the Empty Niche Hypothesis (Stachowicz and Tilman, 2005) unsaturated ecological niches are poorly occupied because of their short evolutionary history (*e.g.* recent volcanic islands), their climatic (glaciation-deglaciation in northern systems), geologic and topographic histories (isolation of mountain ecosystems), or their degree of anthropogenic alteration. The success in non-native populations establishment relies on the assumption of niche differentiation with native populations, involving either the exploitation of unused resources (empty niche), or enhanced competitive ability to access a shared resource (niche replacement) (Chabrerie et al., 2019).

If the dispersal strategy is heritable (Imbert, 1999), thus one may expect to find dispersers on the edge of the colonization front and non-dispersers in the core. Population expansion rate results from population growth and dispersal. If the environmental conditions are favourable, so much the better for dispersers (colonization). If the resources are available outside the original population range where the density is lowest (per capita growth rate is maximal), there is an advantage to disperse to the margin (Deforet et al., 2019). Population expansion seems to select in many cases (plants, fish, crickets, butterflies, and fungi) for better dispersal, even at the cost of slower population growth (Chuang and Peterson, 2016). These findings suggest that a better understanding of conditions favouring dispersal is required to understand evolution in expanding populations.

The problem of evolution in an expanding population has been investigated before both theoretically (Burton et al., 2010) and empirically (*e.g.* Phillips, Brown, Webb et al., 2006). On an expansion front, both low population density at the margin and a strong density gradient are prone to evolutionary processes such as spatial sorting and expansion load (Phillips, Brown and Shine, 2010). Long-distance dispersal (LDD) events may reduce the diversity on the front by affecting the frequencies of genes along the migration road. Populations on the edge, created by a fraction of the initially introduced population (the founders), are expected to be genetically different (founders' effect) because there are selected gene flows. This phenomenon is called spatial sorting. The distance of migration is not the only factor influencing the colonization process. The shape of the dispersal kernel also influences the genetic structure of diversity found in introduced and newly colonized populations along the dispersion corridor (Fayard et al., 2009). For example, fat-tailed dispersal kernel is thought to increase gene mixing on the front of a colonization process. Those two contrasting effects of LDD are in fact dependent upon the frequencies of events of dispersion.

If natal river conditions, migration route, or destination conditions change, so will the benefits and costs of migration. While in theory traits resulting in the highest fitness should fix in a population, balancing selection may counteract and lead to an evolutionary maintenance of trait variation within the population (Hendry et al., 2004). If the resident tactic is advantageous under certain conditions, migratory one could be advantageous under others, relying upon compensatory adaptations to balance the benefits and costs of the tactic (B. Jonsson, M. Jonsson et al., 2016). It is therefore important to acquire better knowledge to compare residents and migrants to shed light on the mechanism of partial migration (Chapman et al., 2011a).

2 Study framework

2.1 The brown trout (*Salmo trutta, L.* 1758)

Studies on salmonids are particularly well suited to address the question of evolutionary response in the decision to migrate, because migration is a conditional strategy. Partial migration illustrates the considerable variation in life-history strategies among salmonids. In the case of fish, partial migration has a very heterogeneous lexicon (Secor and Kerr, 2009). Salmonids are fruitful material for biologists to work on individual variation in life history related to maturation and migration (Dodson et al., 2013). Their life histories can be easily monitored, either by capture-mark-recapture methods (CMR) using telemetry (Davidsen et al., 2014) or pit tagging (Rifflart et al., 2006). The use of the calcified structures is another way to monitor life histories of fish (scales and otoliths) (Burnet, 1969; Campbell et al., 2015; Elliott and Chambers, 1996; Ombredane and Baglinière, 1992). Calcified structures record useful information on fish life histories such as age, growth, reproduction events, and environment of living. Those structures are adequate materials to study the life-history traits quite easy to sample and are chosen tools for many ichthyologists (Borgenson et al., 2014; Ottaway, 1978).

Much work has already been done on the main ecological drivers of partial migration in salmonids. Temperature (Archer, Hutton, Harman, McCormick et al., 2020; Pulido, 2011), food accessibility (Archer, Hutton, Harman, O'Grady et al., 2019; Wysujack et al., 2009) and food quality in fresh water (Marco-Rius et al., 2013; Olsson et al., 2006) have been proven to be involved in the decision to migrate. Across vertebrates, migratory decisions may be inherited, but the role of epigenetics remains unclear (B. Jonsson and N. Jonsson, 2019). Genetics seems to affect the migration decision, by acting on developmental rate and smolting process (inducing physiological, behavioural and morphological changes to cope with environmental conditions that prepare individuals for forthcoming seawater life in spring) (Arawomo, 1981; Bagliniere, 1979; Cuinat and Heland, 1979; Heland, 1980; Nichols et al., 2008; Roussel and Bardonnet, 2002). The choice of one of the alternative migratory tactics relies upon a threshold trait (Roff, 1996), such as threshold size for smolting (Buoro, Gimenez et al., 2012), and individual size-at-age (Carlson and Seamons, 2008).

Dodson et al. (2013) argue that body size in salmonids is the most commonly (and adequately) reported proxy of the liability trait to migration, since migration success depends upon the energy that has been acquired, stored and used by the individual (Acolas et al., 2012; Bohlin et al., 1996; Forseth et al., 1999; B. Jonsson, M. Jonsson et al., 2016; Olsson et al., 2006; Rosenfeld et al., 2015). As an ultimate mechanism, bigger size has been associated with higher fitness (Pettersson et al., 1996; Thompson and Beauchamp, 2016), notably increasing survival at sea and reproductive success (Goodwin et al., 2016). On the adverse side, large size per se is often at the cost of an increase in mortality risks (*e.g.* physiological stress, predation risk (B. Jonsson and N. Jonsson, 2004), or parasitism). Sex-biases in migration has been demonstrated. Migration tendency is generally favoured towards females (Ayer et al., 2018; Rundio et al., 2012) whereas residency is favoured towards males, maturing earlier (Piché et al., 2008). Bigger sizes for females induce higher fertility (number and size of eggs, Carlson and Seamons, 2008).

Egg size, which has an influence on survival and growth, seems to explain most of the among-population variation in offspring phenotypes, mainly through a maternal effect (Thorn and Morbey, 2018). The migration tendency of the offspring is often correlated with their parent's migrating behaviour (Debowski and Dobosz, 2016).

The brown trout (*Salmo trutta*) is a facultative anadromous salmonid, where the anadromous form (migrant) refers to the individual migrating at sea out of the reproductive window. Because migrants and residents morphologically differ significantly, it has long been thought that there were two distinct species. The species' extensive genetic, ecological, morphological and life history variations have led to a long-standing debate about its evolutionary origins (McKeown et al., 2010). The development of genetic techniques and natural release experiments proved that resident and migrant were belonging to the same species, and that the two forms differed by gene expression (Nevoux et al., 2019). Migration destination is often predictable thanks to genes (Nichols et al., 2008; Stabell, 1992). In birds, Berthold and Pulido (1994) demonstrate the heritability of migration, with naive birds having innate information on the appropriate migratory distance and direction.

Brown trout migrants and residents breed sympatrically during winter (*Fig. 2.1*). That is what we call "non-breeding partial migration" (Chapman et al., 2011a). Most migrants are homers, meaning they choose their natal river to breed (Ferguson et al., 2019). Others are strayers, because they disperse to new breeding ground. This behaviour lies upon olfactory cues and migrating as a group, as well as temperature experienced at the embryo stages (B. Jonsson and N. Jonsson, 2009). Oceanic migration which decision occurs in the summer-autumn is accompanied by a smolting process that prepares individuals for seawater life the following spring (Arawomo, 1981; Bagliniere, 1979; Cuinat and Heland, 1979; Heland, 1980; Roussel and Bardonnet, 2002).

Originated from Europe, a decline in the number of migrant trout has been observed, either anadromous in north-western Europe (Ferguson et al., 2019) or lacustrine-adfluvial migrants (Syrjänen et al., 2017). This suggests potential for genetic changes in response to changes in fitness under natural selection. The widespread distribution of the brown trout in many unconnected catchments suggests that migration occurred during glacial periods when the sea temperature was lower. Its distribution has also been increased via human-assisted introductions (Sindermann et al., 1992), and the brown trout is now found in many places all around the world (Budy et al., 2013) recorded as an invasive species (Honda et al., 2012; Young et al., 2010)(*Fig. 2.2*). Oceanic migration which is a spectacular and ubiquitous phenomenon presents a significant risk of further colonization (Honda et al., 2012) since reproduction always happens in fresh water (Goodwin et al., 2016).

The invasion and evolution of salmonids have always been a matter of interest. In a context of climate change, numerous habitat that used to be hostile opened to colonization. Environmental conditions especially changed for estuarine and marine ecosystems which represent 70% of the surface on earth (Cohen, 1997; Dulvy et al., 2003; Vié et al., 2009). The impact of climate change is expected to be greater in the pole than in the median latitude (Hampe and Petit, 2005; Lebouvier et al., 2011; Pitman et al., 2020; Turner and Overland, 2009). Concerning the fresh waters, ice melting could accelerate the erosion of coastal zone, decrease the salinity of coastal water, increase the number of accessible rivers, and potentially increase the rivers flow rate characteristics. Brown trout, as most of the salmonids, is a viable candidate to colonize those newly opened habitats (Klemetsen et al., 2003).

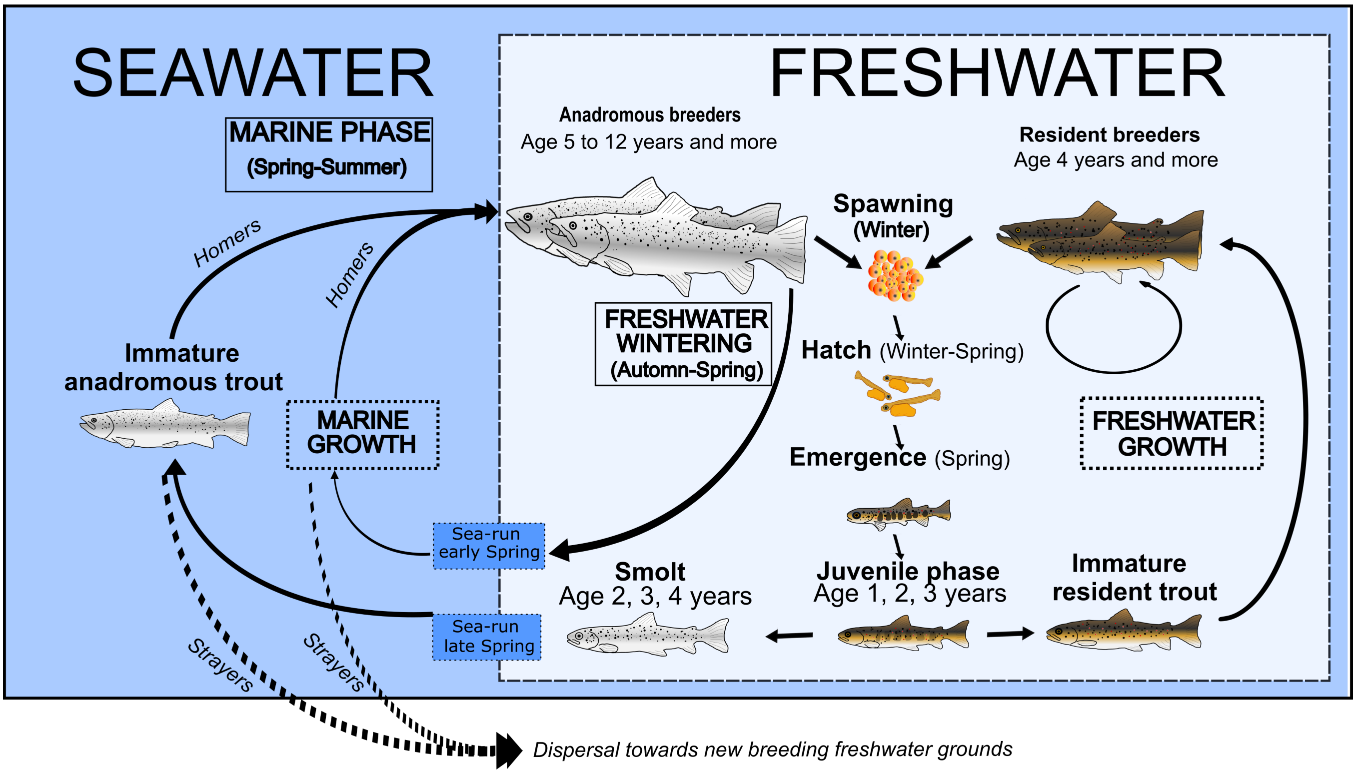

Figure **2.1**: Life cycle of the brown trout. Adapted from Aymes et al. (2014).

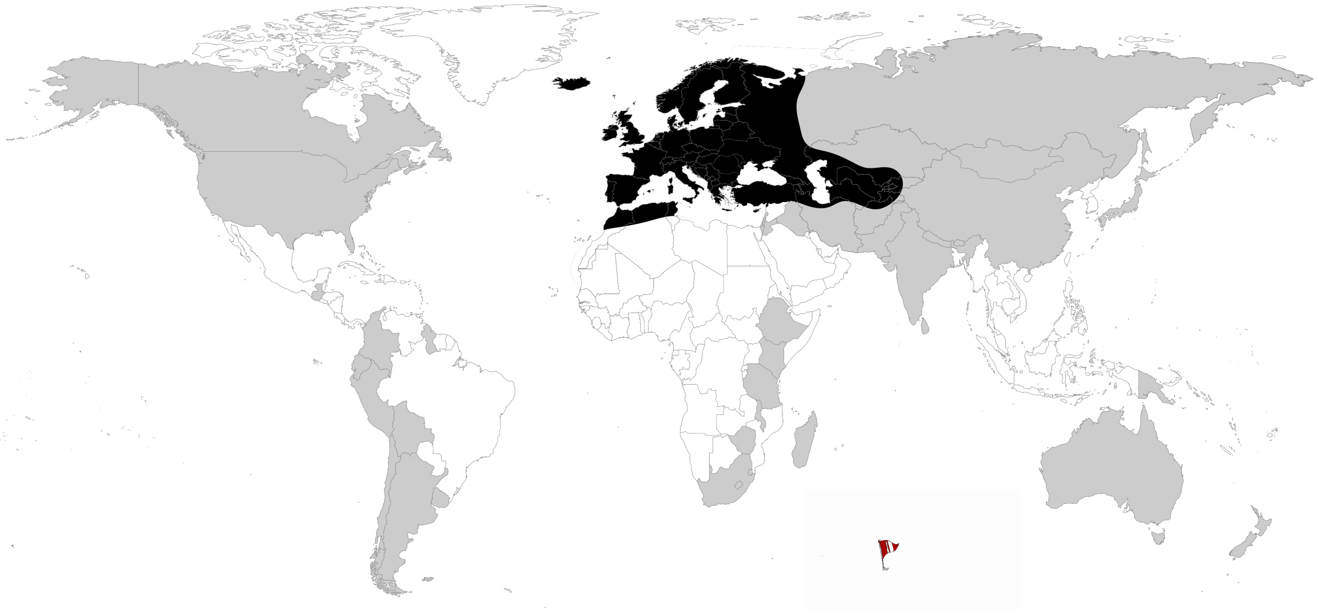

Figure **2.2**: Global distribution of the brown trout. Adapted from Závorka et al. (2018). *The black area represents the 'maximum' native range and the grey area the 'minimum' non-native range where non-native range is defined at the country level. The flag represents the location and introduction of brown trout in the Kerguelen Islands.*

Located at the confluence of the Indian and the Southern oceans waters (69°30'E-49°30'S), the 7,215 km^2 Kerguelen Islands archipelago (*Fig. 2.2*) belongs to the French Austral and Antarctic Territories (TAAF). It was originally free from freshwater fishes. To 'improve' these pristine territories for military men, civilians and scientists' settlements, some voluntary fishes' introductions were made during the 50's. With its original pristine state, the Kerguelen Islands provides the opportunity to study the modalities of introduction while offsetting anthropogenic effects. In a context of climate change, understanding species dispersal and processes of colonization in the Kerguelen Islands are of major interest to acquire useful population's dynamic information to manage appropriately the islands that are now part of a National Natural Reserve (RNN). Funded by the French Polar Institute Paul Emile Victor [1], a long-term monitoring program was undergone to understand the evolution of salmonids species and their ability to spread into new freshwater systems. Long-term monitoring of migration in fish provides the opportunity to study the evolution of life-history traits related to dispersal and their potential for rapid evolution (Dodson et al., 2013; Hutchings, 2011; Quinn et al., 2001). The complete history of the salmonids introduction in the Kerguelen Islands is recorded in Lecomte et al., 2013. The work presented in this dissertation is based on data collected during the long-term monitoring led in the Kerguelen Islands from 1954 until 2019.

2.2 Objectives of the dissertation

In this doctoral project, I investigated the evolution of life-history traits related to dispersal through the study of migration in the brown trout introduced in the Kerguelen Islands. My specific objectives were (1) to extract relevant data from the tremendously large amount of available data collected on fish caught in the Kerguelen Islands, (2) determine an appropriate methodology to reconstruct life-history traits related to migration using the scales of fish, (3) investigate the implication of freshwater growth as a driver to migration, (4) determine whether growth rate and body size of fish (liability traits) changed in time (according to time since colonization within population) and space (along an expansion range) and (5) finally investigate if the threshold value of the liability trait that triggers the migratory strategy at first migration changed in this spatial and temporal frame, with a particular interest in cross-referencing the two last part to disentangle the role of evolutionary forces and phenotypic plasticity on the evolution of partial migration.

A first part of the presented work is focused on technical and methodological questions to reconstruct the life-history traits related to dispersal, focusing on migration as a pre-requisite to dispersal. In **Chapter 3**, I describe the huge amount of data that are available thanks to a long-term monitoring launched in the 50's in the Kerguelen Islands. I analysed the characteristics of fish registered in the database, which is still under implementation. In order to obtain a balanced dataset, I determined a decision rule to select fish which scales would be mounted and study to rebuild their life-history traits. Then I finally describe the final datasets used in this manuscript. In **Chapter 4**, I focused the study of the scalimetric database and reveal the several problems we are confronted with when reconstructing life history based on scales reading. Therefore, I decomposed hierarchically the sources of variance that may affect the determination of age and growth of fish. This chapter intended to determine the final methodology we applied on the scalimetric selected data. To end the first part, I discuss the main results of those two first chapters.

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[1] https://www.institut-polaire.fr/ipev-en/the-institute/

In a second part, we modelled and studied the evolution of freshwater growth, body size at age and alternative migratory tactics, using the data and methodology described in the previous part. In **Chapter 5**, I studied changes in the liability traits to migration: the growth rate and the body size of the fish. In a first section, I modelled changes in individual freshwater growth according to time and space (location on the colonization front) using the scalimetric dataset. I investigated (1) whether future migrant and resident had a differential growth in fresh water prior to the first migration, (2) whether freshwater growth changed in time (mainly through density-dependence of growth) and (3) whether the temporal pattern was reproducible in space or not (meaning whether there was a spatial evolution as well). I went further and studied changes in body size at age in the same manner, looking at temporal and spatial evolution of body size. Concerning the changes in body size, I used two different and complementary datasets, one directly based on fish capture-at-age and the scalimetric dataset (reconstructed life-history traits). In **Chapter 6**, I used the theoretical framework of reaction norm to study changes in the threshold value at first migration to determine how partial migration would evolve in the context of expansion range in the Kerguelen Islands. The probabilistic migration reaction norm developed in a Bayesian framework, allowed us to discuss about the plastic response of alternative migratory tactics and other evolutionary forces that may facilitate or prevent migration. I finally end this part, discussing about the main findings on life-history traits related to dispersal (as migration is a prerequisite to dispersal). I cross-referenced the results of the two last chapters to highlight the evolutionary pattern of migration in the case of the shifting expansion range of the brown trout in the Kerguelen Islands.

I end this manuscript with a general discussion synthesizing the main results of both parts, to highlight the complex evolution of dispersal across space and time, and to highlight the potential decrease in invasion rate in the Kerguelen Islands. Then I make some suggestions about research perspectives to go further on the understanding of trade-offs driving partial migration.

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Part II

From fish and scales sampling to the implementation of an analytical methodology ...

Objectives and organization of the part

Reconstructing life-history traits of fish is a key point to understand whether traits related to migration has evolved along space and time. For ichthyologists, scales and otoliths are widely used tools to reconstruct the histories of the fish (Goodrich, 1907; Panfili et al., 2002). Because of their external position, scales are easy to remove, and give access to numerous life-history traits, such as age (*e.g.* Erickson, 1983; Gunn et al., 2008, age at migration (Bagenal et al., 1973), age at maturity), and growth (Kipling, 1962). The introduction of the brown trout (*Salmo trutta*) in the Kerguelen Islands provide a good opportunity to study whether the life-history traits of fish related to migration has evolved through space and time.

Nevertheless, the monitoring in the Kerguelen Islands gives access to a huge dataset of fish and the allocation of time to the scalimetry procedure does not allow studying all the individual captured. Choices are to be made concerning which fish should be studied. To evaluate spatial variations, we must select rivers among the 62 locations (rivers and ponds) where the brown trout is present (among which 60 locations colonized). To select individuals in a comparable temporal framework, we also have to determine the cohort to which they belong to (*i.e.* year of birth). Therefore, we developed models based on known size-at-capture and age to select the individuals. Criterions of selection are explained in the first chapter.

Once the fish have been selected, their scales must be studied to rebuild individual life history. Unfortunately, different scales from the same individual can tell contradicting stories. Measurements of age and growth may vary across readers and scales (Beamish and McFarlane, 1983). Over time, ichthyologists have come to the acceptance that multiple readings are more reliable to study the life history of fish (Panfili et al., 2002). However, it is hard to find one defined and appropriate methodology to determine accurately age or growth by studying a certain number of scales (Chilton and Beamish, 1982). To extract the most reliable information from the scales and to understand the main sources of variation in the determination of life-history traits, we decomposed variance hierarchically in a nested crossed manner Fish-Reader-Scale. How to select the appropriate methodology to reallocate time to the purpose of interest? This is the subject of the second chapter. This chapter is based on a published paper in Marine and Freshwater Research (Aulus-Giacosa et al., 2019).

3

Individual selection in a spatio-temporal framework

3.1 Fish caught during the long-term monitoring in the Kerguelen Islands

Long-term monitoring in the Kerguelen Islands began in 1955 with first introductions of eigth salmonids species (Coho salmon (*Oncorhynchus kisutch*), Rainbow trout (*O. mykiss*), Chinook salmon (*O. tshawytscha*), Arctic char (*Salvelinus alpinus*), Brook trout (*S. fontinalis*), Lake trout (*S. namaycush*), Atlantic salmon (*Salmo salar*) and Brown trout (*S. trutta*)). After 22 introduction attempts and 23 rivers seeded (Labonne et al., 2013; Lecomte et al., 2013), natural colonization was achieved by anadromous individuals. Among the eight species introduced, three failed to establish local population (rainbow trout, chinook salmon and lake trout). Since 1962, 81184 fishing data were collected as recorded in *Table 3.1*. The database used in this work is still being updated. Therefore, not all fish caught are represented in the database we have been working on. The last update considered in this work dates from the end of 2019. When referring to "fish caught", "sampling" or "available data", we mean implemented data in this database.
The complete history of the salmonids introduction in the Kerguelen Islands is recorded in Lecomte et al., 2013 (*Fig. 3.1*). The major introductions of brown trout (mainly originated from Bidarray in the French Pyrenees), brook trout and rainbow trout occurred from 1955 to 1962. From 1975 to 1981, Atlantic salmon, brown trout (originated from the Baltic Sea, River Slupia in Poland) and rainbow trout were released under control. Meanwhile a transfer experiment was launched to study the colonization process along the coast (reproduction, colonization, and speed of the process). The ten next following years were devoted to a sea ranching experiment of chinook salmon, brown trout, brook trout and arctic char (originated from Lake Leman, France) in Armor. In 1997, 33 rivers were recorded as colonized. In 2019, natural colonization was proven only for brown trout, brook trout, Arctic char and Coho salmon. The brown trout represents a major part of the database with 74%, followed by brook trout and Atlantic salmon. This number of data does not reflect the real number of available fish. The explanation stands in the capture-mark-recapture campaign (CMR) that was lead during the 70's. The idea was to mark fish with tags to follow their migrating movement. The fish belonging to that program were caught regularly. Their size and phenotype-at-capture (resident/migrant) were noted, and scales were removed for ageing and growth analysis. According to their movement, some fish were caught several times, so that one line in the database is representative to one capture event of fish and not representative of one fish. The available number of fish is approaching 70000. *It is important to note that the database used in the present work is the one updated in 2019. Because of an important work of implementation of the database made by F. Guéraud, the status of the database changes rapidly. This work is in progress. For information, more than 151000 fishing data are available at present.*

All the introduced species in the Kerguelen Islands belongs to the Salmoninae subfamily of the Salmonidae. They all originate from the Northern hemisphere and reproduce in cold fresh waters either one (semelparity, most *Oncorhyncus*) or several time (iteroparity, *Salmo* and *Salvelinus*). After eggs deposition under the appropriate substrate, the fry emerges and grow in fresh water at juvenile stage.

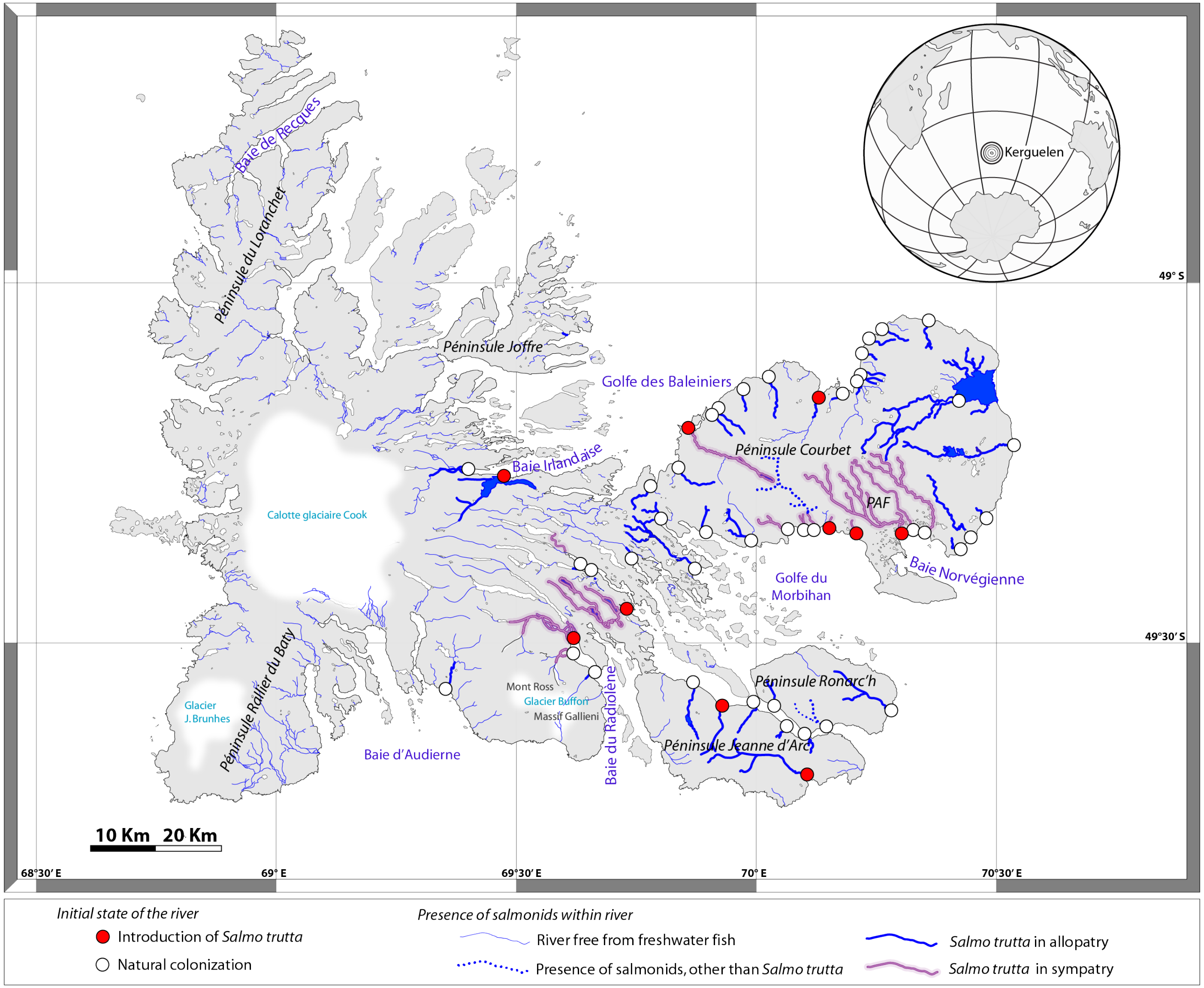


Figure **3.1**: General map of the colonized rivers in the Kerguelen Islands, their state and salmonids presence. *The salmonids that are still present in the Kerguelen Islands are Oncorhynchus kisutch, Salvelinus alpinus, S. fontinalis, the hybrid of the two Salvelinus, Salmo salar and S. trutta as recorded in Table 3.1.*

At that stage, they are either able to undertake a seaward migration or stay as resident in their native river. After the growth season, the migrant either come back to their natal river (homing) or reproduce in another river (dispersal). If the reproduction in the new river is successful and the fry at the following season survive, the colonization process is completed. Nevertheless, some species can also exist as exclusive freshwater population (Klemetsen et al., 2003). The origin of each introduced species and their life cycle is described in Lecomte et al., 2013.

The brown trout is the dominant fish species caught in the Kerguelen Islands (*Table 3.1* and *Fig. 3.2*). Successfully introduced in 10 rivers (either introduction or transfer), in 2013 the colonization of some 32 new rivers in only 10 generations was observed (Davaine and Beall, 1992; Labonne et al., 2013; Lecomte et al., 2013). The dispersal success of the brown trout in the Kerguelen Islands could be related to the high propagule pressure (with 160.000 eggs imported) (Simberloff, 2009). Originated from different source population, the introduction effort has increased the chance of successful brown trout settlement (Chabrerie et al., 2019). This settlement highly depends upon the characteristics of the environment itself and the intrinsic characteristics of the species (*i.e.* invasiveness). The plasticity of functional traits is one of the key determinants of species invasiveness. With its high phenotypic plasticity, the brown trout is already considered one of the world's worst invaders (Závorka et al., 2018). In sympatric conditions, numerous studies have also shown the relative success of the Brown trout to compete other species in term of growth and completion for food (Imre et al., 2005; McHugh and Budy, 2006; Zwol et al., 2012). In experimental conditions, trout are often more aggressive compared to salmon (Berg et al., 2014; Houde et al., 2015). Also, body size is an important feature to win territorial competition within salmonids (Gaudin and Heland, 1995; Heland et al., 1995; Johnsson et al., 1999) but density can counterbalance the advantage of being large, this advantage decreasing as group size increases (Pettersson et al., 1996).

Table 3.1: Number of samples (n) by species recorded in the long-term monitoring database.
The percent line gives the total represented by each species in the sampling.

Species	Non identified	Coho salmon	Rainbow trout	Chinook salmon	Arctic char	Brook trout	Atlantic salmon	Brown trout
n	3388	864	8	43	362	10215	5833	60471
Percent	1.1	4.2	<0.010	<0.10	0.45	13	7.2	74

Among the 68 locations (rivers and ponds) where fish were caught during the monitoring, the brown trout is present in 62 of them (91%). Among those 68 locations, there are 46 locations where allopatry is observed (more than 99% of the fish caught belong to only one species) (41 with the brown trout (89%)). There are 18 locations where the brown trout is in sympatry (one other species) and dominant on 12 locations. On the other locations, the brook trout is predominant. For more information about the repartition of salmonids in the different locations, see **Appendix A.1**. However, as the brown trout successfully invaded the Kerguelen Islands, the fishing effort could have been reinforced for monitoring purpose. Indeed, except for the brown trout, salmonids in the Kerguelen Islands form spatially defined and restricted set. Over time, the fishing effort was not continuous (*Fig. 3.2*). Higher fishing effort are recorded in the late 70's, the early 90's and 2000 whereas gap period are observed in the late 90's and from 2012 until 2016.

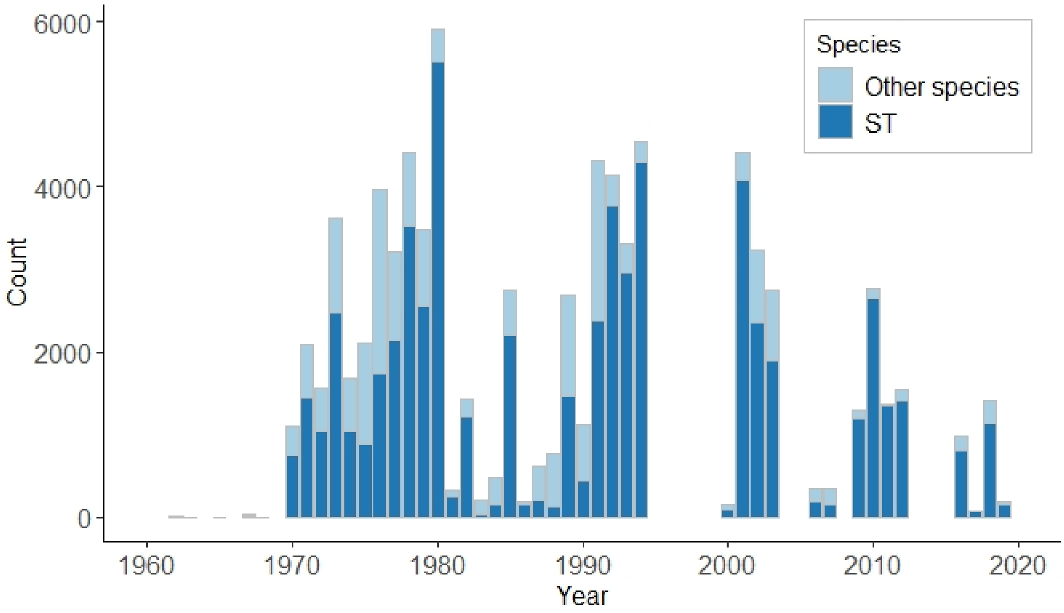


Figure **3.2**: Number of fish recorded in the long-term monitoring database by species and per year. *Other species stands for all species except from Salmo trutta (ST).*

For sampling purpose, different type of fishing exist and lead to different selective bias. The 3 main method used in the Kerguelen Islands are electro-, recreational or net fishing (**Box 3**). The *Table 3.2* summarises the number of fish caught by each fishing method. Electro-fishing represents 65% of the fish caught. We refer here to electro-fishing as fishing practised to evaluate fish density. The density evaluation has evolved over time (**Box 4**). This is the less selective methodology, because the totality of the sampling zone is covered. Selective fishing is the application of electro-fishing method used in a particular sampling objective (*e.g.* fish size selection) or to describe habitat. Recreational fishing was one of the first purpose of the salmonids' introduction. Nowadays recreational anglers voluntarily contribute to the acquisition of data (5%). Recreational and electro-fishing probably make up non-defined method in the database (18%). Finally, net, and lading net represent less than 1% of the sampled fish.

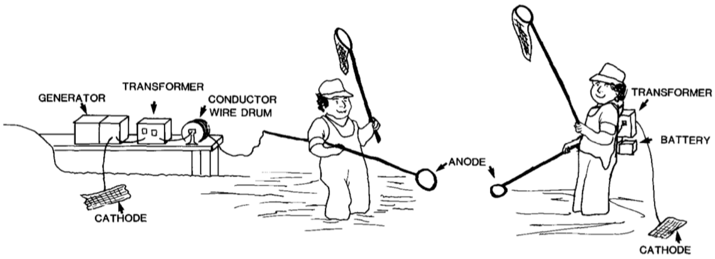
Until now, the studies of the salmonids in the Kerguelen Islands present a large variety of topics, from genetic to population levels. During the 90's, the main question was the characterization of salmonids colonization thanks to the reading of their scales. Beall and Davaine (1988) demonstrated the annual formation of scales annulus. With other collaborators, they worked on scale readings errors and the relationship between growth of fish and environmental factors (Beall, Davaine and Bazin, 1991). Later on, the studies focused on the genetic differentiation and colonization strategy (Ayllon et al., 2006; Launey et al., 2010), the use of otoliths to study life-history traits (Aymes et al., 2016), the reassessment of the carnivorous status of salmonids (Marandel et al., 2018) or growth of sea trout (Jarry et al., 2018).

Table 3.2: Number of samples (n) per species for each fishing method recorded in the long-term monitoring database.

The percent line gives the total represented by each fishing method in the sampling.

		Fishing method					
Species		Electro-fishing	Non defined method	Selective fishing	Recreational fishing	Net and lading net	
Non identified	864	401	323	101	39	0	
Coho salmon	3388	1578	1136	655	19	0	
Rainbow trout	8	0	0	0	8	0	
Chinook salmon	43	28	15	0	0	0	
Arctic char	362	24	40	231	19	48	
Brook trout	10215	5350	2552	1326	987	0	
Atlantic salmon	5833	4505	388	908	32	0	
Brown trout	60471	41232	9754	6222	3238	25	
		53118	14208	9443	4342	73	***n***
		65	18	12	5	1	*%*

Box 3: Main sampling method used to catch fish in the Kerguelen Islands



Equipment used for electro-fishing with stationary (left part) and mobile systems.

Electrofishing is a method developed in the 50's, which permitted careful trapping of fish. It uses alternative or continuous electric current to temporally stop the swimming activity of fish in the device electric field (Figure from Bohlin et al., 1989). This method is effective, simple, and relatively harmlessness for fish. All fish species and size category electro-fished are caught, even if the efficiency of the recapture is in general close to 0.3 (Peterson et al., 2004). **Net fishing** is a method using gill nets to capture fish. The net stays for a certain amount of time in a location. The probability to catch a fish depends on the probability of the fish to encounter the net and the probability of the fish to be retained in it (Hamley, 1975). The first component depends on the size of the fish because the swimming activities is thought to be linked with size of fish (Rudstam et al., 1984). This method is selective for the bigger individuals. **Recreational fishing** is a poplar human activity, practised either for leisure or for harvest. In both case, fish are caught and released in the natural environment, or taken based on species and size selective criterion (Cooke and Cowx, 2004; Lewin et al., 2006).

Box 4: Fish population density estimation

To evaluate fish population density, two main methods exist the one form Peterson and the one from De Lury. Peterson method consists in the electro-fishing of a river transect made two consecutive times. The first passage consists in catching m fish marked and released in the transect. The second passage consist in fishing n fish with r marked during the first passage and u fish not marked. This method allow the calculation of the fishing efficacy $\frac{r}{u+r}$ and the probable density of the population $\frac{m\times(u+r)}{r}$. This method was used in the Kerguelen Islands until the early 80's. De Lury method supposes that the fishing effort is constant over space and time. It does not need to release nor mark the fish caught during the first passage. This method has always been used in the Kerguelen Islands because it is advantageous in term of manipulation. Moreover, in the case of salmonids in river, small fish that are hardly marked represent a large part of the population (Laurent and Lamarque, 1975)

3.2 The brown trout in the database

More than 74% of the fish in the database are brown trout (60471 individuals) (*Table 3.3*). They represent on average 70% of the collected samples, scales, or otoliths sampling. Less than 3% of the fish in the database were sacrificed for otoliths studies. In the case of the brown trout, the sampling was done in 62 different locations in the Kerguelen Islands. The last fishing campaign was led from December 2018 until February 2019. For further information on the last sampling in the field, see **Appendix A.2**.

To characterize the life-history traits of fish and colonization dynamic of salmonids, fish sampling was mainly performed to collect calcified structure of fish (scales and otoliths). Scales were sampled in the optimal zone, located near the dorsal fin above the lateral line (Elliott and Chambers, 1996). Method of fishing, localization (rivers, coordinates) and date are recorded. Body-size (fork length in millimetre (mm)), weight in gram (g), and species are noted. The phenotype at capture is also defined when possible. As partially migratory species, resident and migrant brown trout differ by their phenotype. They are differentiated by morphological traits (*i.e.* length/weight relationship (Jonsson, 1985), silver-grey colouration (Quigley et al., 2006)). Additional information was taken if available, such as sex, or health state. Depending on the study, other samples are taken, some non-lethal such as fin sampling, some lethal such as otoliths or stomach content. Investigations were conducted according to the guiding principles for the use and care of laboratory animals and in compliance with French and European regulations on animal welfare (Décret 2001-464, 29 May 2001 and Directive 2010/63/EU, respectively).

Table 3.3: Number of fish, scales and otoliths recorded in the long-term monitoring database.

Two categories of species are in lines (All species and brown trout). The numbers in parenthesis correspond to the percentage of line category. The final line gives the percentage of Brown trout among the total sampled fish, scales and otoliths.

	Number of fish	Scales	Otoliths
All species	81184	36598 (45.1)	2235 (2.8)
Brown trout (ST)	60471	28968 (47.9)	1499 (2.5)
Percent of ST among other sampled fish	74.5	79.1	67.1

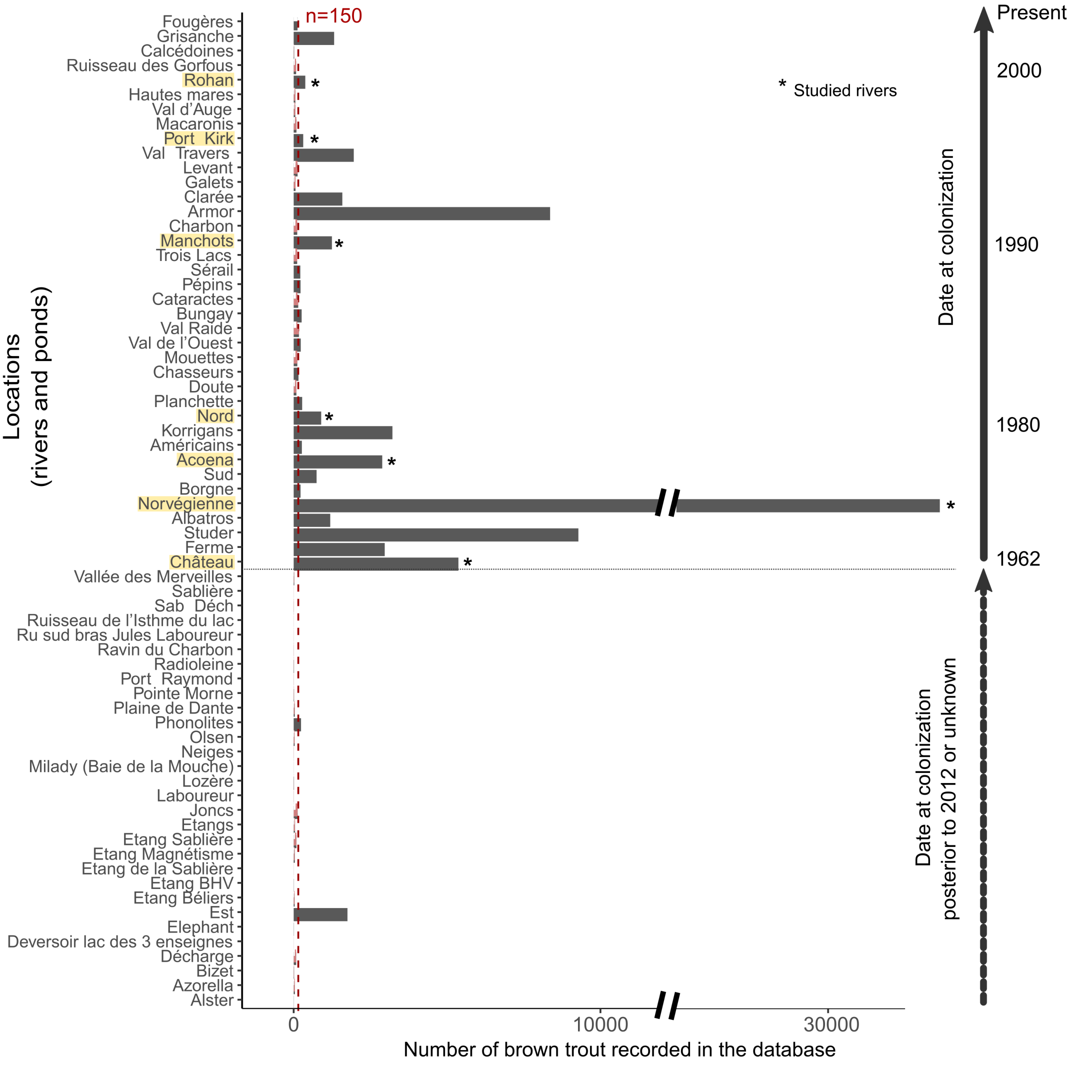


Figure **3.3**: Number of brown trout recorded in the database on each sites ordered by their date at colonization.

The abscissa scale is cut from 12000 to 25000 to facilitate the reading. The vertical dotted line represents the below limit of 150 fish. The 7 main rivers studied in this manuscript are highlighted (*).

As we want to study the evolution of traits, numerous fish should represent each population (river) and cohort. On the 68 locations recorded in the database (rivers and ponds), 34 locations were discarded because less than 150 fish were sampled (*Fig. 3.3*). Among the remaining location, we were only interested into rivers. Several criterion were used to select the most appropriate pseudo-replicated dataset in term of date at colonization, where date at colonization stands for the first reproduction observed. Two different categories of rivers are depicted, the one that were chosen for introduction purpose (hereafter referred as introduced) and the one that were naturally colonized by anadromous individual (hereafter referred as colonized). Rivers were selected more specifically to cover the largest possible time range from old to recent colonized/introduced rivers (*Fig. 3.4*): Rivers Château and Norvégienne in the 60's, Rivers Acœna and Nord in the 80's and Rivers Rohan and Port Kirk around 2000. An additional river colonized naturally during the 90's was added (River Manchots). On the 7 rivers selected (*Fig. 3.5*), 5 have more than a thousand samples and two have around 300 samples (*Fig. 3.3*). Sympatry only occurs in Rivers Château and Norvégienne and pure allopatry is observed in the 5 others.

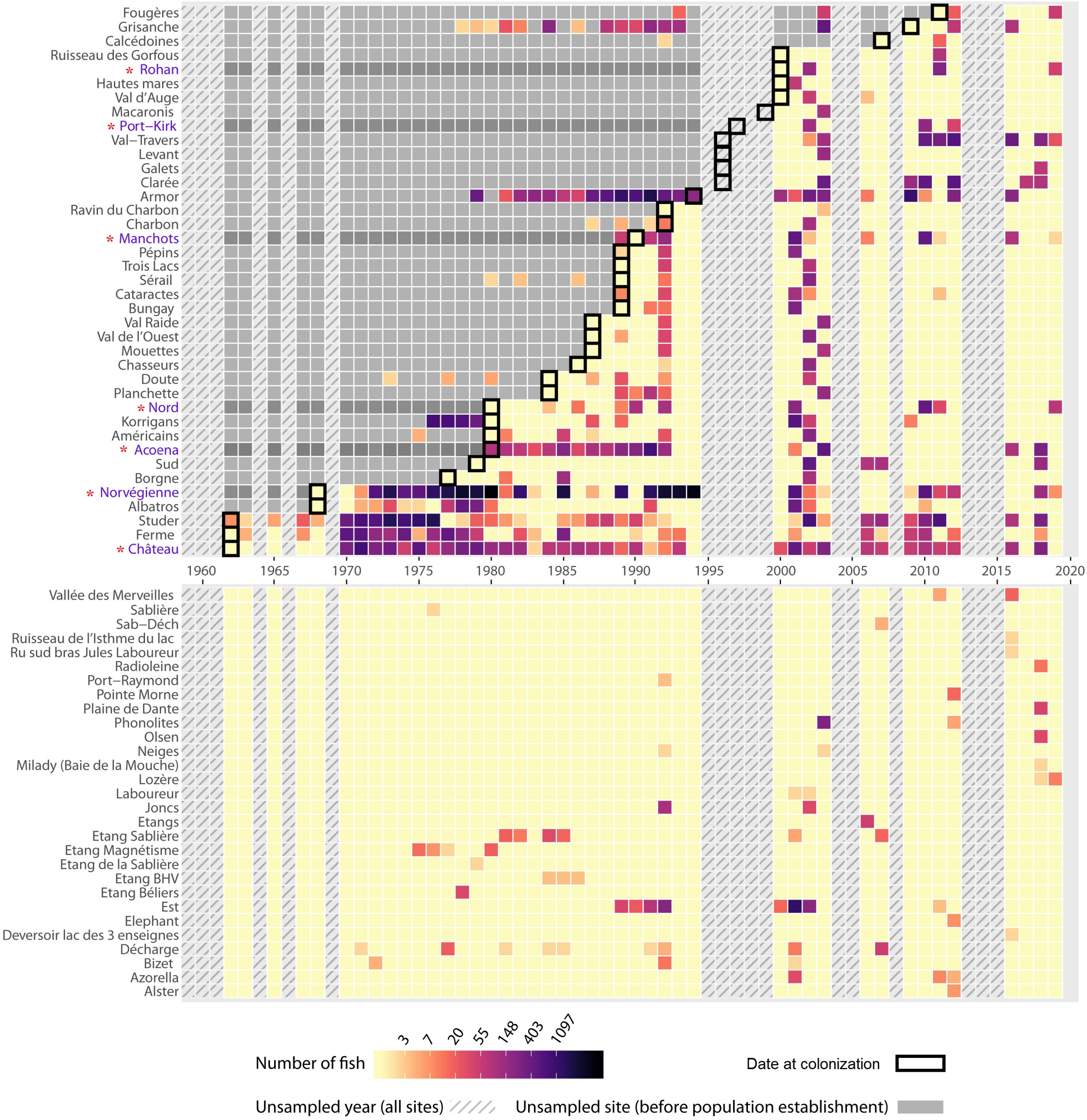


Figure **3.4**: Number of samples collected on each rivers of the Kerguelen Islands.

The dataset is ordered by date at colonization when known (above part of the figure). The establishment of the population is unknown for the rivers below the abscissa time. The information about establishment of population are recorded in Labonne et al. (2013). Some period over the long term monitoring have been unsampled an all site because no campaign was launched. The darkgrey lines correspond to the studied rivers in this manuscript.

There are 42112 samples on those 7 rivers, among which 16771 had their scales collected during the long-term monitoring (40%). The rivers selected and their features are described below. The date given in parenthesis is the first known reproduction event (date at colonization,). A summary is given in *Table. 3.4*.

River Château (1962) is a river where fish were introduced on purpose. From 1954 to 1958, French fish farming eggs were introduced, but the reproductive success of those attempts is uncertain. A successful translocation from fish originated from River Ferme, a river next to the base Port au Français, led to the first reproductive success in 1962. On River Château, 4141 fish are available. **River Norvégienne** (1968) is a river that was colonized naturally. The population was probably founded by anadromous fish from River Château because of the proximity of the two rivers estuary linked by the Baie Norvégienne. The large amount of caught fish on River Norvégienne is due to a capture-marked-recapture (CMR) experiment conducted at the beginning of the colonization. Numerous fish were marked with different method to understand the pattern of migration of smolts and anadromous individuals in the catchment. On the 8710 samples available in the dataset, 2752 fish were caught more than once (32%). Their size and age were defined each time they were captured. Because measurements were repeated on those fish at several capture date, individuals in that river were selected with caution. **River Acœna** (1983) is a river belonging to the category of the introduced river. In 1979, the river was deliberately stocked with fish of a wild population from Poland (River Slupia). On the 1413 available fish, a small fraction was given a phenotype before the 2000's. On those first 3 rivers, a decrease in the sampling is observed, especially on River Norvégienne congruent with the end of the CMR experiment. Although, a high proportion of fish was not given any phenotype at capture before the 80's (*Fig. 3.6*), either because it was impossible or because it is resident trout. Afterwards, and around the 2000's, monitoring was done by period of 3 years followed by 3 years of no campaign. All size classes are well represented in the sampling design of Rivers Acœna and Château, and there are less intermediate size on River Norvégienne (*Fig. 3.7*). **River Nord** (1986) is a river that was introduced on purpose. In 1981, the river was deliberately stocked with fry of fish acclimated to the Kerguelen Islands and originated from River Château. There are 581 fish available. **River Manchots** (1990) was naturally colonized by anadromous individuals probably because of the presence of a fresh water lagoon (Lagune du Doris) in the estuary of the river. This estuary is thought to be a sanctuary for individuals. The localization of the site in the middle of the eastern coast probably makes a refugee for fish migrating along a south-North pathway. The presence of a penguin colony and elephant seals are also thought to increase the productivity of the lagoon. There are 957 fish available. In the present work, the fish living in the lagoon were considered as resident trout based on microchemistry analyse results (**Appendix A.3**). **River Port-Kirk** (1997; with 224 fish) and **River Rohan** (2000; with 305 fish) are rivers that were colonized naturally. They are the western studied river and the latest reported as colonized, so the majority of the fish caught are resident individuals (*Figs. 3.6* and *3.7*).

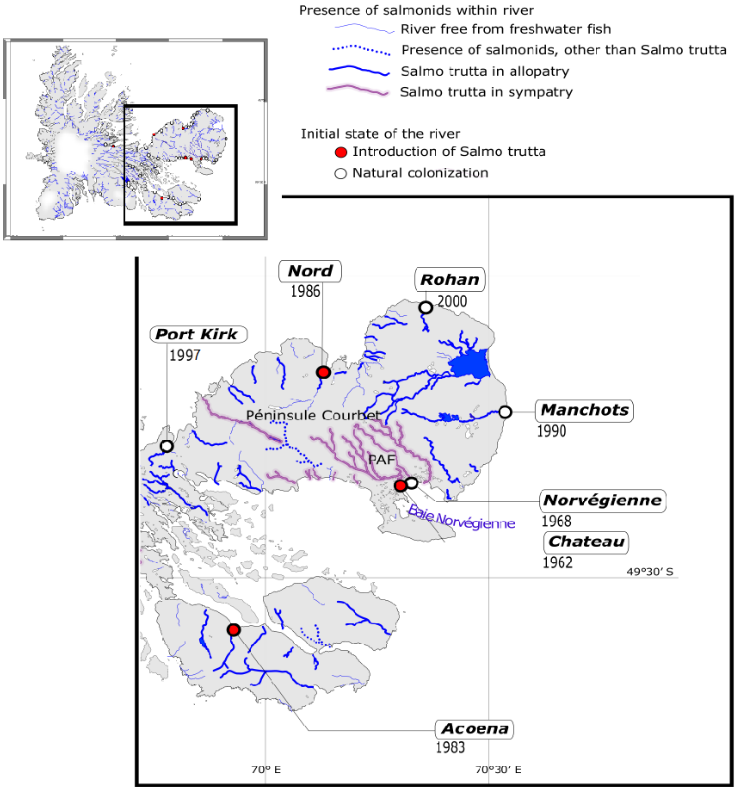


Figure **3.5**: Zoomed map of the studied rivers in the Kerguelen Islands.

Table 3.4: Description of the selected rivers, with the number of samples (n) collected on each sites, since the beginning of the monitoring.

Rivers	Acœna	Château	Manchots	Nord	Norvégienne	Port-Kirk	Rohan
Date of colonization	1983	1962	1990	1986	1968	1997	2000
Type of colonization	Human induced introduction	Human induced introduction	Natural colonization	Human induced introduction	Natural colonization	Natural colonization	Natural colonization
Origin	Poland (Slupia)	Bidarray	unknown	Château	Château	unknown	unknown
n	1413	4141	957	581	8710	224	305
Concurence state	allopatry	sympatry	allopatry	allopatry	sympatry	allopatry	allopatry
Length of main tributary (km)	9,7	22,2	19.8	11.3	16.7	3.9	3.6
Catchment area (km^2)	35	115	94.5	74	36.3	13	16.2
Estuary		Wide and protected oceanic bay (Baie Norvégienne)	Wide lagoon area (Lagune du Doris)		Wide and protected oceanic bay (Baie Norvégienne)		Short and dropping sheer into the ocean (Cap de Rohan)
Upstream lake			Grand Etang		None		Small lakes

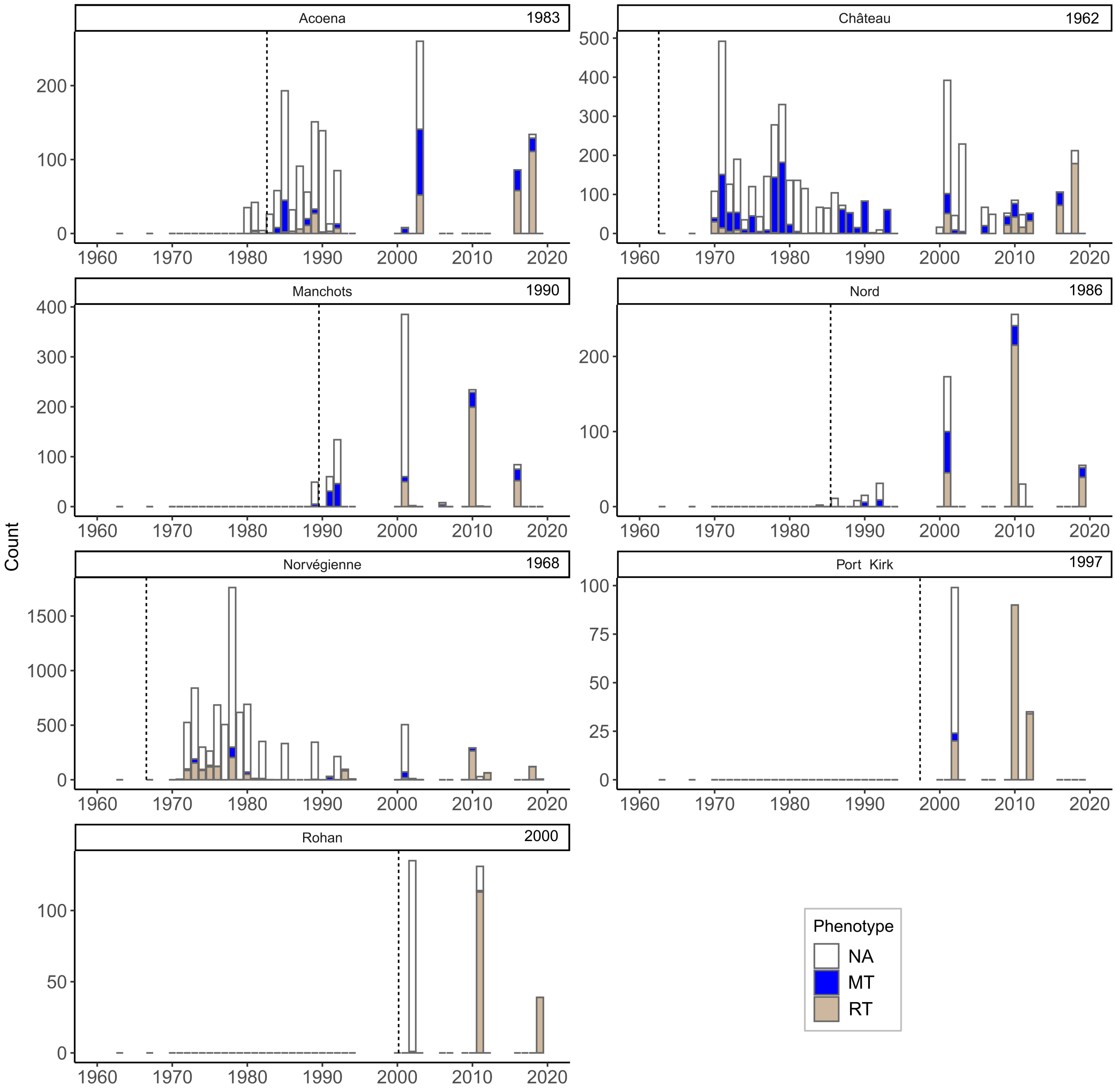


Figure **3.6**: Number of samples by phenotype at capture, year and river.

Phenotype at capture are grouped in three categories. NA stands for for unknown phenotype at capture. MT stands for migrant trout. RT stand for resident trout. Dotted lines represent the date at colonization.

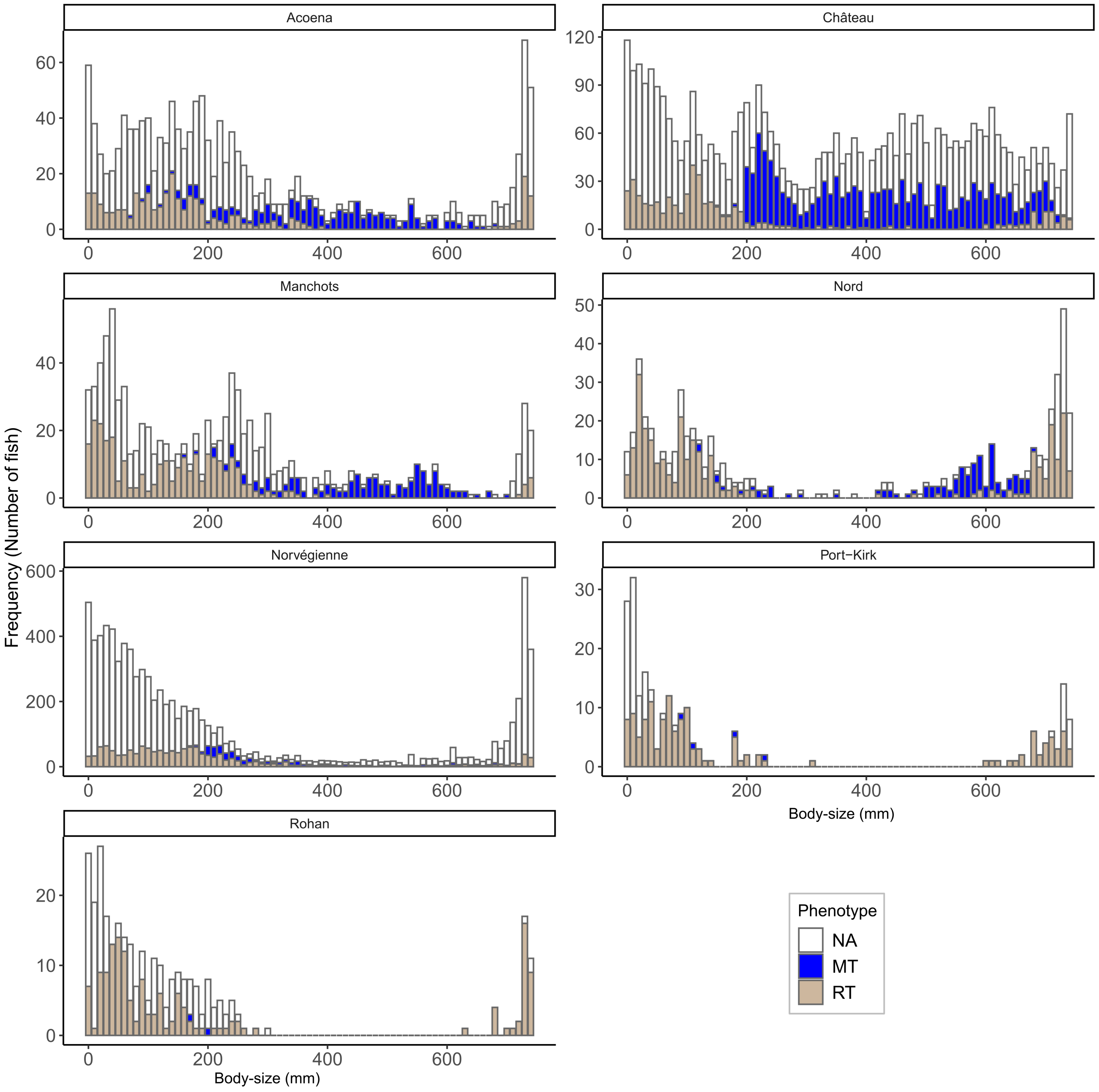


Figure **3.7**: Number of fish distributed per size (fork length (mm)) and phenotype in each studied river. *Phenotype at capture are grouped in three categories. NA stands for for unknown phenotype at capture. MT stands for migrant trout. RT stand for resident trout.*

3.3 How to select the fish in the database: description of the decision rule

To study the spatio-temporal variation of life-history traits taking data dispersal into account, we need to select fish in a spatio-temporally comparable framework. Along a temporal continuum ranging from 1962 until now, fish must be chosen in the same river (spatial effect) and the same cohort (temporal effect, where cohort is defined as groups of individuals born the same year). By doing so, we will have fish experiencing comparable environment of growth, as we expect density of population and temperature to change through time. To select fish within cohorts, we need to infer their probable age knowing their size. To do so, scales are often used to access the life-history traits, by counting the annuli deposited yearly in the structure (Beall and Davaine, 1988). Nevertheless, using scalimetry to empirically determine the individual age of more than 60 000 samples can be time-consuming. As already mentioned, the long-term monitoring in the Kerguelen Islands gives access to a huge dataset and the allocation of time to the scalimetry procedure does not allow studying all of them.

Another solution to infer the age of fish is to establish a relationship between the age and body size at capture based on aged fish. On the 28968 Brown trout in our dataset (measurement of fork length at capture and collection of scales) (see *Table 3.3*), 6775 fish have already been aged through other studies (23%) lead in the Kerguelen Islands. The already aged fish in the database belongs to 7 rivers, Rivers Acœna, Albatros, Château, Nord, Norvégienne, Studer, and Val-Travers, some common with our study and others. The relationship between age and body size at capture can be estimated from those samples. 22193 fish remain to be aged. According to the phenotype at capture, migrant are bigger than resident, and numerous fish were not attributed a phenotype when captured (*Figure 3.8*). The majority of the fish caught belongs to a size category inferior to 400 mm (*Fig. 3.8a*) but all the size classes are represented among the aged fish (*Fig. 3.8b*).

Nevertheless, the relationship between the age and body size is also thought to depend upon the phenotype at capture. The expected increase in body size depends upon conditions and availability of resources in the environment in which the fish is growing (Davaine and Beall, 1992). As the brown trout is a facultative anadromous species, we can expect resident to grow slower than migrant at least out of the reproductive period (when migrants are at sea). Even if pristine fresh water habitats in the Kerguelen Islands may allow good access to the resources, fish growth at sea is expected to be better (Beall, 1979; Jarry et al., 2018. The size classes distribution of phenotypes (*Figure 3.8*) is congruent with this hypothesis. The non-identified phenotype (NA) is mainly represented in the lowest size classes, nevertheless a non-negligible part of the samples belong to the highest size category (superior to 400 mm). In the database, the phenotype is described by 115 levels. The first selection rule was to homogenize the phenotype in 4 categories: resident trout (RT), migrant trout (MT), lake trout and non-identified (NA). As lake trout are not consistent enough in the sampling, we considered them as resident trout to reassign an age to the non-aged fish. The smolting individuals had size ranging from 94 to 667 mm. We decided to reassign smolting individuals to the category of migrant trout when their size was superior to 200 mm. If not, as for the remaining fish, the phenotype was non-identified. The number of fish (n) in each category is summarized in *Table 3.5*.

The objective of this part is to define a methodology aiming at redistributing an age to the fish that have not yet been aged through scalimetry. We alternatively chose a method called out-of-bag error, also called out-of-estimate. This method is used to measure the prediction error (PE), where PE (or also accuracy) is a measure of how close model predictions are to their true value on average (De'ath, 2007). Different techniques are used to evaluate models' performance, such as random forest, averaging, shrinkage, bagging or boosting trees. The principle of random forest is to bootstrap sub-sample of the data set to create training set to fit the model (multiple trees) with a random subset of predictors (Prasad et al., 2006). This step is repeated a high number of times. For our analyses, we used 20000 bootstraps. The training sample was used to reassign an age to the bootstrapped samples according to the decision rule. We tested for two decision rules to calculate a probability to belong to a discrete age knowing the size at capture.

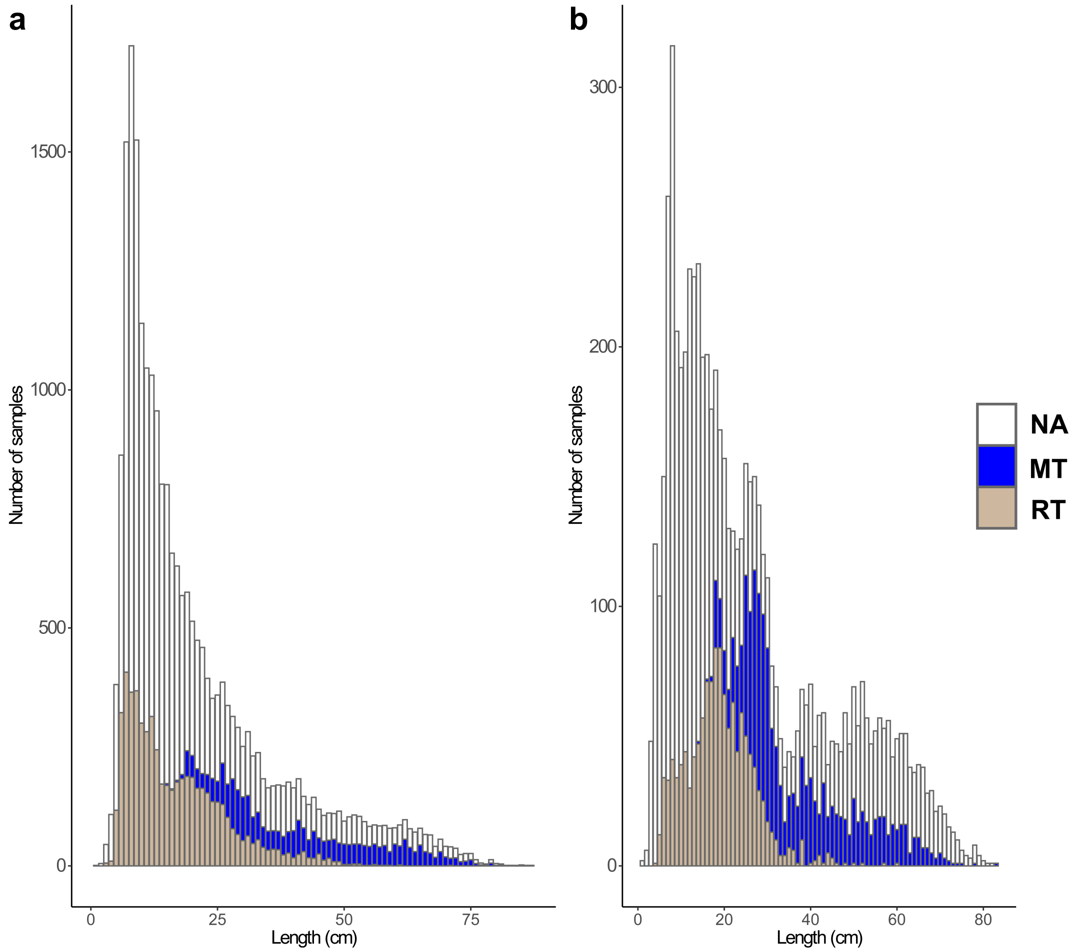


Figure **3.8**: Distribution of the number of fish in each size category at capture with **(a)** all the captured fish recorded in the database (28968 samples) and **(b)** the aged fish (6675 samples).

Phenotype at capture are grouped in three categories. NA stands for for unknown phenotype at capture. MT stands for migrant trout. RT stand for resident trout.

Table 3.5: Number of samples (n) available in each phenotype category.

Resident trout stands for all fresh water trout (i.e. fish caught in lakes or rivers). Details per locality are given in ***Appendix A.4***.

	Unknown phenotype at capture (NA)	Resident trout (RT)	Migrant trout (MT)
n	19458	6741	2769

The first decision rule was to use the known frequency distribution of age classes knowing the size of fish (*Fig. 3.9*). In the dataset, the samples range from 36 mm to 891 mm. We created matrices with lines corresponding to age ranging from 1 year to 14 years and columns corresponding to size classes that were arbitrarily cut each 5 mm from 30 to 900. Then 4 matrices were created, corresponding the phenotype at capture considered: all phenotypes, resident trout (RT), migrant trout (MT) and non-identified (NA) based on the previous shown distributions (see *Fig. 3.8*). On the *Figure 3.9b*, RT ranges from 2 to 10 years and have in general a size inferior to 500 mm whereas MT (*Fig. 3.9c* ranges from 2 to 12 years old and are bigger than 200 mm. For the NA, the 3 first year's classes are probably all represented by RT (freshwater parr or fry that may subsequently migrate to sea or not). It is harder to classify fish which age is superior to 4 because of the bimodal distribution, coming from that both RT and MT are mixed in the NA category.

The second decision rule was based upon the assumption that size at age are distributed as Gaussian distributions (*Fig. 3.10*). Gaussian mixture models are statistical models expressed as function of mixed densities to estimate the distribution of the variable of interests. Here we were searching for the distribution of size according to the age of fish (as many distributions as age categories). Clusters of size-age relationship were built using the function normalmixEM available in the R package mixtools (*ver. 1.1.0*, Benaglia et al., 2009).

Each of the two decision rules were tested for 4 relationship between size and age according to the phenotype at capture (all phenotypes, RT, MT, and NA). By bootstrapping, eight tables of probabilities of body size at age were built (2 methods with 4 phenotype categories). In each table, we chose to attribute an age to fish that had a certain threshold chance x to belong to a size-age distribution. We define x as the probability to belong to the size-age category. We tested for different values of x (50 to 90 percent) and calculated the error of age-attribution on the 6775 fish that were already aged. Those tables are used to reassign an age to each fish knowing their size and phenotype at capture. When the phenotype is known, the corresponding tables are used in each method. The two tables "All phenotype" are thus unused. By doing so, the probability of reassigning an age is known with its error. For both methods, we created two output error tables in reassignment with different threshold of x. We calculated the number of fish re-aged on the 6775, the percentage of fish not re-aged among those 6775 fish and applied the decision rule to the entire dataset (6775 aged plus 22193 not aged) to calculate the total percentage of fish that would not be aged. The final output error in age reassignment is given in *Table 3.6*. Reading the first column of this table will give this: Keeping a threshold probability (x) to belong to a size-age category at 50%, the error in giving an age reaches 27%. In that case, 4474 fish will be analysed. 34% of fish that were aged will not be re-aged and in total 25.7% will not be aged.

Higher the probability to belong to a certain size-age category in the sampling (x) lower the error of age reassignment and higher the percentage of fish that were not aged (either re-aged or aged in the total sampling). However, this also means a drastic reduction in the fish that were selected to be age in both methods (decrease in the number of fish aged according to the increase in the probability to redistribute an age). Using the first decision rule (frequency distribution) leads to less error in redistribution than the use of Gaussian mixture models. The Gaussian distributions does not perfectly fit and represent the real distribution of size-age relationship. While using the data frequency distributions, the error varies from 2.6% to 27% where the Gaussian distributions give an error comprised between 54.9% and 59.5%. According to these results, more fish are aged using the Gaussian mixture models at the expense of the error in age reassignment. According to the *Table 3.6*, on the 6775 fish that have already been aged,

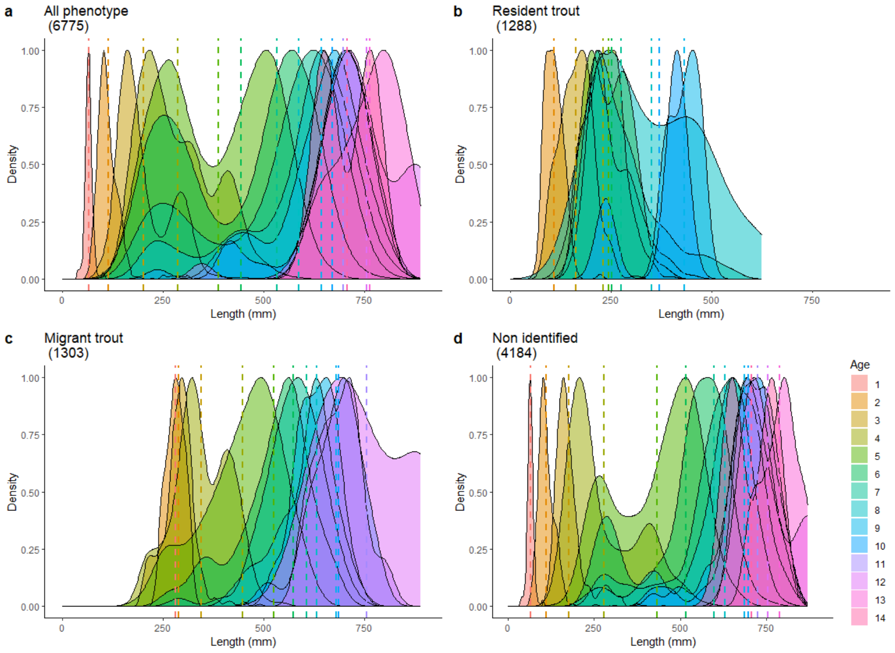


Figure **3.9**: Density distribution of the fish sizes by age classes based on the dataset frequency **(a)** all phenotype considered, **(b)** resident trout, **(c)** migrant trout and **(d)** non-identified phenotype.

All the fish used to create those graphs (6775) were aged and measured at capture. The number in parenthesis corresponds to the number of fish used to generate the distributions.

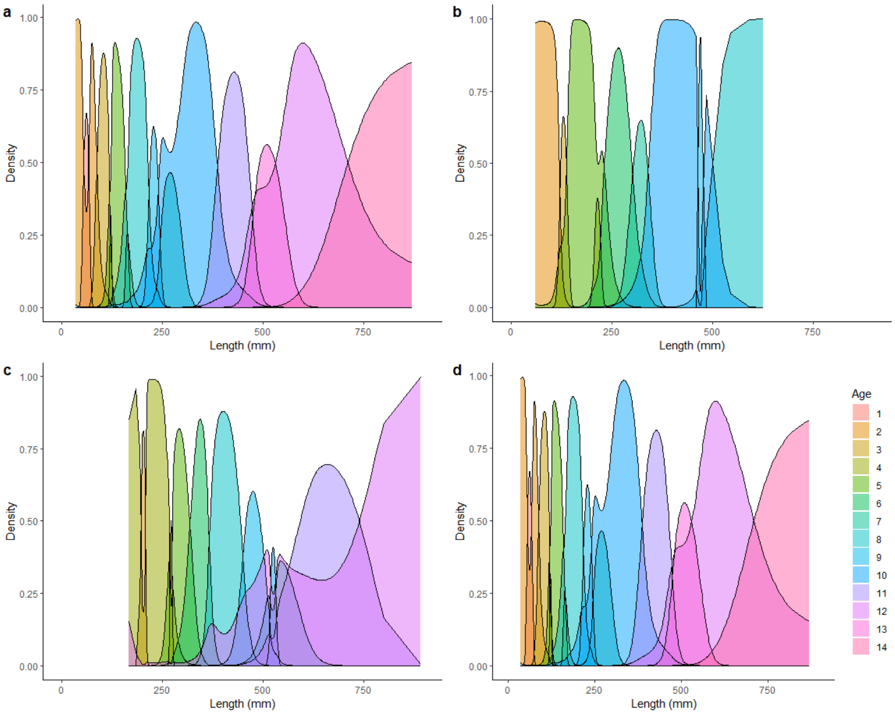


Figure **3.10**: Density distribution of the fish sizes by age classes obtained with the package mixtools **(a)** all phenotype considered, **(b)** resident trout, **(c)** migrant trout and **(d)** non-identified phenotype.

All the fish used to create those graphs (6775) were aged and measured at capture.

4474 are re-aged using the frequency distribution with a threshold probability x fixed at 50%. Using this criterion, there is 27% chance to redistribute a false age. Nevertheless, this criterion seems the less restrictive to redistribute an age to the 22193 fish that were not aged in the database. We can thus expect to age 16490 fish (because 25.7% will not be aged on the 22193 fish) among which 4452 might be wrongly reassigned in an age category. Finally, it seems that using the frequency distribution of body size at age is more powerful than the Gaussian mixture model to redistribute an age to the fish in the database with less error.

Table 3.6: Comparison of the two out of bag error in age reassignment considering two decision rules and different threshold probability.

Decision rule	Threshold probability to belong to a size-age category (x)	50%	60%	70%	80%	90%
Frequency distribution of age classes	Error in age reassignement (%)	27.0	21.2	13.3	6.3	2.6
	Number of fish aged	4474	3382	2165	1386	1019
	Non re-aged fish (%)	34.0	50.1	68.0	79.5	85.0
	Non aged fish (%)	25.7	40.8	57.9	70.1	76.0
Gaussian mixture models (normalmixEM)	Error in age reassignement (%)	59.5	57.8	55.4	59.3	54.9
	Number of fish aged	6544	5614	4698	3551	2602
	Non re-aged fish (%)	3.5	17.1	30.7	47.6	61.6
	Non aged fish (%)	3.8	16.3	28.5	49.4	60.8

Prior to scalimetry analyses, we chose the frequency distribution with a threshold probability fixed at 50% to primarily redistribute a cohort to the fish. Even if the fish might be wrongly redistributed with 27% or not aged with a 25.7% chance, this method helped us to choose fish belonging to the same cohort and rivers for the analysis in this manuscript (*Table 3.6*). After the application of the method on our dataset (described below), we obtained 47% that were not redistributed to a cohort (not-aged fish). This result is higher than our expectations (25.7%). First it is due to the strong body size at age distributions overlap. The variability of size within age class can be either explained by the inter-individual variability in growth or inter-river variability (environmental effect). Secondly, we added recently caught fish in the dataset, after the predictions have been run. Such not aged fish are present in all rivers of our dataset, and in all cohorts (after ageing). A higher proportion of not-aged fish are found among migrant trout (59%) and within age classes from 3 to 8 years old, which is congruent with the previous distribution figures. Among the fish that were aged, 48% (3036 samples) were wrongly redistributed (compared to the age given by the reader). The error of age redistribution increases as age increase. In general the attributed age overestimates by at least one year the real age of the fish (*Table 3.7*). The same pattern is observed in space (all rivers) and time (all cohorts).

There are 14851 samples available on the 7 main rivers we selected. Fish were aged and measured according to their location, phenotype at capture and cohort (year of birth). We primarily selected the fish that were attributed to an age-class based on the frequency distribution method. Because of the numerous uncertainties of scales reading (Bereiter-Hahn and Zylberberg, 1993; Kacem et al., 2013), we decided to select more fish and thus also selected fish that were not attributed to an age-class. Those fish were selected by their size and phenotype at capture manually (according to the expertise of *François Guéraud*). A total of 5713 samples for 4750 fish were analysed to study the evolution of life-history traits related to dispersal (*Fig. 3.11*). For each studied rivers, details of the samples distribution over time since colonization (t = 0 corresponds to the first reproductive event observed in the river, also denominated date at colonization (Labonne et al., 2013)) are given in *Fig. 3.12* and details by phenotype are given in *Fig. 3.13*. The oldest rivers colonized record the highest number of samples. Despite a few holes in the sample, it is quite homogeneous regarding our a priori selection. It can be noted, however, that very few migrant trout were captured in the most recently colonized rivers. The *Table 3.8* records the final sample by studied river among the total available samples.

Table 3.7: Comparison of age redistribution and real age given to the fish.

Error is the difference between the real cohort to which the fish belong and the predicted cohort. When the value is negative, it means that the age of the fish is overestimated compared to its real age. The numbers given in the table corresponds to the number of fish in each age class.

Age	1	2	3	4	5	6	7	8	9	10	11	13	14
Error													
-6	0	0	0	0	0	0	0	0	0	0	2	0	0
-5	0	0	0	0	0	0	0	1	4	1	0	0	0
-4	0	0	0	0	0	1	2	10	4	1	2	0	0
-3	0	0	0	0	0	15	39	12	5	1	1	0	0
-2	0	0	0	3	109	134	40	12	6	5	0	0	1
-1	0	23	95	297	282	155	14	13	7	2	2	1	1
0	42	392	425	441	213	25	11	11	1	3	1	0	0
1	5	16	49	54	9	2	3	2	5	0	0	0	0
2	1	1	0	0	1	3	3	6	0	0	0	0	0
3	0	0	0	0	0	1	2	2	1	0	0	0	0
4	0	0	0	0	0	2	0	0	0	0	0	0	0

Table 3.8: Final samples analysed by rivers and their equivalent in number of fish.

The final studied samples are given in numbers and in percent of the total available sample by river.

Rivers	Acœna	Château	Manchots	Nord	Norvégienne	Port-Kirk	Rohan	All rivers
Available sample in the database	1585	4039	1270	448	6551	224	430	14851
Final sampling	218 (14%)	2331 (58%)	518 (41%)	752 (60%)	1816 (28%)	104 (46%)	278 (65%)	5713 (38%)
Final number of fish	70	769	129	134	681	138	45	1966

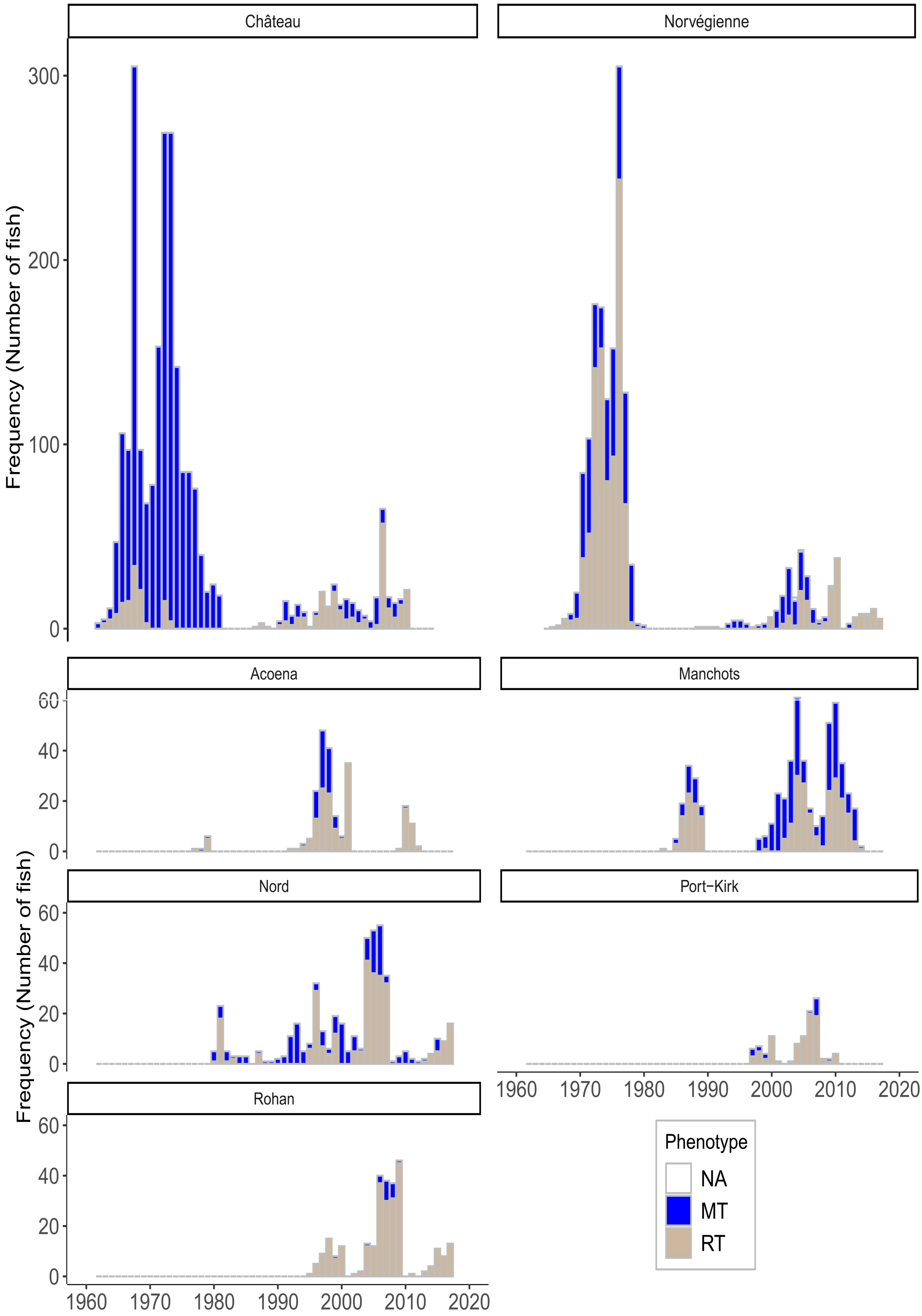


Figure 3.11: Distribution of the fish selected by rivers, cohorts and phenotype.

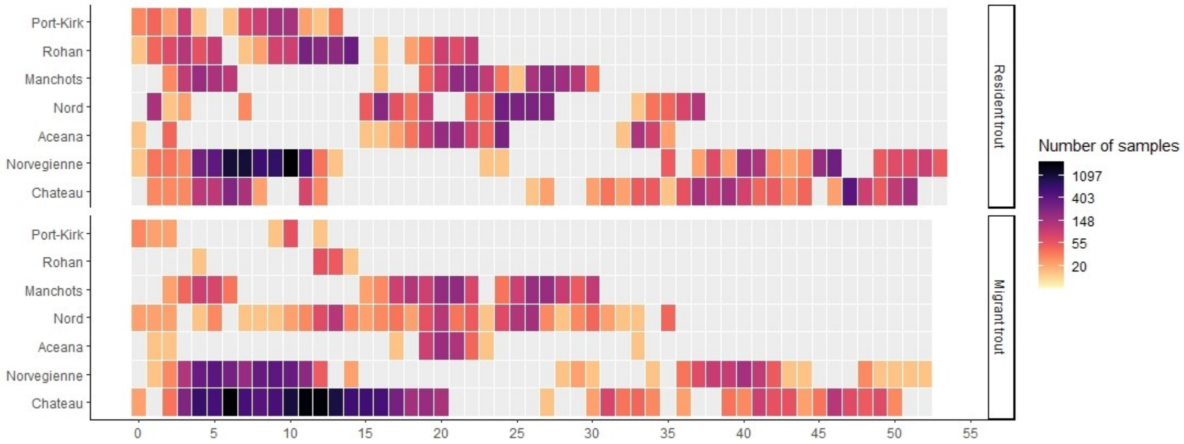


Figure **3.12**: Samples selected by rivers and phenotype, over the time since colonization.

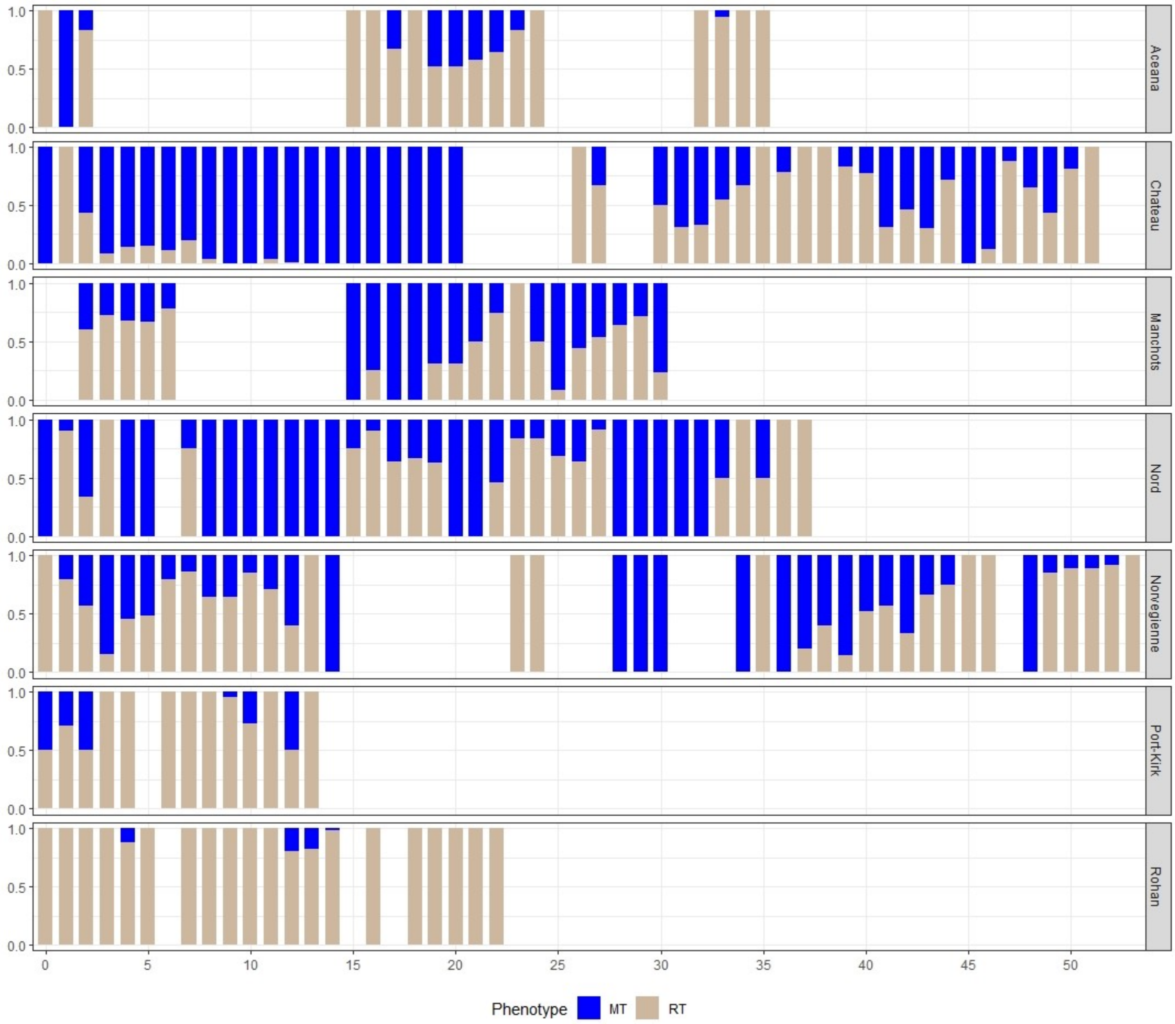


Figure **3.13**: Proportion of migrant and resident trout in each river selected over time since colonization.

3.4 Conclusion

Since 1962, 81184 fishing samples have been implemented in the database, where the brown trout represents 74% of the fish caught in 62 different locations. On the 60471 brown trout caught, 28968 fish had their scales sampled. 6675 fish had already been aged prior to the present work for this manuscript. Scales are very interesting tools to rebuilt life-history traits of fish, especially their age. Nevertheless, obtaining age-size information for the almost 22000 fish remaining to be aged in less than three years is not possible, because scalimetry is time consuming. Because of data dispersion and because we want to study spatio-temporal evolution of life-history traits, we need to select individual along a temporal continuum ranging from 1962 until now. Therefore, we selected rivers in a spatio-temporal comparable framework, *i.e.* fish were chosen in the same rivers (spatial) and the same cohort (temporal, where cohort is defined as groups of individuals born the same year). To select the fish studied in this manuscript, we used an out of bag methodology with random forest to redistribute an age to fish knowing their size at capture. By comparing two methods (frequency distribution versus Gaussian mixture models), we used the criterion of frequency distribution to reassign each fish in an age category based on their size at capture. A total of 5713 samples for 4750 fish were analysed to study the evolution of life-history traits related to dispersal. In the present work, the scalimetric samples were the main support for the advanced work. However, other complementary data were used, such as the catch sizes of the fish for which scales were not available. These data were used either for comparative purposes or to obtain additional information not available in our selected scaled data set. Some scalimetric data already studied in previous work were also used, either because they provided data from other systems or because they allowed us to expand the size of our dataset (*Table 3.9*). To the purpose of this manuscript, the scalimetric dataset described in this chapter and another dataset were used. The second dataset records all the individuals captured at the age of one and was used in a comparative purpose to study the evolution of body size (see *Chapter 5*).

Table 3.9: Description of the datasets used in each section of this manuscript.

	Scalimetric dataset	Fish captured at age 1
Composition	**4750 fish** **7 rivers** Fraser-Lee back-calculation model	**22160 fish** **44 rivers** Log-linear back-caluclation model
Advantages/Inconvenients	Pseudoreplicated dataset Selection a priori of a balanced dataset Selective mortality Several age-classes Selection a priori	Large dataset Absence of selective mortality Uneven catchment
Referenced chapters	* *Chapter 4.* Section 4.2. Hierarchical variance decomposition On 60 fish from 3 rivers. * *Chapter 5.* Section 5.2. The evolution of freshwater growth All dataset * *Chapter 5.* Section 5.3. The evolution of body size (D2) All dataset * *Chapter 6.* Section 6.2. Towards the evolution of the threshold size at migration? On 4044 fish from 5 rivers.	* *Chapter 5.* Section 5.3. The evolution of body size (D1) 19974 fish from 12 rivers

4 The use of scales to reconstruct life histories

4.1 The general use of calcified structures

To reconstruct life histories of organisms, scientists have searched for structures able to record variations in the individual and environmental conditions, at short or long-time scales. Calcified structures have been widely used to that purpose, because of the periodic aggregation of a carbonate matrix. The periodicity of the aggregation is synchronous with the growth of organisms, and the deposition of the matrix varies according to the studied structure, from daily to annual deposition. In fishes, calcified structures are scales, otoliths and bones. Scales are external calcified structures present in the fish skeleton (*Fig. 4.1 A*). Their principal role is the protection of the organism. They are mainly made from collagen and are more or less mineralized depending on the species. There are different types of scales (Goodrich, 1907). Brown trout scales are from cycloid type, the oldest form of elasmoid scales. Elasmoid scales are thin, flexible, transparent imbricated and lamellar (Ombredane and Baglinière, 1992) (*Fig. 4.1 B1*). Otoliths are calcified structures made out of successive concentric layers of proteins and calcium carbonate located in the inner ear (*Fig.4.1 A and C1*). There are three pairs of otoliths named *Sagitta*, *Lapillus* and *Astericus*. In most species, the sagitta is the biggest otolith explaining why it is the most used (*Fig. 4.1 C2*). They are implicated in the mechanic reception, acting as transducers of sound and movements. Bones (in the large sense and definition) are present in osteichtyans and their structure is like the one of Mammals. Cartilaginous chondrichtyan fishes do not possess bones (Panfili et al., 2002).

The study of scales is widely used in ichthyology since its introduction by Hoffbauer about 1898. The sampling of scales is not costly nor invasive and does not necessitate killing the fish. Multiple sampling of the same fish is possible; thus scales are useful to validate observations made with capture-mark-recapture Method (CMR). Their use has been amplified because they are easy to collect and store, which is interesting in the case of long-term monitoring to create huge collections. Most scales are easy to prepare and analyse in laboratories. The interpretation of scales readings can be used for many purposes such as species classification (Goodrich, 1907; Ombredane, Tanguy et al., 1992), and age, growth or even environmental determination (*Fig. 4.1 B2*). Since annulus formation and seasonal patterns have been demonstrated in numerous species (Fabre and Saint-Paul, 1998; Machias et al., 2002), the use of scales to determine the age of fish has become a standard (*e.g. Alosa alosa* (Mennesson-Boisneau and Baglinière, n.d.), *Sargochromis codringtonii* (Moyo and Fernando, 2000), *Salmo trutta* (Rifflart et al., 2006)). The relationship between calcified structures and somatic growth (Thomas et al., 2019) justifies the use of scales to determine individual growth. In many cases, readings are made on scales, and scalimetric measurements are converted into somatic body size at age using back-calculation (Pompei et al., 2011) (*Fig. 4.1 B3*).

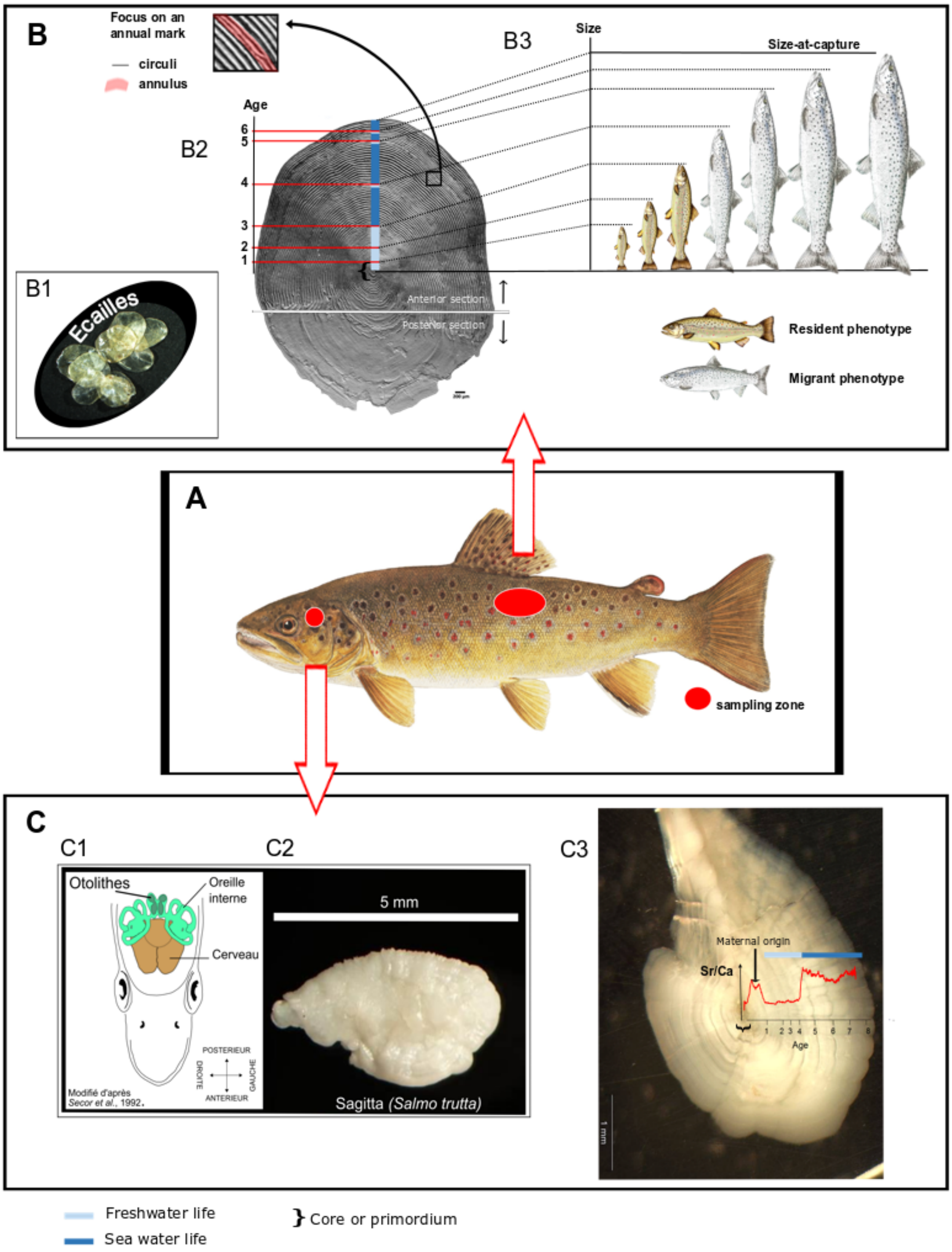


Figure **4.1**: The location (A) of the two principal calcified structures to rebuild life histories: scales (B) and otolithes (C). B1. Microscopic view of scales. B2. The determination of age and environment of growth by reading scales. B3. The correlation between scalimetric and somatic growth of fish. C1. The localization of the otoliths within the head of fish. C2. The external structure of a sagitta. C3. The internal structure of a sagitta (after preparation), and its use to determine age, maternal origin, and migration (LAICPMS microchemistry determination).

This figure consists of original images taken in the schlerochronology laboratory, and modified to illustrate points of interest.

Scales are also individual mineral storage. Some species may store more than 20% of their calcium content in their scales. Thanks to the development of microchemistry analytical technologies such as the Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS), the content of any solid samples (elements and isotopes) can be analysed (Adey et al., 2009; Elsdon and Gillanders, 2005). The analyses of scales or otoliths isotopic contents (Wainright et al., 1993) can give information on the maternal migratory status, the migratory status of the fish itself (Bagenal et al., 1973; Campbell et al., 2015) or on food webs (*Fig. 4.1 C3*).

There are also disadvantages to scales readings. First, scales are not present in all fish species. For example, there are no scales in lampreys or sturgeons. In that case, there is no other choice than using other calcified structures or methods to rebuild life histories. When scales are present, only fish with ctenoid or cycloid scales enable readings. In addition, the accuracy of age determination is often only proven for younger individuals (Gunn et al., 2008; Hining et al., 2000), older fish suffering more from event prone to regenerating scales, or false annuli formation (Bagliniere et al., 2020; Ibáñez et al., 2008). Almost all teleost fish lose their scales during their life, either because of environmental conditions or relatively to specific habits (*e.g.* sexual maturity, holes burrowing). In that case, scales are immediately replaced by regenerating ones, that do not contain early life-history information anymore. This phenomenon increases with age (*Fig. 4.2 A,B and C*). False-checks formation on scales are growth checks with patterns of circuli spacing that suggests an annual mark (annuli). Their formation on scales is caused by stressing external factors such as changes in temperature, manipulation of fish (*e.g.* CMR by the deposition of a mark or tag) or important changes in diet. The formation of multiple false checks is particularly problematic to determine age accurately by simply counting annual marks. Because scales are mineral storage, they are also prone to resorption (Kacem et al., 2013). The cause of resorption is the osteoclastic activity during an individual event that requires energy (*e.g.* sexual maturation, migration, reproductive event). The resorption of scales results in a more or less highly deformed shape of the scales that can be regenerated afterwards (*Fig. 4.2 D*). The resorption during reproduction is useful to characterize spawning marks. In all the cases, either because scales reading is not possible or is subject to life-history determination errors, other calcified structures can be used. The otoliths are good tools to determine age, growth and other environmental variables of the fish life (Gillanders et al., 2015). But other calcified structures may be used to rebuilt life-history traits. The information obtained can then be compared and allow for a finer analysis of the observed patterns (Burnet, 1969; Casselman, 1990; Erickson, 1983). Moreover, not all life-history traits can be rebuilt using a single calcified piece, sometimes justifying the use of multiple structures (Campbell et al., 2015; Hining et al., 2000).

The use of fish scales to determine their life-history traits is common (Ombredane and Baglinière, 1992). However, the diversity of fish species and their scales does not make a commonly applicable methodology possible. Knowledge according to the studied species is prerequisite to determine the most appropriate methodology to be implemented. Thus, many general or species-centred books exist and give the basic keys to reading calcified pieces (Elliott and Chambers, 1996). Multiple readings (either several scales or several readers) are often required to ensure accuracy (Haraldstad et al., 2016). The number of scales analyzed after preparation can vary from 3 to 8 depending on the species (Baglinière et al., 1992) or even within species. The possible loss and regeneration of scales explains why a bigger number of scales are collected to be analyzed (Bereiter-Hahn and Zylberberg, 1993). As scalimetry has become a standard, it is quite common reading *"age has been determined by scalimetry"* in many articles.

But underneath this sentence lies a diversity of methodologies that are more or less precise or accurate in the determination of life-history traits. What has to be remembered is that “scales are just estimates” (Borgenson et al., 2014). Therefore, numerous questions still remain: ***How many scales to sample? How many to read for age determination and for growth estimates?***

Figure **4.2**: Example of different regeneration degree of trout scales (A-B-C) and resorption (D), Adapted from Bagliniere et al., 2020.

4.2 Hierarchical variance decomposition of fish scale growth and age to investigate the relative contributions of readers and scales

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Summary. Taking measurement error into account in a biological model may be of particular interest depending on the context in which the measurements are to be used. Repeatability in growth and age estimation at the individual level has a significant effect on estimating parameters at the population level. In this study we determined to what extent inter-scale (intra-individual) and inter-reader effects were negligible compared with inter-individual variability, providing a rationale for selecting an appropriate sampling strategy.

Abstract. Correct estimation of inter-individual variability is of primary importance in models aiming to quantify population dynamics. In a fisheries context, individual information such as age and growth is often extracted using scales; however, the rationale for using a given scalimetric method (i.e. number of scales per individual and number of readers) is rarely discussed, but different sources of variance may affect the results. As a case study, we used scale growth and age of brown trout (*Salmo trutta*) caught in the Kerguelen Islands. Based on a nested design (readings of four scales per fish by two independent readers), we decomposed variance in growth and age according to fish (inter-individual level), scales (intra-individual level) and readers by using repeatability analysis. The results highlight that most variation is attributable to fish. Readers and scales contribute little to inter-individual variance, suggesting that inference was insensitive to intra-organism biological variation. Using additional scales or readers was an inefficient use of sampling resources. We argue that variance decomposition should be widely used for studies aimed at modelling natural variability in life-history traits. This would improve our knowledge of the implications of measurement error, helping rationalise and define appropriate sampling strategies.

Additional keywords: introduced species, measurement errors, sampling strategy, scalimetry.

Introduction

Understanding patterns of natural variability is a major issue in evolutionary ecology, because variability can be described at the taxonomic, community, population, individual and evolutionary levels (Landres et al., 1999). However, populations have long been studied without concern for individual variability or inter-relationships within populations (Łomnicki, 1999). With the rise of the holistic approach, most recent studies confound the organisational components of ecosystems from the individual level to the ecosystem organisational level. In particular, individuals in a population obviously differ in terms of behaviour, habitat use, reproduction or migratory strategy to optimise their fitness (Fromentin et al., 2009; Roff, 1996).

Inter-individual variability has attracted much attention during the past two decades because it could have severe consequences on the estimation of population dynamics. Thus, identifying sources of variability underlying inter-individual differences is important for developing relevant sampling designs aimed at answering evolutionary questions with appropriate statistical power (Johnson et al., 2014). In this field, significant developments have been based largely on the use of mixed and individual-based modelling that explicitly considers individuals as variable entities (Baayen et al., 2008; Thorson and Minto, 2015). As an example, in fish biology, as with many other taxa, individual growth is modelled using the von Bertalanffy growth function (vBGF). Growth parameters are highly dependent upon an accurate description of the individual age–length relationship (Hatch and Jiao, 2016). Moreover, estimates of individual growth in population models can be significantly different while accounting for or failing to account for inter-individual variability, leading to evolutionary misinterpretations or to inappropriate conservation decisions (Harris et al., 2018; Shelton and Mangel, 2012; Vincenzi, Mangel et al., 2014).

Teleost scales are an important and widely used tool in ichthyological studies (Goodrich, 1907; Panfili et al., 2002). Among other applications, scales provide access to life-history traits, such as age (Erickson, 1983), growth (Kipling, 1962; Ottaway, 1978) and migration (Bagenal et al., 1973). Readings of the calcified structure can provide accurate estimates of growth and age at both daily and yearly scales. This offer a basis for recording growth patterns from the individual to the population level (Casselman, 1990; Schreck and Moyle, 1990). Over time, researchers have come to accept that analysing several scales from the same individual provides more reliable information (Panfili et al., 2002). On a theoretical basis, the number of scales required to determine growth and age depends on the species studied (Chilton and Beamish, 1982), but the reason for using a given number of scales is rarely mentioned explicitly in the literature. In addition, inconsistency appears among studies dealing with the same fish species for the same purpose. Even if the accuracy of age data has been demonstrated in the published papers initially (Dahl, 1907; Ward Cutler, 1918; through mark–recapture datasets), Beamish and McFarlane (1983) pointed out that only a few consecutive studies have re-examined the methodology of those initial studies. Campana (2001) and Spurgeon et al. (2015) concluded that over the past 30 years the number of age validation studies has increased; however, there are still some deficiencies in integrating variability in models or in justifying the selected methods. Given the prominent importance of individual variation, the number of scales used for recording relevant individual life history (age, growth, migration) is a matter of interest. Setting up a sampling design with the minimum number of scales required is, indeed, a reasonable shortcut to avoid redundancy and a waste of resources. Variability in growth and age among individuals can be assessed by means of repeatability (characterised as the degree of agreement among measurements). By delineating annuli (yearly rings deposited during winter) and measuring the associated inter-annuli spacing, one can estimate an individual's growth trajectory and migratory status (Elliott and Chambers, 1996); however, measurements may vary across readers and scales. Establishing measurement repeatability is important in order to disentangle methodological from biological variance and to increase reliability in the study of evolutionary patterns.

To investigate to what extent biological variability in scale growth and age arises from either individual variation or methodological variation, the brown trout was used as a case study. Variation in scale growth and age was decomposed in an explicit nested quantitative manner (*i.e.* extracting the respective contribution of readers, scales, and individuals). Decomposition of variance is necessary to assess the sensitivity of growth and ageing measurements to realistic levels of scale or reader variability and to efficiently reallocate laboratory time to ecological issues.

Material and methods

Species and study area

The brown trout is a facultative anadromous salmonid species (Acolas et al., 2012; Dodson et al., 2013), with some individuals spending their entire life cycle in fresh water (resident fish), whereas others migrate to sea (anadromous fish). Among other salmonids, brown trout was successfully introduced into a dozen rivers in the subantarctic Kerguelen Islands between 1955 and 1979. This archipelago, located in the Southern Ocean (49°S, 70°E), was previously a fish-free landscape. The complete history of salmonid introduction to the islands is recounted in Lecomte et al. (2013). Since the introduction of fish to the Kerguelen Islands, long-term monitoring has been implemented for a better understanding of the causes and processes of colonisation (Labonne et al., 2013).

To test for the robustness of observations of the growth and age of captured brown trout, three rivers with contrasting environments were selected, namely the Rivers Norvégienne, Manchots and Rohan (*Fig. 4.3*), hereafter named Norvésgienne, Manchots and Rohan respectively. The main characteristics of the rivers are described in *Table 4.1*. Electro- and net fishing were conducted between 2010 and 2016. Because brown trout is a migratory species, resident and migrant (anadromous) fish (hereafter referred to as 'phenotype') were primarily identified based on morphological criteria: length–weight relationship (Jonsson, 1985) and colouration (Quigley et al., 2006). A total of 60 brown trout were analysed, with 20 individuals per site in a calibrated resident: migrant fish ratio of 75% residents : 25% migrants for Rohan and 55 : 45% for the two other rivers (*Table 4.2*). The fork length (FL) of the fish at capture ranged from 88 to 770 mm (mean ± s.d. = 333.2 ± 183.2 mm).

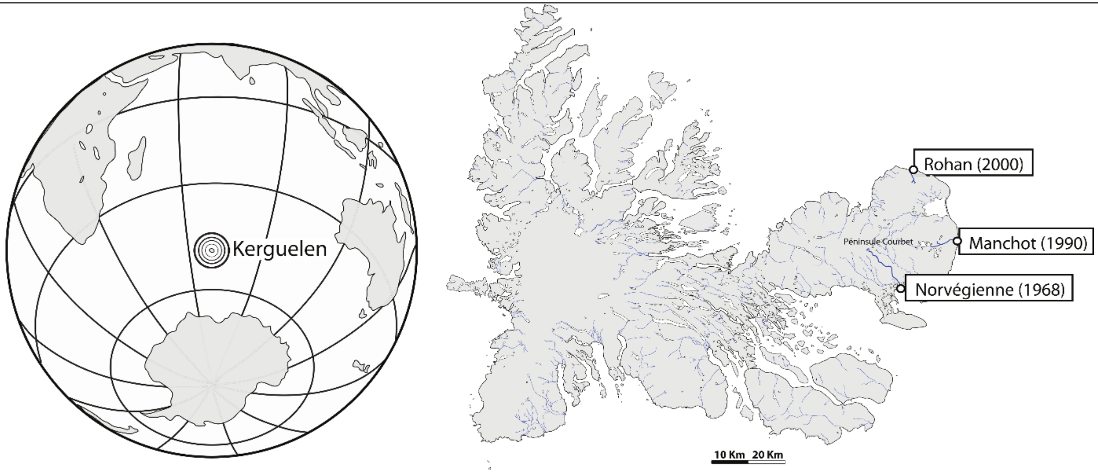

Figure **4.3**: Locations of the studied rivers in the Kerguelen Islands. The location of the rivers are shown on the right, with names and year of colonization by salmonids.

Data collection

Because the scales collected could be damaged and thus rendered useless by regeneration (Borgenson et al., 2014) and resorption (Kacem et al., 2013), numerous scales from each fish were removed from the optimal zone, specifically the second rank, below the dorsal fin and above the lateral line (Elliott and Chambers, 1996). For each fish, four scales that were not regenerated nor resorbed were selected and investigated (Bereiter-Hahn and Zylberberg, 1993). Selected scales were mounted and photographed (original scale in micrometres (μm)) under transmitted light using a stereomicroscope (Olympus SZX-16) and attached camera (Olympus DP72). Photographs were processed and saved using CellSens Entry microimaging software. Ageing and measurements were done by two readers (F. Guéraud and L. Aulus-Giacosa) with different degrees of expertise (2 *vs.* 10 years' experience) using ImageJ software (*ver.* 1.51u, National Institute of Health, see https://imagej.net/Downloads; Abràmoff et al., 2004) on a total of 240 scales in a double-blind and independent manner.

Migrant fish were distinguished from resident fish because the growth rate of brown trout in fresh water is generally less than the growth rate recorded at sea (Elliott and Chambers, 1996; Jarry et al., 2018). Because scale growth is used as a proxy for somatic growth, an increase in the intercirculi spacing on scales is a good proximate indicator of migration. This criterion was used for migrant fish to determine the size of scales at migration (measured from the core to the circulus corresponding to migration) and age at migration (counts of annuli until the intercirculi spacing increases).

Age was determined by counting the number of annuli on a scale (Borgenson et al., 2014) and total age (TA) was recorded. Freshwater age (FA) corresponds to the number of years spent in fresh water. For migrant fish, FA was determined by counting the number of annuli before marine migration using the criterion of intercirculi spacing. For resident fish, FA was equal to TA.

Scale growth (interannuli spacing (μm)) was measured along the main longitudinal axis from the core to the total radius (TR). The freshwater radius (FR) corresponds to freshwater growth. For migrant fish, FR was measured on a scale from the core until the circulus before migration according to the criterion of intercirculi spacing. For resident fish, FR was equal to TR. The mean (± s.d.) position of the annuli for freshwater growth are given in *Table 4.3*. Further details on the mean position and mean freshwater growth by phenotype are given in *Fig. B.1*, available as Supplementary material to this paper (**Appendix B.1**).

Table 4.1: Catchment details for Rivers Rohan, Manchots and Norvégienne.

The date of colonisation for each of the rivers is given as year. Additional descriptions of the estuary and proximity to first neighbouring river are provided.

River	Year of colonisation	Length of main tributary (km)	Catchment area (km^2)	Estuary	Upstream lake
Manchots	1990	19.8	94.5	Wide lagoon area (Lagune du Doris)	Grand Etang
Norvégienne	1968	16.7	36.3	Wide and protected oceanic bay (Baie Norvégienne)	None
Rohan	2000	3.6	16.2	Short and dropping sheer into the ocean (Cap de Rohan)	Small lakes

Table 4.2: Details of fish sampled for Rivers Rohan, Manchots and Norvégienne.

Characteristics are given by phenotype (migrant or resident) and river. Unless indicated otherwise, data are given as the mean ± s.d.

		Rohan	Manchots	Norvégienne
Migrant	Number of fish studied	5	9	9
	Size at capture (mm)	185.9 ± 38.3	509.5 ± 149.5	533.1 ± 128.7
	Age at capture (years)	3 ± 1	6 ± 2	6 ± 1
Resident	Number of fish studied	15	11	11
	Size at capture (mm)	200.7 ± 71.2	277.4 ± 69.2	214.7 ± 105.9
	Age at capture (years)	3 ± 2	5 ± 1	4 ± 2

Table 4.3: Mean position of annuli recorded on scales categorised by age at capture.

Annuli (years)	Mean (±s.d.) annuli position (μm) for		
	All fish	Fish caught at age (±3 months)	Fish caught older
1	218.7 ± 44.1	221.21 ± 40.57	216.19 ± 47.67
2	582.92 ± 129.36	673.26 ± 148.15	492.58 ± 110.57
3	831.67 ± 220.25	903.61 ± 259.48	759.74 ± 181.02
4	1063.20 ± 244.07	1128.65 ± 220.43	997.76 ± 267.71
5	1231.87 ± 259.47	1329.01 ± 294.64	1134.73 ± 234.30
6	1324.47 ± 268.79	1371.33 ± 350.89	1277.6 ± 186.7
7	1428.60 ± 203.94	1374.35 ± 227.12	1482.86 ± 180.76
8	1657.35 ± 104.41	1657.35 ± 104.41	

Hierarchical decomposition of variance

Variance was decomposed hierarchically in a nested and crossed manner, namely fish–reader–scale (*Fig. 4.4*) to determine which levels account for the variance in growth and age. Sixty fish were sampled from three rivers (Population) with samples taken from two phenotypes (Phenotype). For each fish (Fish), two readers (F. Guéraud and L. Aulus-Giacosa) (Reader) made independent readings on four selected scales (Scale) in a double-blind manner (*i.e.* two readers independently read each scale; this could be done on several scales for each fish).

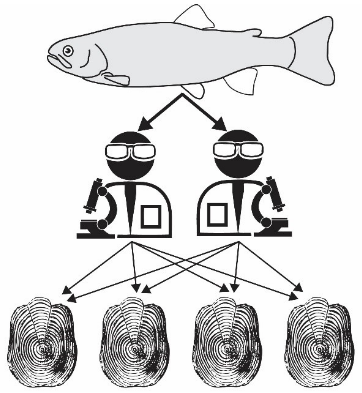

Figure **4.4**: Schematic drawing of the hierarchically crossed design of the study Fish-Reader-Scale.

To decompose the variance, two response variables were examined through measurements of repeatability (r). The repeatability of scale measurements (an approximation of somatic growth) and age estimates was investigated. Repeatability ranges from 0 to 1 and expresses the proportion of variation explained by the considered level (Bell et al., 2009; Wolak et al., 2011). For each variable, the value taken by r is the proportion of variance explained by the variable and reflects its contribution to overall variance. To estimate repeatability, we used the newly developed method from Stoffel et al. (2017) as implemented in the *rptR* R package (*ver.* 0.9.21 in R, *ver.* 3.4.4). This package fits mixed-effects models by parametric bootstrapping (two Monte Carlo simulation steps) to quantify the uncertainty of repeatability. In our case, we simulated models with 1000 parametric bootstraps and tested the null hypothesis using a likelihood ratio test.

Population and Phenotype were both added as fixed effects in the variance decomposition. Fish, Reader and Scale were considered random variables to explain the variance of scale growth and age. Because growth is sharply contrasted between marine and freshwater habitats, we considered Phenotype as a fixed effect. Similarly, Population was considered a fixed effect because it maximised the log-likelihood.

In addition, we considered Reader as random because we hypothesised that readings subjectively correlated with scales and therefore should more widely reflect the inter-reader effect. Calculations considering Reader as a fixed effect were also performed and did not change the results (**Appendix B.1**, *Fig. B.2*). To compare phenotype, we omitted the Phenotype fixed effect and accordingly divided the datasets into two parts, each of them being analysed as stated previously (focusing exclusively on Fish, Reader and Scale effects).

For the present study, variables related to age (FA and TA) were treated as Poisson-distributed data (Chi-squared goodness of fit for Poisson distribution, $P = 1.70 \times 10^{-14}$ for TA and $P = 1.00 \times 10^{-8}$ for FA) and scale growth was approximated and treated as Gaussian (D'Agostino normality test, $P_{SkewnessTest} = 2.55 \times 10^{-9}$, $P_{KurtosisTest} = 1.30 \times 10^{-1}$ for TR; $P_{SkewnessTest} = 1.10 \times 10^{-13}$, $P_{KurtosisTest} = 0.01$ for FR). Codes and fully worked examples are available in SCRIPT.R and data.RData of the Supplementary material (**Appendix B.1**). The results for r are given with 95% confidence intervals ($CI_{95\%}$) and the P-value of the likelihood ratio test. For the Poisson-distributed data, the original scale approximations were used because they are the exact solution of the general linear mixed model (GLMM) compared with link scales approximations, which are approximations; however, in this study, the two approximations gave very similar results.

Results

Population accounted for most of the variance (40% for growth measures (TR, FR) and 15% for annuli counts (TA, FA)), highlighting an important contrast among the three localities in terms of growth and age.

Variance decomposition of scale growth: TR and FR

Variance in growth as interpreted with scale measurements was primarily explained by inter-individual differences. Exact values of repeatability are given in *Table 4.4* with 95% confidence intervals ($CI_{95\%}$) and P-values. Fish alone explained more than 96% of the phenotypic variance of TR (*Fig. 4.5a*) and 53% of FR (*Fig. 4.6*). In contrast, the proportions of variance explained by Reader and Scale were not consistent in the decomposition of growth (*Fig. 4.5 b, c*, and *Fig. 4.6*). For both TR and FR, the combined effect of Reader and Scale corresponded to <1% of the total variance and Reader for FR. In addition, growth was harder to decompose for anadromous fish. Although Phenotype was not consistent in accounting for the variance of TR ($r = 4.55 \times 10^{-3}$; $CI_{95\%} = [6.71 \times 10^{-4}; 1.36 \times 10^{-2}]$), its effect on FR became greater ($r = 0.364$; $CI_{95\%} = [0.202; 0.536]$), reflecting the difficulty of locating the circulus corresponding to migration at sea.

Table 4.4: Mean repeatability estimates (r) of scale growth (total and freshwater radii) according to Fish, Reader, Scale and Phenotype, with corresponding 95% confidence intervals ($CI_{95\%}$) and P-values.

*Scale growth (interannuli spacing) was measured along the main longitudinal axis from the core to the total radius (TR); the freshwater radius (FR) corresponds to freshwater growth. Significant P-values are denoted by: ***, P ≤ 0.01; and **, 0.01 < P ≤ 0.05. There are no P-values for Phenotype because it was considered a fixed effect in the repeatability model and so was not included in the calculation of ratios of variance per se.*

	TR			FR		
	r	$CI_{95\%}$	P-value	r	$CI_{95\%}$	P-value
Fish	0.965	[0.945; 0.976]	4.16×10^{-245}***	0.536	[0.428; 0.631]	1.29×10^{-120}***
Reader	0	$[0; 6.00] \times 10^{-4}$	1	4.69×10^{-3}	$[0; 2.48 \times 10^{-2}]$	3.62×10^{-3}***
Scale	5.58×10^{-4}	$[0; 2.41] \times 10^{-3}$	3.95×10^{-2}**	3.76×10^{-5}	$[0; 1.93 \times 10^{-3}]$	0.48
Phenotype	4.55×10^{-3}	$[6.71 \times 10^{-4}; 1.36 \times 10^{-2}]$		0.364	[0.202; 0.536]	

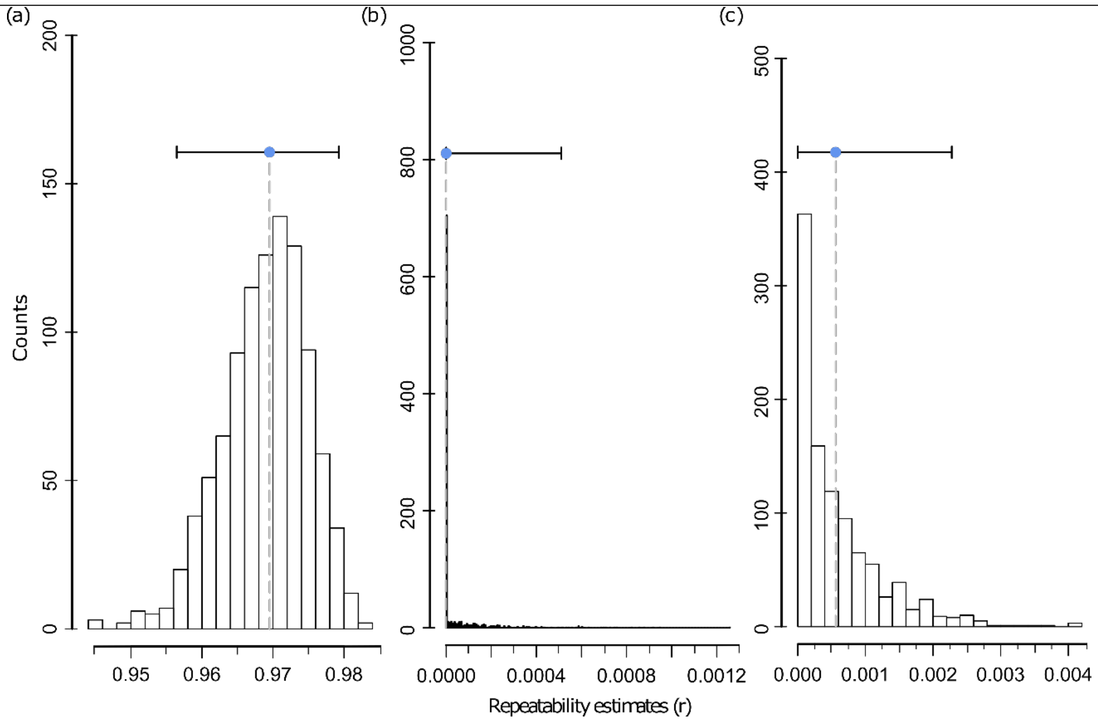

Figure **4.5**: Variance decomposition of measures made on the total radius of scales (TR). Symbols and dashed lines indicate the median of the repeatability estimates (r) for (a) Fish, (b) Reader and (c) Scale, with uncertainty (*i.e.* 95% confidence intervals) indicated, obtained over 1000 bootstraps.

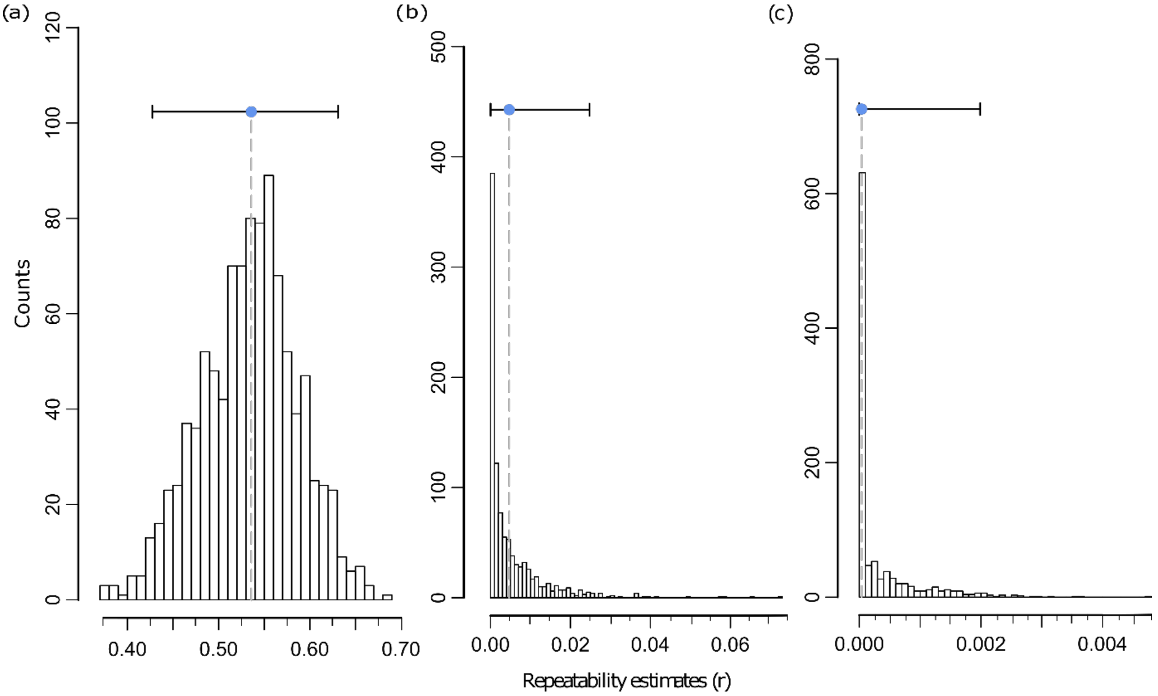

Figure **4.6**: Variance decomposition of measurements made on the freshwater radius (FR), which corresponds to freshwater growth. Symbols and dashed lines indicate the median of the repeatability estimates (r) for (a) Fish, (b) Reader and (c) Scale, with uncertainty (*i.e.* 95% confidence intervals) indicated, obtained over 1000 bootstraps.

Table 4.5: Mean repeatability estimates (r) of age (total and freshwater) according to Fish, Reader, Scale and Phenotype, with corresponding 95% confidence intervals ($CI_{95\%}$) and P-values.

*Total age (TA) was determined by counting the number of annuli on a scale (Borgenson et al., 2014); freshwater age (FA) corresponds to the number of years spent in fresh water. Significant P-values are denoted by: ***, $P \leq 0.01$; and **, $0.01 < P \leq 0.05$. There are no P-values for Phenotype because it was considered a fixed effect in the repeatability model and so was not included in the calculation of ratios of variance per se*

	TA			FA		
	r	$CI_{95\%}$	P-value	r	$CI_{95\%}$	P-value
Fish	0.539	0.372–0.632	1.31×10^{-57}***	0.392	0.246–0.495	1.89×10^{-38}***
Reader	1.98×10^{-6}	0–4.93×10^{-3}	1	3.43×10^{-4}	0–7.08×10^{-3}	0.453
Scale	5.59×10^{-7}	0–6.65×10^{-3}	1	1.11×10^{-9}	0–6.79×10^{-3}	1
Phenotype	2.04×10^{-2}	2.86×10^{-3}–8.15×10^{-2}		6.49×10^{-2}	2.92×10^{-2}–1.43×10^{-1}	

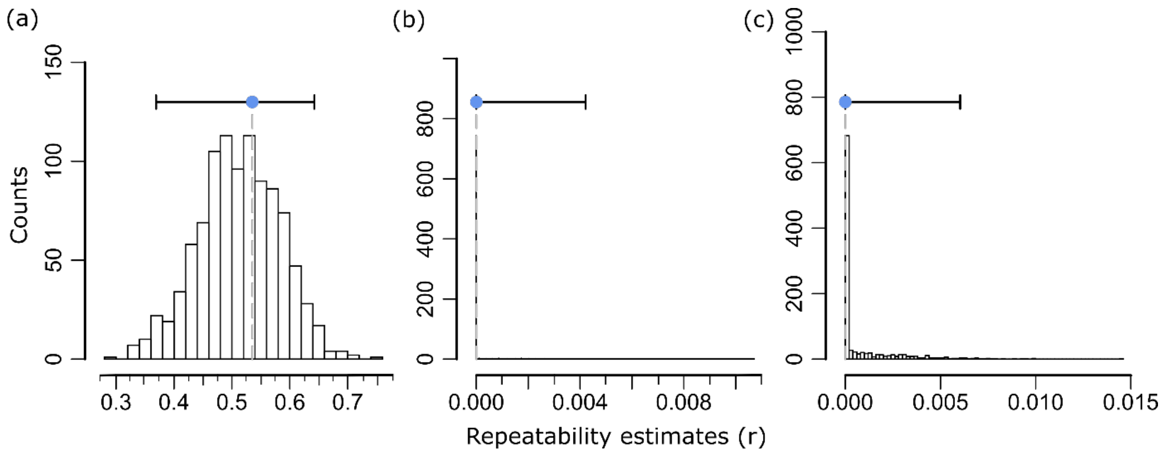

Figure **4.7**: Variance decomposition of total age (TA). Symbols and dashed lines indicate the median of the repeatability estimates (r) for (a) Fish, (b) Reader and (c) Scale, with uncertainty (*i.e.* 95% confidence intervals indicated), obtained over 1000 bootstraps.

Variance decomposition for TA read on scales and FA

Exact values of repeatability are given in *Table 4.5*, with $CI_{95\%}$ and P-values. Fish explained the main proportion of the variance in ages read on scales: 53% for TA (*Fig. 4.7a*) and almost 40% for FA (*Fig. 4.8a*). In contrast, Reader and Scale were inconsistent factors for explaining the variance in TA and FA (*Fig. 4.7b, c*, *Fig. 4.8b, c* ; *Table 4.5*). In addition, Phenotype explained 2% of the variance in TA and 6% in FA. Contrary to measures of growth (TR and FR), Phenotype explained a greater proportion of variance in age models (TA and FA), meaning that environmental conditions (*i.e.* freshwater *vs.* marine) increase the difficulty of age readings, especially for migrant fish, where an age at migration had to be determined. The number of annuli counted before migration (FA) was less repeatable than total age (TA) for Fish ($r = 0.392$ and 0.539 respectively, (*Fig. 4.7a*, *Fig. 4.8a*).

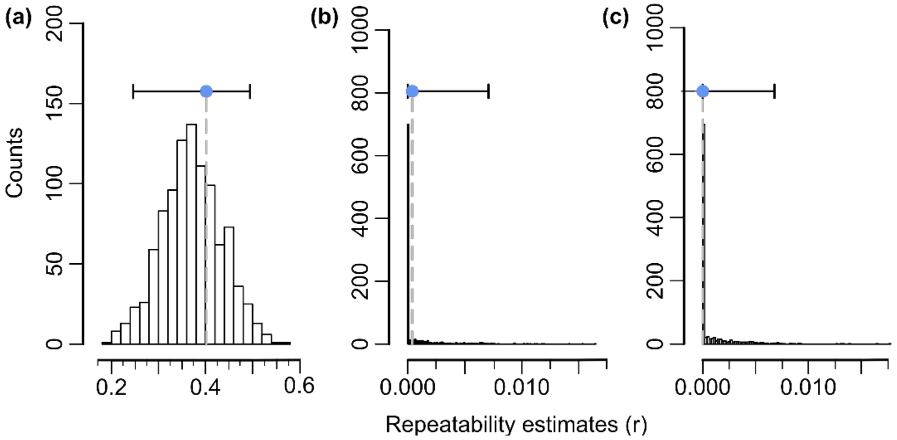

Figure **4.8**: Variance decomposition of freshwater age (FA), which corresponds to the number of years spent in fresh water. Symbols and dashed lines indicate the median of the repeatability estimates (r) for (a) Fish, (b) Reader and (c) Scale, with uncertainty (*i.e.* 95% confidence intervals indicated), obtained over 1000 bootstraps.

Table 4.6: Mean repeatability estimates (r) for scale growth and age according to by Phenotype (resident *vs.* migrant), with corresponding 95% confidence intervals ($CI_{95\%}$).

Scale growth (interannuli spacing) was measured along the main longitudinal axis from the core to the total radius (TR); the freshwater radius (FR) corresponds to freshwater growth. Total age (TA) was determined by counting the number of annuli on a scale (Borgenson et al., 2014); freshwater age (FA) corresponds to the number of years spent in freshwater.

		Resident		Migrant	
		r	$CI_{95\%}$	r	$CI_{95\%}$
TR	Fish	0.944	[0.903; 0.964]	0.96	[0.934; 0.975]
	Reader	0	[0; 0.002]	0	[0; 0.001]
	Scales	0.003	[0; 0.014]	0	[0; 0.003]
FR	Fish	0.944	[0.905; 0.964]	0.693	[0.554; 0.783]
	Reader	0	[0; 0.002]	0.007	[0; 0.041]
	Scales	0.003	[0; 0.013]	0	[0; 0.012]
TA	Fish	0.58	[0.357; 0.712]	0.455	[0.254; 0.584]
	Reader	0	[0; 0.009]	0	[0; 0.011]
	Scales	0	[0; 0.014]	0	[0; 0.017]
FA	Fish	0.584	[0.381; 0.732]	0.167	[0.031; 0.271]
	Reader	0	[0; 0.01]	0	[0; 0.011]
	Scales	0	[0; 0.013]	0	[0; 0.02]

Comparison of repeatability for resident and anadromous fish

The results obtained by separating Phenotypes are given in *Table 4.6*. Because TR was equal to FR and TA was equal to FA for resident fish, the results are the same for both pairs of variables. Variance decomposition was globally similar between resident and migrant fish, with the notable exception of FA and, to a lesser extent, FR. The variance explained by Fish was reduced for FA and FR compared with TR and TA respectively for migrant fish, highlighting the difficulty and subjectivity in locating the circulus corresponding to age at migration. The repeatability of interindividual differences in FA was sharply reduced for anadromous fish compared with resident fish ($r = 0.167$ and 0.584 respectively). In addition to the abovementioned fact that Phenotype has a noteworthy effect on FA decomposition, the proportion of variance in TR explained by Fish remains high for any phenotype, supporting our previous results that total scale growth is primarily explained by interindividual differences, regardless of Reader and Scale.

Discussion

The motivating problem for our study was how to most effectively sample, based on biological variance, in order to appropriately model dynamics. Apart from the consensus acceptance that the correct zone for sampling scales in salmonids is the first rows around the lateral line between the pectoral and the anal fins (Ombredane and Richard, 1990) and that measures have to be taken along the major scale axis (maximal length from the core of the scale to the border), the number of scales that need to be read to explain relevant individual information is still vague in the literature. Furthermore, a statistical issue in scalimetry is how many scales from fish should be used to improve precision in readings (Haraldstad et al., 2016).

Decomposition of repeatability on growth and age was performed and shows that most of the variability in repeatability is attributable to Fish. More generally, at least 50% of the interindividual variance is related to real interindividual variability, not to methodological or artefactual issues (Scale or Reader related), when investigating growth and TA. TR had the highest Fish repeatability, regardless of the reader and the chosen scale; therefore, increasing the number of scales examined is not necessary for capturing interindividual variability in growth because no significant effect has been recorded for Scale.

This study also suggests further issues associated with identifying migration. Compared with total variables (*i.e.* TR and TA), both freshwater variables (FR and FA) exhibited lower Fish repeatability, highlighting the difficulty and subjectivity in locating the migration point; however, the results arising from the global dataset encompass two distinct phenotypes. Consequently, when separating the phenotype into two datasets, we observed that the repeatability of Fish increased for FR (by a factor of 2) and decreased for FA (by a factor of 3). Those results globally confirmed that the determination of size through scale size and age at migration is a difficult task. Given the importance of this task to studies aiming to investigate ecological or evolutionary patterns of migration in many anadromous fish species, it is essential to quantify the uncertainty associated with locating the migration point.

In this paper, as in many others (Kimura and Lyons, 1991), the percentage of agreement in age estimations between readers was reasonably low: 65 and 60% for TA and FA respectively. The difficulty for readers in ageing fish from multiple structures (scales, otoliths) has long been an issue in many species. To avoid a potential lack of precision, some studies have made the choice to only conserve scales where agreement between scales or readers was established. Nevertheless, by doing so, only a fraction of a fish's life history may be selected and investigated. Consequently, the variability of life histories present in a population may be biased towards some more understandable pattern that does not necessarily reflect overall natural variability. Alternatively, one can estimate in a quantitative way the respective contributions of readers, scales, and individuals to the precision of the information to be analysed. Quantifying the effect of those confounding factors allows extraction of relevant interindividual variability. Only such a decomposition can determine the legitimacy of ignoring scale-related variance. Even if methodological biases in interindividual variability are not significant in this study, they could be substantially reduced by appropriately quantifying reader variance by river and environment (fresh water *vs.* sea).

The present study provides a case study that quantifies the sources of variance in age and size. Because errors frequently arise either from disagreements between scales or between readers, associated variances should be explicitly integrated into admitting-errors models, such as growth models (Cope and Punt, 2007; Hatch and Jiao, 2016; Shelton and Mangel, 2012). This is particularly true in an evolutionary context when the proper determination of fish length and age at migration, used as threshold traits in the decision to migrate, is necessary to produce reaction norms for migration (Dieckmann and Heino, 2007; Hutchings, 2011; Jonsson et al., 2016). Indeed, preliminary analysis to quantify errors should be a prerequisite to any study because it could provide valuable insights for accurate modelling of individual variability. Such understanding of interindividual variability should serve to better estimate population dynamics and could have several applications in stock assessment and conservation (Harris et al., 2018).

Inferring growth for fish or other taxa intrinsically depends on an accurate description of the age–length relationship, which may be undermined by measurement errors and ageing errors. Growth is an important life-history trait potentially associated with fitness through sexual maturity and the mortality rate (Pettersson et al., 1996; Wysujack et al., 2009). In many taxa, such as mammals (English et al., 2012), birds (K. M. Tjørve and E. Tjørve, 2010) or reptiles (Lehman and Woodward, 2008), growth is widely modelled using the vBGF (Von Bertalanffy, 1938). Not considering individual variability may lead to over- or underestimation of the vBGF parameters such as theoretical maximum length (L_∞) and the growth coefficient k (Harris et al., 2018; Vincenzi, Crivelli et al., 2016; Vincenzi, Mangel et al., 2014 (see **Appendix B.1**, *Fig. B.3*; *Table. B.1*). Such errors affect our ability to understand the evolution of life-history traits by comparing populations whose locations differ at different times.

A surprisingly high number of studies ignore the decomposition of variance and the implications of their methodologies on the estimation of parameters. Every researcher aims to answer a scientific issue while designing effective studies in terms of both time and funding. Not extending enough effort in data acquisition leads to underpowered analysis, whereas the reverse leads to overpowered analysis. The waste of resources can be considerable in both cases (Johnson et al., 2014; Wolak et al., 2011). Repeatability is an important feature in research, both to be able to reproduce our own studies and to compare with others (Cassey and Blackburn, 2006). Unfortunately, the rationale for using a given scalimetric method in fish biology is rarely discussed, and even neglected; it is sometimes nearly impossible to access the precise methodology (numbers of scales or readers), precluding exact reproduction of experiments. In the present study, the data highlight the importance of individual variability within populations of brown trout in the Kerguelen Islands and enable us to avoid the unnecessary and time-consuming use of multiple scale readings (see **Appendix B.1**, *Fig. B.3* and **Appendix B.1**, *Table. B.1*). In other contexts, the methodological approach (numbers of readers and scales by fish) should be similarly justified and discussed on a case-by-case basis.

In conclusion, decomposition of variance should be a prerequisite to any study aiming to quantify population dynamics through the growth of individuals. If neglecting methodological variance influences the variables studied, the time spent in the laboratory cannot be adequately allocated to focus on biological variability. In addition, failing to disentangle the effects of biological and methodological variance could prevent the relevant investigation of ecological and evolutionary patterns.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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4.3 From the back-calculation of size at age to the estimation of individual growth

Based on the variance decomposition work and because scales are estimators of life-history traits, in this work we used four scales to determine the age of fish (age at migration and total age) and considered a single scale for associated growth measures. The scales were prepared and read according to the same methodology as previously described, except for double reading by different readers. All measures of growth (position of annulus) and the same variables (total age TA, freshwater age FA, total radius TR, freshwater radius FR) were noted for all the scales making up our data set.

In many species, the growth of calcified structures is correlated with somatic growth (Casselman, 1990; Günther et al., 2012; Ottaway, 1978). When the size of the fish at each age cannot be obtained from CMR-type monitoring, the growth recorded on the scales, whether daily or annual, makes it possible to rebuild the probable size of the fish at a given age. The use of calcified structures to infer the size of fish at a previous age is called back-calculation (Casselman, 1990; Ibáñez et al., 2008; Kipling, 1962). A back-calculation model is used to estimate the length of the fish at age i : L_i, from known values of length at capture (total length, L_T), and measurements made on scales : total radius (TR or R_T) and distance between the core and the radius at age i : R_i. Numerous back-calculation models exist (Ogle, 2013). Models are described hereafter, and the main mathematical equations are recorded in *Table 4.7*. Widely used back-calculations methods are the one of Dahl and Lea (1910), Fraser-Lee (1916-1920), the body proportional hypothesis (BPH, also called Whitney and Carlander) and the scale proportional hypothesis (SPH, also called Hile). Different assumptions are underlying all these models. Dahl and Lea suggest that scales growth is an exact proportion of fish growth (1). Fraser-Lee implemented the previous model by allowing fish to grow before the formation of the first scales (2). The SPH assumes that if a scale is bigger than the average scale for that size of fish (catchment size), then this difference would be conserved throughout the lifespan (3). The BPH is the exact same thought but turned the other way round. Meaning that if a fish is x percent smaller or bigger at capture than the average fish for that size of scale, then this difference would be conserved throughout the lifespan (4). Other numerous models exist such as nonlinear SPH, nonlinear BPH but the preferred back-calculations model is often the Fraser Lee model (Duncan, 1980; Kouhestan Eskandari et al., 2018). However, it is interesting to note that studies are carried out to choose the best back-calculation model in accordance with the study species or the calcified part chosen (Horppila and Nyberg, 1999; Ibáñez et al., 2008).

Table 4.7: Referenced back-calculation models.

Depending on the assumption of the model, parameters of the function of the mean scale radius for fish of a given age (i.e., E(R|L)) or a function of the mean length for fish of a given scale radius (i.e. E(L|R)) will be used (Ogle, 2013). E(R|L) = a + bL and E(L|R) = c + dR, where E(R|L) is estimated from the regression of R on L and E(L|R) from the regression of L on R.

Dahl Lea	$L_i = \frac{R_i}{R_T} L_T$	(1)
Fraser-Lee	$L_i = \frac{R_i}{R_T}(L_T - c) + c$	(2)
SPH	$L_i = \frac{c + dR_i}{c + dR_T} L_T$	(3)
BPH	$L_i = \frac{R_i}{R_T}(L_T - \frac{a}{b}) + \frac{a}{b}$	(4)

The Brown trout is no exception to the rule of using back-calculation through the use of fish scales. (Kipling, 1962). Most often, an allometric growth relationship is established between the size of the calcified structure and body size. However, the growth phase at sea, for migrant trout, seems more favourable to establish models based on isometric relationships. Referring to the results of Beall (1979), the relation between L_T and R_T was considered as biphasic, with an allometric relation during freshwater life and an isometric relation after migration. In the present manuscript, we used the Fraser Lee model in a Bayesian framework, using rjags R package (*ver.* 4.6 in R *ver.* 3.4.4, an interface from R to the JAGS library for Bayesian analysis), to back-calculate the freshwater body size at age of fish. The reasons for this choice are the followings:

- First of all, because of the evolution of the equipment and the progress made in scalimetry, we had different types of measurements taken on the scales. This forced us to go through back-calculation, using a model with ratio of growth (R_i/R_T), to be able to study the evolution of growth according to our spatio-temporal grid.
- Secondly, we are only interested in the first phase of growth: freshwater growth. This means that we only need one allometric model.
- Based on the previous work on variance decomposition, we used only one scale since the major source of variance is the fish level. A single back-calculation model was generated, with no spatial or temporal effects, on the assumption that the relationship between scale size and fish size does not vary either in time or space. However, the use of the Bayesian framework allowed us to consider the variability of size at age estimates in models using these back-calculated sizes.

The results of the mean size distribution at age for ages ranging from 1 to 5 years were then compared with the actual size distribution observed at capture for each of these ages (*Fig. 4.9*). It is important to remember that the fish in this dataset are almost never caught at full age (with the 1st of July as birthday) but are often caught during the southern summer. This means that the fish have restarted growing at this time, and this growth is visible on the scales with the deposition of new circuli after the last annulus. A fish with 2 visible rings and re-growth is therefore more than 2 years old and its age is 2^{+}. The back-calculated sizes, on the other hand, give the sizes at full age since these estimates are obtained from direct measurements of the annulus on the scales. The model we have chosen performs well in predicting correct sizes during the first three years of life. However, the median estimated for the fourth and fifth years is higher than the median respectively of the 4^{+} and 5^{+} that were captured later. However, the estimated values as well as the dispersion remain consistent to allow comparison between the selected populations.

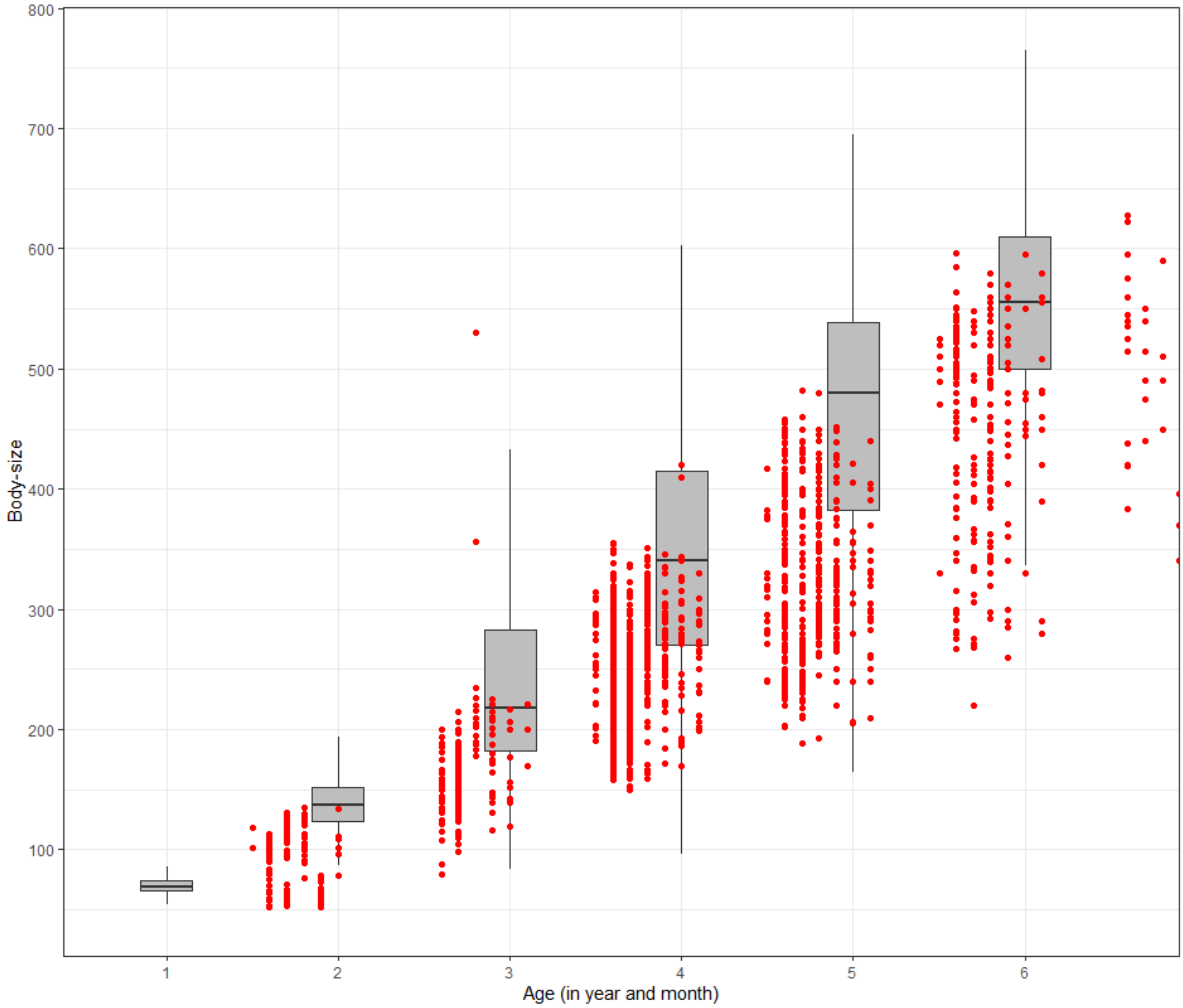

Figure **4.9**: Comparison of the backcaculated body size at age (plain boxplot) with the real size-at-capture in our studied dataset (red points).

Back-calculated body size at age are really useful when biologist want to study the growth of fish especially when few data are available (Contreras-Reyes et al., 2018; Mohdeb and Kara, 2015). The back-calculated sizes are then used as known data, allowing the estimation of fish growth patterns, individual or population patterns, in time and space. Different growth models exist, the most commonly used being that of Von Bertalanffy (Katsanevakis, 2006; Katsanevakis and Maravelias, 2008; Von Bertalanffy, 1938). Nevertheless, because back-calculated body sizes at age are non-independent, some growth models' assumptions are violated when biologists want to study the growth of fish (Jones, 2000). The accuracy and use of back-calculation models are of paramount importance for growth analysis (Fontez and Cavalli, 2014). Another way to model growth is to directly study scalimetric growth instead of rebuilding proximate of somatic growth (Marco-Rius et al., 2013). The advantages of this method are to offset the use of back-calculation models. One problem is that it is more complicated to figure out what corresponds the micrometric growth of scale compared to the growth of an organism. Unfortunately, because methodology changed throughout the time, we were not able to do that kind of study to observe a spatio-temporal evolution of growth.

4.4 Conclusion

Fish scales are a very useful biological material for reconstructing fish life-history traits. However, due to their external position, the scales can be damaged causing a loss of information. Other individual internal processes can also cause loss of information such as maturation. Other calcified pieces may sometimes be more suitable for the study of life-history traits, such as otoliths. However, the advantage of taking scales is that they are not lethal and allow many samples to be taken.

In general, scales are used to determine the age and growth of fish, but it is often difficult to find an exact methodology to determine the appropriate number of scales to be used or read. The scales give estimates of the variables of interest. Knowing the variability of these estimates appears to be of prime importance before reusing these data to predict growth curves and compare population and temporal parameters. Based on a nested design (readings of four scales per fish by two independent readers), we decomposed variance in growth and age according to fish (inter-individual level), scales (intra-individual level) and readers by using repeatability analysis. The results highlight that most variation is attributable to fish. Readers and scales contribute little to inter-individual variance, suggesting that inference was insensitive to intra-organism biological variation. Based on these published results, we decided to use four scales to determine the most likely age of the fish and carried out the measurements on a single scale.

To study freshwater growth patterns in our dataset, the age and growth estimates (scale measurements) were then converted to fish body size using a back-calculation model. We decided to use a single common model for our dataset and selected the Fraser-Lee model which we applied in a Bayesian statistical framework. This model provides estimates of the probable size distributions at age per individual. These estimates of body size at age were subsequently used to study the evolution of growth and reaction norms models as presented in this manuscript.

Discussion on the sampling design and the chosen methodology

Several thousands of data were collected as part of the long-term monitoring carried out in the Kerguelen Islands. Faced with such a large database, it was necessary to make choices about which individuals to study to answer questions about the evolution of life-history traits. This pre-selection is a necessary work. In this work, I have chosen to develop two selection models based on size distributions at age. It turns out that the most appropriate model is based on the actual frequencies of observed size-at-capture and age. I selected 7 study rivers for reasons of pseudo-replication, integrating several criteria, such as the date of colonization of the river and its original state (introduced versus naturally colonized). This main dataset ultimately comprises 4750 fish caught in seven rivers and will be the central dataset used in the rest of the manuscript. However, several things can already be noted about this dataset. First, compared to the samples available on each of these 7 rivers, the fish selected represent on average 38% of the data actually available (*Table 3.8*). This percentage varies by river, *i.e.* some rivers are better represented by the final sampling than others. Notably, the River Acœna where only 14% of the fish caught were analysed. On the other hand, as I am interested in migration, I have selected individuals whose migratory phenotype is known at capture. But on some rivers, especially the most recently colonized (Rivers Port-Kirk and Rohan), very few migrant are being caught, which may be problematic to model the probabilities of departure at sea (*Fig. 3.13*).

This scalimetric dataset will be the main dataset of this manuscript. It will be used to study the evolution of freshwater growth, body size at age and migration probability. However, another important dataset has been incorporated in the section on the study of body size at age (see *Chapter 5, section 5.2*). This dataset includes several thousand fish caught at the age of one. This dataset is used in a comparative aim in the section of the evolution of body size at the age of one along the colonization front. Indeed, caught at one year of age, this dataset presents the opportunity to relax the hypothesis of selective mortality. As this particular dataset only appears in Chapter 5, full details are provided in this chapter.

There is a wide diversity of studies relying on scales or other calcified structures to rebuilt the life histories of fish (*e.g.* Borgenson et al., 2014; Boughamou et al., 2014; Elliott and Chambers, 1996; Ibáñez et al., 2008). In this manuscript, I focused on the use of scales because the long-term monitoring in the Kerguelen Islands offered the opportunity to study a uniquely large dataset. Otoliths are also available, but I did not make the choice to use them for several reason. First, there are fewer otoliths in the database because sampling otoliths necessitate fish sacrifice. Second, if scalimetry is time consuming, otolithometry is as well. Nevertheless, there are several problems linked with the use of scales (Bereiter-Hahn and Zylberberg, 1993; Haraldstad et al., 2016; Jensen and Johnsen, 1982; Kacem et al., 2013) that could be disentangle while using available otoliths in a conjoint way (Boughamou et al., 2014; Campbell et al., 2015; Hining et al., 2000; Machias et al., 2002).

As I am interested in the evolution of traits related to dispersal, I made the choice to focus on the migratory tendency of fish. Thus, I had to rebuilt life histories through scales readings but I also had to back-calculate the body size at age. Using back-calculated body size at age is common in studies willing to rebuilt growth and body size (Contreras-Reyes et al., 2018; Guezi et al., 2017; Günther et al., 2012; Mohdeb and Kara, 2015). Nevertheless, there could be some biases introduced using such methodology. As we were mainly interested into the first stages of freshwater life, we used the Fraser Lee model (Duncan, 1980; Ogle, 2013; Pierce et al., 1996) in a Bayesian framework, which was the best model. Back-calculation of body size at age could also be problematic while comparing the real size at capture and the back-calculated size, especially for these ages superior 4 (*Fig. 4.9*). Novel methodologies are developing on how to model growth of fish directly using incremental growth observed on scales (Marco-Rius et al., 2013). Unfortunately, it was not possible to do so to the purpose of the study, due to change in scalimetric methodologies since the beginning of the long-term monitoring.

Despite some methodological biases, the work developed in this methodological part allowed me to determine an appropriate method to select the fish studied in an efficient way and to optimize the working time to study the evolution of life-history traits related to dispersal.

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Part III

... To study the evolution of life-history traits

Objectives and organization of the part

Based on the previously determined dataset, this part is willing to fully exploit information given by scales on life-history traits related to migration. We focused on the evolution of the age at migration, the freshwater growth before migration, and body size at age. Our aim was to quantify variations in the traits of interest according to our spatio-temporal frame.

In a first chapter, we were interested into the evolution of freshwater growth rate and body size at age because they have widely been demonstrated to relate to migration propensity. The growth of individuals depends on the environmental conditions in which they live. Thus, the same individual in different environments may experiment different growth trajectories (spatial effect). In addition, within a population the number of individuals changes over time (density), so population density may influence competition for the resource within the habitat (temporal effect). The context of expanding populations is a perfect frame to study the spatio-temporal evolution of such trait. Furthermore, along a colonization front, spatial sorting may happen, if dispersers have different growth abilities than residents, and if these abilities are transmissible (in a direct or indirect manner) then individuals in newly founded populations could show different growths than those observed in core populations. We have decided to answer these questions in a section devoted to the evolution of the growth rate.

However, a high rate of growth does not always mean a larger body size at age. Body size at age is considered by many authors (at least in salmonids) to be a key feature in migration. Indeed, the largest individuals at a given age are often considered to be the fastest to migrate because they are likely to have better survival chance and they will have stored more reserves. Thus, changes in body size at age among individuals could lead to changes in migration tactics. Especially because of density, body size at age is bound to decrease. In a context of expansion, it is expected that fish in old populations will be smaller than fish in new populations, but that time (and thus density) will have a similar effect on all populations regardless of their location on the colonization front. Moreover, under the spatial sorting hypothesis, one could hypothesize that the traits favouring dispersal will be favoured on the edges. We decided to deal with the evolution of body size at age in a section, which is the subject of a paper in preparation.

In a second chapter, we were interested in the evolution of the migratory tactic itself along the colonization front. Alternative migratory tactics are considered as threshold traits because of their polygenic nature (Dodson et al., 2013). Alternative phenotype may respond to the evolution of a normally distributed liability trait (body size) and the evolution of the threshold that will determine the limit value of the liability trait under which one tactic is expressed and above which the other (*i.e.* residents *vs.* migrants). In fact, the evolution of growth and body size towards lower value may lead to a decrease in the migratory tactic if the threshold value itself does not evolve (considering that future migrant must be the bigger). In this chapter we were interested in the evolution of the probabilistic migration reaction norm according to the time since colonization, on the different selected rivers located on a shifting expansion range. This section is the subject of a paper in preparation.

5

The evolution of growth and body size at age

5.1 Growth rate or body size? How to model the variable driving migration?

Somatic growth is one of the most important life-history traits across taxa since it acts indirectly on reproduction abilities and survival rate, that are fitness component. Body size and growth rate are frequently demonstrated to relate to sexual maturity (Thorpe et al., 1990), survival (Thompson and Beauchamp, 2016), reproductive success, movement, or migration (in birds: Jahn et al., 2010, in fish: Peiman, Birnie-Gauvin, Midwood et al., 2017). In fish, most evidence suggests that environmental pressure on individual growth affects the migratory phenotype as well as the timing of migration (Peiman, Birnie-Gauvin, Larsen et al., 2017). For example, those environmental pressures can relate to change in temperature or food supply (Archer et al., 2019).

Which variable best explains the individual decision to migrate? Much research often compares somatic growth and body size at age as explanatory drivers (Acolas et al., 2012). High individual growth rates are often correlated with higher individual physiological needs and is observed for individuals of different body sizes. Energy resources and reserves are essential for individuals to cope with the new needs they will face during the migration phase (*e.g.* predation risks, migration distance). Thus, it is often demonstrated that individuals with the highest energy demand are those who grow fastest and are the fastest to migrate (Bohlin, Dellefors et al., 1996). This result is congruent with the fasting endurance hypothesis (Millar and Hickling, 1990) and the 'increasing food availability hypothesis' (Gross, 1987). On the other hand, studies have also shown that individuals with slower growth and less energy tend to migrate earlier within populations (Peiman, Birnie-Gauvin, Midwood et al., 2017), which is more consistent with the competitive release hypothesis (Yeaton and Cody, 1974). In both cases, the development time (Abrams et al., 1996) and the earliest stage of life seem to be of great importance (Cucherousset et al., 2005). Both phenomena have been observed or demonstrated and show that the state of organisms and the environment in which they live condition the migratory fate of individuals within populations. It is essential to understand these effects because they affect the evolutionary dynamics of populations and therefore their future in the context of global change. Body size at age is a life-history trait involved in survival (Acolas et al., 2012) but also in the decision to migrate (Bohlin, Dellefors et al., 1996). Individuals need to reach a certain size to be able to migrate because migration is a conditional strategy in partial migratory populations. Adaptation of conditional strategies requires the evolution of either the environmentally influenced cue (*e.g.*, body size at age) or the state (*e.g.* threshold size) at which an individual switches between alternative tactics (Phillis et al., 2016). The notion of reaction norm and the state evolution (threshold size) will be developed and discussed in the next chapter. Larger size confers competitive advantages to individuals, in terms of resource acquisition, competition, and survival. However, the "Bigger is better" hypothesis is not always true (Ulaski et al., 2020), with the competitive advantage of large body size decreasing with increasing group size (favouring sneak-in strategies at higher densities) (Pettersson et al., 1996). With change in population dynamic, and particularly change in population density, being large may no longer be an advantage.

The objective of this chapter is to analyse the evolution of freshwater growth prior to migration and body size at age along the colonization front to understand the potential evolution of the drivers of migration. More specifically, we investigate in the second section the spatial and temporal evolution of growth during the six first year of life using the Von Bertalanffy model on our dataset. Information contained in this section also results from reflections on the work of several interns (Gautier Magné, Valentin Santanbien, and Hervé Rogissart, *see* **Appendix D**). The third section is an article in preparation centered on the evolution of body size at age based on the comparison of two datasets: our back-calculated dataset and data collected at capture.

5.2 On the evolution of freshwater growth prior to migration

Introduction

The growth rate of individuals is often described as a proximate mechanism in the decision to migrate. Growth is the phenomenon of the increase in size per time unit. Some species grow during a certain period of their life cycle, what is called determinate growth, to reach their adult size (*e.g.* birds, mammals), some others exhibit an indeterminate growth (*i.e.* the organism grow during all its lifespan). This is the case of numerous fish species such as brown trout (*Salmo trutta* L.) (Mommsen, 2001; Warren and Davis, 1967). The energy acquired by the fish is allocated as a compromise between traits related to reproduction and survival, *i.e.* the fitness of the organism (Dieterman et al., 2012; Vincenzi, Mangel et al., 2014; Werner and Gilliam, 1984). As they age, fish might allocate less energy to growth and invest in general more into reproduction. As already mentioned in the introductive section, the growth rate is involved in the migratory fate of individuals, whether it is the fast-growing or slow-growing individuals who migrate first.

Statistical models have become widely used in the study of organisms' growth. Studying growth in applied or theoretical contexts requires good knowledge of the shape of the growth trajectories to select a reasonable model of approximation (Vincenzi, Crivelli, Jeseňsek et al., 2019). A great diversity of models exists to model the growth of vertebrates. The most famous are Gompertz (GGF) and Von Bertalanffy (vBGF) models. Many studies have looked at which model was most appropriate to simulate the growth of their studied organism (Finco et al., 2016; K. M. Tjørve and E. Tjørve, 2010). In many cases, both models (GGF and vBGF) exhibit similar performance (Vincenzi, Crivelli, Jeseňsek et al., 2019). In the case of the indeterminate growth of fish, the vBGF hypothesizes that the growth of an organism is the result of a dynamic balance between anabolic and catabolic processes. The anabolic factors are proportional to the surface area and catabolic factors are proportional to mass (Vincenzi, Crivelli, Jeseňsek et al., 2019). The form of the specialized vBGF equation is given in the equation (5.1), where the size of an individual at a given age is expressed as a function of three different parameters. L_∞, the asymptotic size, is the upper limit of the size towards which an individual could converge through time. k is the rate of growth (in $time^{-1}$ units). t_0 is the hypothetical age at which length is equal to 0. This model seems appropriate to study the evolution of the different parameters that affect growth, such as the emergence, the growth rate and the asymptotic size (Pompei et al., 2012; Von Bertalanffy, 1938).

$$L_t = L_\infty(1 - e^{-k(t-t_0)}) \tag{5.1}$$

In most studies, the model has been applied to theoretical questions about the population growth to understand the ecology and the evolutionary biology of the studied species. The interpretation of such results corresponds to the growth of a hypothetical average individual within the population. However, variation among individuals within a population is a ubiquitous feature of natural population (Shelton and Mangel, 2012). Over the last decade, many models taking inter-individual and environmental variations into account have emerged. They demonstrated in majority the importance of these stochastic effects on the evaluation of growth (Dieterman et al., 2012; Harris et al., 2018; Vincenzi, Crivelli, Munch et al., 2016; Vincenzi, Mangel et al., 2014). Consideration of these individual effects is even more important when the dataset is fragmented and made up of sparse longitudinal back-calculated data.

In partial migratory population, it is of paramount importance to study growth before migration to understand which key processes are involved in the tactics chosen by the individual. According to the future migratory status, differences in growth have already been observed in fish (Gillanders et al., 2015), and the energetic status determines the migration destination (Boel et al., 2014). In expanding population along a colonization front, environmental conditions may vary in space and time as the population settle down. The diversity of environments along a colonization front may condition individual growth rate within rivers. This spatial variation in growth expected along a colonization front may have implications on the migratory strategy adopted by individuals. Moreover, as the population grows (in term of number of individuals, *i.e.* density), the available resources per individual are expected to decrease, so does the freshwater growth with time since colonization. If the freshwater growth evolves, individual's migration fates are expected to evolve as well. Under the main assumption of the fasting endurance hypothesis and density dependence, one can expect that growth will decrease with time, and delay the migration decision of individuals, making old population less prone to produce young migrants than new ones located on the border of the colonization front.

In the present work, we use our longitudinal dataset obtained through the long-term monitoring of the brown trout populations in the Kerguelen Islands to show the evolution of fish growth during their first years of life. We were particularly interested in the change in growth rate, as a function of spatial (river) and temporal (time since colonization) factors. We propose in this section an individual-based formulation of vBGF in a Bayesian framework to test for the spatial and temporal change of freshwater growth. Moreover, the growth rate was decomposed according to the future migratory fate, to highlight a possible differentiation in growth prior to migration. In addition, we gathered exploratory work on growth of several interns under my co-supervision (see **Appendix D**).

Material and methods

Data

Brown trout caught in the Kerguelen Islands (69°30'E-49°30'S) were used to study the evolution of freshwater growth. To the purpose of this study, we used our longitudinal dataset containing 4750 fish sampled in 7 different rivers (Acœna, Château, Manchots, Nord, Norvégienne, Port-Kirk and Rohan) during a long-term monitoring in the Kerguelen Islands from 1952 until now. Further information about the location are given in the *Table. 3.4*. We focused the analysis on the 6 first year of individual life in fresh water, either they stayed resident or became migrants. For migrants, only the freshwater growth before migration was considered. Interns under my co-supervision performed preliminary works on various subsets of this final dataset. Two sub-samplings were carried out, grouping together comparable rivers in terms of time at colonization. Subsampling S1 records the Rivers Acœna and Nord[1], and subsampling S2 records Rivers Château and Norvégienne[2].

Model selection

To study the influence of space and time on the estimation of vBGF parameters, we first fitted models according to three main variables: river, period, and phenotype. Period corresponds to the year of birth of the individuals (*i.e.* cohort) and phenotype to the future migratory behaviour of the individual (*i.e.* resident *vs.* migrant). In both *S1* and *S2*, vBGF models were fitted using the bmrs R package (respectively *ver.* 2.3.1 and *ver.* 2.9.0) (Bürkner, 2018).

Concerning *S1*, 49 models were compared using WAIC and LOOIC criteria (Vehtari et al., 2017). The 49 models come from the different combinations of variables that could influence either one, two or three of the vBGF parameters. The variables considered were: river (spatial effect (H in *Fig. 5.1*)), period (temporal effect, recorded as grouped cohorts (individual year of birth) (C in figure *Fig. 5.1*)) and phenotype (P in *Fig. 5.1*). In *S1*, C corresponds to two grouped cohorts' period: individuals born between 1989 and 1994 (C1) and individuals born between 1995 and 2000 (C2). Any combination of variables could influence any parameters. Unmentioned parameters in the vBGF model name were considered constant over the different groups (*Fig. 5.1*).

Concerning *S2*, a conditional inference trees that embed tree-structured regression models was used (Rusch and Zeileis, 2013). The vBGF parameters L_∞, k and t_0 are calculated in a recursive manner, as the dataset is split under the categorical variables influence (river, period and phenotype). In *S2*, periods are split into three grouped cohorts: [1960-1970], [1971-1980], and [2000-2010].

Statistical analysis of the evolution of freshwater growth

The empirical Bayes method refers to a traditional statistic where the fixed effects and variance of random effects are estimated through maximum likelihood (Vincenzi, Mangel et al., 2014). Several modelling tools are now available to deal with noisy, large, and sparse data to fit parametrized non-linear models in efficient ways. However, maximum likelihood method applied in classical frequentist approaches can reach their limit such that the Bayesian approach becomes the solution to fit complex models (Gelman, 2006). In that way, the Bayesian approach seems more flexible to study unbalanced data. Another advantage of the Bayesian approach is the ability to incorporate explicitly prior information about parameters onto the specified model. The brms R package allows computing a wide range of Bayesian single-level and multilevel models that are fitted with the probabilistic programming language Stan behind the scenes (Bürkner, 2017; Bürkner, 2018). Non-linear relationship, such as vBGF models can be fitted using non-linear predictors.

Based on the preliminary model selection and vBGF fitted in the preliminary works (**Appendix C.1**), we studied change in growth rate parameter (k) according to spatial and temporal variables (river, time and phenotype). The reason for this is that we were particularly interested in the evolution of the growth rate as a function of the spatial (river) and temporal (time since colonization) factors. Time

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[1] Work developped by Gautier Magne (intern under my co-supervision). This work is partially presented in this manuscript.

[2] Work developped by Valentin Santanbien (intern under my co-supervision). This work is partially presented in this manuscript.

since colonization acts as a proxy of change in density within populations. As the population grows with time (increase in density), the growth rate is expected to evolve towards lower values or simply decrease via plasticity. The future migratory behaviour (phenotype) also seems implicated in the variation of the freshwater growth, with future migrants expected to grow faster. The conditions with which the individuals have to deal, depends on their locations. The best and easily modelled variable that should spatially impact k is the river (spatial effect). The hypothetical age at which length is equal to 0 (t_0) was considered to be homogeneous across space and time. Finally, it is hardly believable that the asymptotic size (L_∞) should differ among individuals if they lived forever, whatever the river, the period, and the phenotype.

According to our hypothesis and to test for the evolution of growth rate across space and time, we fitted a hierarchical vBGF model described in the equation (5.2), using the independent platform JAGS in R using rjags (*ver.* 4.10). We performed 500 000 iterations on two parallel chains, after adaptation (20000) and burn-in (20000) steps. Posterior distributions were obtained through the Monte-Carlo method (Hastings, 1970; Metropolis et al., 1953). The convergence of the chains was checked with the Gelman diagnosis test (Brooks and Gelman, 1998).

$$\begin{aligned} L_{i,j} &\sim N(m_{i,j}, \tau) \\ m_{i,j} &= L_\infty(1 - e^{-(k_{r,p}+\varepsilon_t)(j-t_0)}) \end{aligned} \tag{5.2}$$

where i is the individual and j its age, r is the river in which the individual lives, p its future migratory phenotype, and t the time since colonization.

The priors of the equation (5.2) are given below (5.3), details for the convergence of the chains are given in **Appendix C.2**. The symbols N, U ad G respectively stand for normal, uniform, and gamma distributions (Balakrishnan and Nevzorov, 2004).

$$\begin{aligned} L_\infty &\sim U(500, 1500) \\ k_{r,p} &\sim U(0, 1) \\ \varepsilon_t &\sim U(0, 1) \\ t_0 &\sim U(-10, 10) \\ \tau &\sim G(0.001, 0.001) \end{aligned} \tag{5.3}$$

In this model, we presume that growth rate may vary according to river and phenotype ($k_{r,p}$). We also hypothesize temporal inter-cohort fluctuations (ε_t). Median estimates of each parameter are given with their confidence intervals at 50% ($CI_{50\%}$) and 95% ($CI_{95\%}$).

Results

Preliminary model selection

The first approach lead on *S1* concludes, either with WAIC or LOOIC, that the equally best models take river and phenotype (PH) into account on the parameters k and t_0 (**Kt**) or on the parameters L_∞ and t_0 (**Lt**). Other models taking river, period and phenotype (PCH) on any combinations of the three vBGF parameters (except from only t_0) performs as good as the two first cited models.

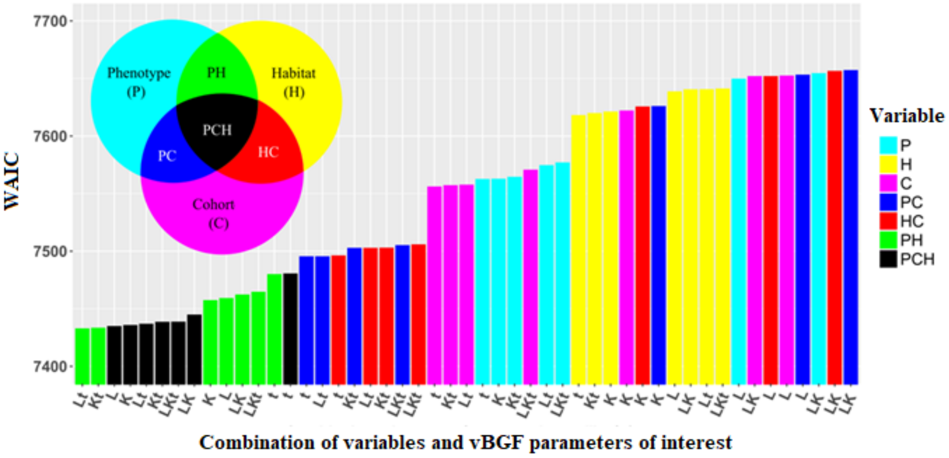

Figure **5.1**: WAIC score for the 49 vBGF models, ordered by increasing score. From Gautier Magne's work.

In the preliminary work lead on *S2*, the best driver of growth is the period (*Fig. 5.2*). In the first period, only rivers discriminate the growth of fish, but later differentiation of growth between phenotypes is visible. This method gives complementary information of the study performed on *S1*, of the ordered importance of river, period, and phenotype on the vBGF parameters.

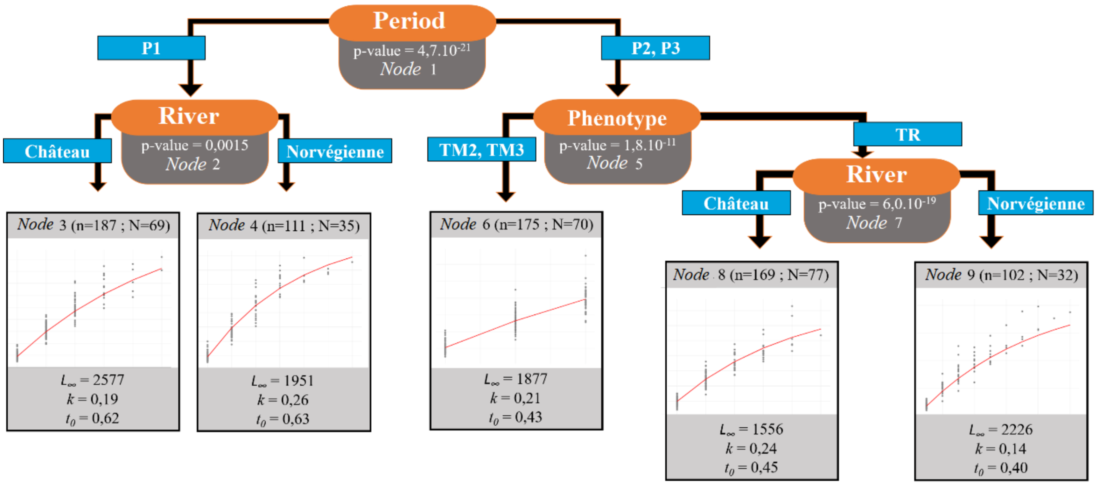

Figure **5.2**: Resulting tree from the recursive partitioning method, considering river , period and phenotype, and their modalities (n=number of data, N=number of individuals).

TM stands for migrant trout and TR for resident trout.

These preliminary works confirm that river, period and phenotype should be taken into account in our vBGF model. The variables river, period, and phenotype seem to differently affect the vBGF parameters estimates (L_∞, k and t_0). What seems best biologically acceptable is that growth rate (k (in $time^{-1}$ units)) may vary according to space (river), time (period considered), and phenotype (future migratory behaviour of the individual within population).

Parameters estimates

We obtained convergence of the algorithm for the vBGF model parameters estimation in JAGS (**Appendix C.2**). The parameters estimates of L_∞ and t_0 were biologically consistent considering freshwater growth of fish (*Fig. 5.3*). The average asymptotic size that an individual could reach in fresh water would be 593 mm ($CI_{50\%}$ = [575; 612]; $CI_{95\%}$ = [547; 647]). The age at which an individual should be of size 0 is approximately 0 (t_0-1), where t_0 = 1.06 year ($CI_{50\%}$ = [1.06; 1.07]; $CI_{95\%}$ = [1.04; 1.09]). The reason for this difference comes from that in our dataset the first age considered j is 0. For computational reason, it had to be turned in 1, so all age in the matrices should be *j-1*.

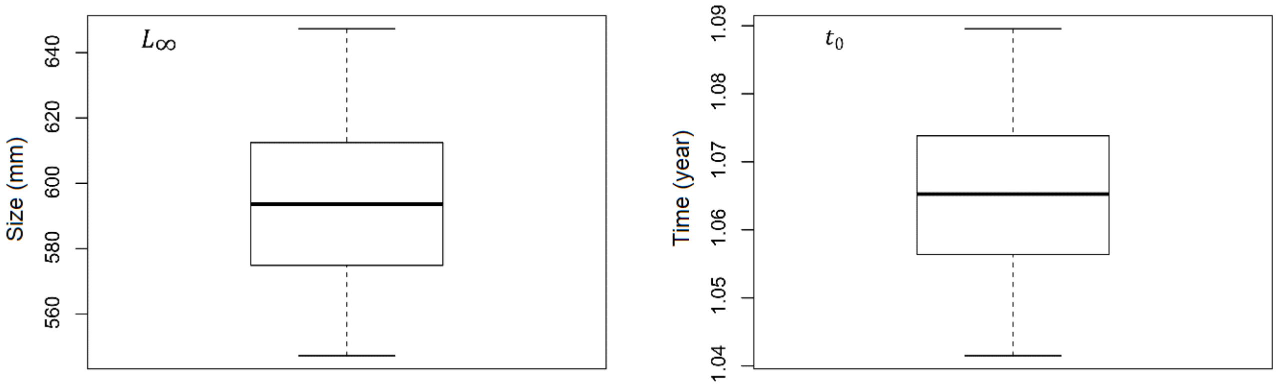

Figure **5.3**: Parameters estimates of L_∞ and t_0.

The median value (bold dark line) is given with the confidence interval at 50% ($CI_{50\%}$, plain boxplot segments) and the confidence interval at 95% ($CI_{95\%}$, thin dotted segments).

Temporal change in growth

Our model did perform well to demonstrate that there were great temporal inter-cohort fluctuations in growth rate. The estimates of the parameter ε are positive but decrease over time (*Fig. 5.4*). Caution has to be paid to the unbalanced amount of data for each time since colonization (t) since in our dataset we had 7 rivers colonized for more or less long time. All systems are nevertheless colonized for more than 20 years, represented by the bold dotted line. According to this truncation, the decrease of the growth rate is clear. Afterwards, the signal is variable but seems quite random.

The differentiation in growth rate (k) according to future migratory status (phenotype) but no spatial effect recorded (river)

In the different studied rivers, there is no variation on the average growth pattern recorded (P-value = 0.9474) whereas the future migratory behaviour of the individuals affects the growth rate (P-value = 0.0171) (*Fig. 5.5*). The higher freshwater growth rate of future migrants is more or less visible according to the studied river, either for sampling purposes or for environmental/biological reasons. The total growth rate in our model is $K = k_{r,p} + \varepsilon_t$, and varies from 0.05 to 0.22.

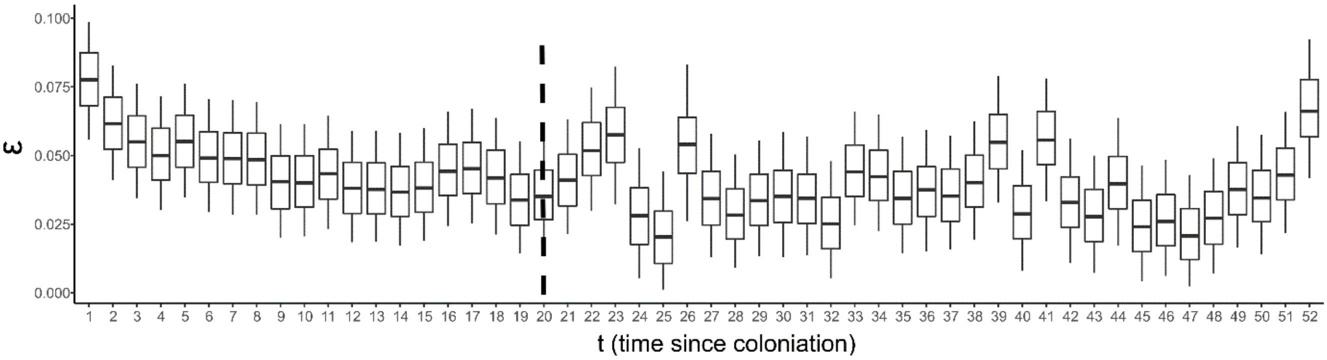

Figure **5.4**: Parameters estimates of the evolution of growth according to the time since colonization (ε_t).

The median value (bold dark line) is given with the confidence interval at 50% ($CI_{50\%}$, *plain boxplot segments) and the confidence interval at 95%* ($CI_{95\%}$, *thin segments).*

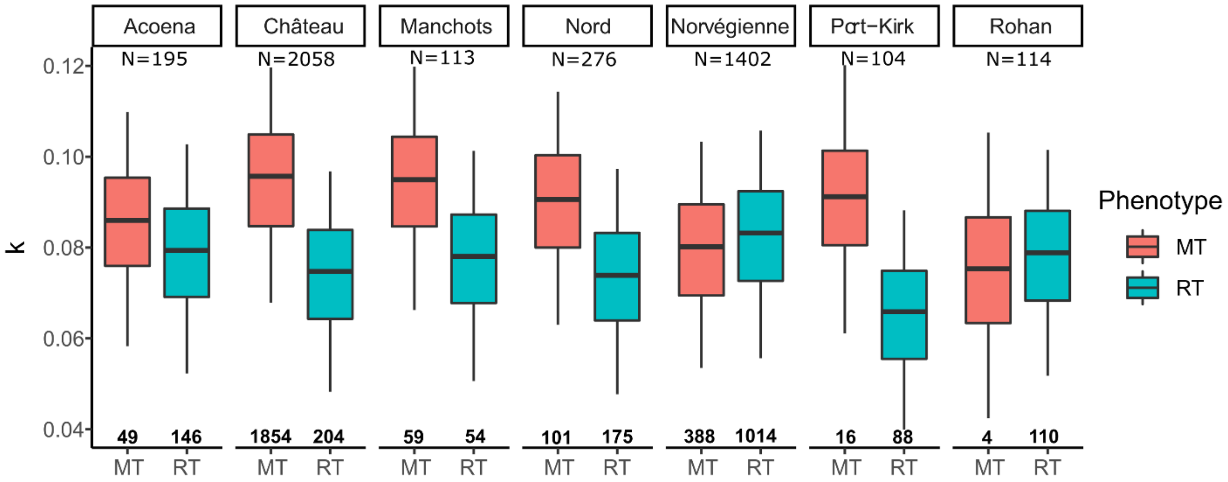

Figure **5.5**: Parameters estimates of the evolution of growth according to river (spatial effect) and phenotype ($k_{r,p}$).

The median value (bold dark line) is given with the confidence interval at 50% ($CI_{50\%}$, *plain boxplot segments) and the confidence interval at 95%* ($CI_{95\%}$, *thin segments). MT stands for future migrant trout and RT for resident trout. N summarize the number of total available samples by river. The number of sample by phenotype-category is given n bold below each boxplot.*

The general evolution of the growth curve, and the estimation of body size at age

As an example, we calculated the average body size at age within the two oldest populations, Rivers Château and Norvégienne (details for other rivers are given in **Appendix C.3**). A general pattern of decrease in body size whatever the age class is observed over time (*Fig. 5.6*). The differences in size within phenotypes are not very significant, but the biggest difference observed over time occurs in the first 5 years. The overlap in body size at age is also less important for the two first year of life, meaning that a greater difference in body size at age is observed for younger individuals through time since colonization. The difference in size between the phenotypes is observable on River Château, but on River Norvégienne the future migrant trout do not seem to be larger than resident. The decrease in body size at age seems also to be sharpest on River Château than on River Norvégienne.

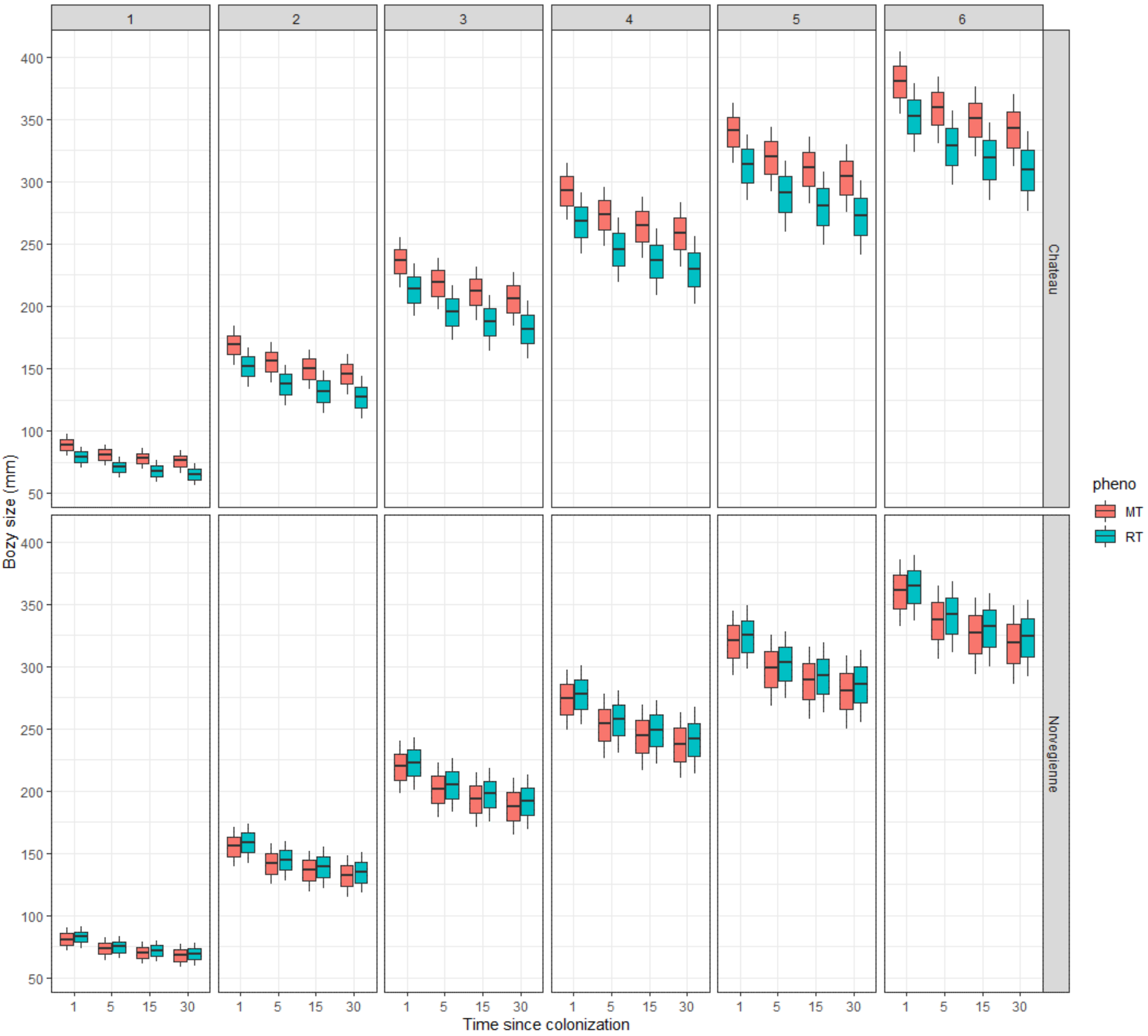

Figure **5.6**: Evolution of the estimated vBGF body sizes, according to the age class, the phenotype, and the river.

The median value (bold dark line) is given with the confidence interval at 50% ($CI_{50\%}$, plain boxplot segments) and the confidence interval at 95% ($CI_{95\%}$, thin segments). MT stands for future migrant trout and RT for resident trout. Results are given only for Rivers Château and Norvégienne (the two oldest population) for different time at colonization. Times at colonization were chosen arbitrarily at 1, 5, 15, and 30 years after the first reproductive event.

Discussion

Model selection and parameters estimates

There is a rich literature about the selection of growth function to infer the growth processes in species (Katsanevakis, 2006; Katsanevakis and Maravelias, 2008; Vincenzi, Jesensek et al., 2020). When developing a mathematical and statistical model in biology and ecology we face a trade-off between model complexity and biological interpretability. The vBGF model we tested gave convergent parameters estimates, under the assumption that t_0 and L_∞ are not evolving parameters through the effect of space and time. Under these assumptions, the values of the estimated parameters appear to be biologically correct ($L_\infty = 593$ mm, $CI_{95\%} = [547; 647]$ et $t_0 = 1.06$ year, $CI_{95\%} = [1.04; 1.09]$). For example, resident trout sizes in Patagonian rivers are comprised between 23.6 cm and 42.2 cm for 4 to 7 years old fish (O'Neal, 1999). L_∞ is often defined at the species level, there is no clear reason to think that the location on the colonization front should affect significantly the value of L_∞. Moreover, it has been demonstrated that the brown trout displays higher body sizes (superior to 400 mm) out of their native range (Budy et al., 2013). The growth rate values ($K = k_{r,p} + \varepsilon_t$) comprised between 0.04 and 0.22 is congruent with values obtained in other studies, either thanks to pit-tagging (Dieterman et al., 2012) or vBGF model fitting (Vincenzi, Mangel et al., 2014). Finally, t_0 can be seen as a proxy of egg deposition. At age 0 ($t_{age=0}$), the body size is positive and equal to the size at hatching. The hypothetical age at which length is equal to 0 is therefore expected to be negative, and the differences: $t_{age=0} - t_0$ could be seen as the development time required between egg deposition and hatching date. The development time (calculated in degree-days) may vary according to environmental conditions such as flow and temperature recorded, but the variation among rivers is not expected to be significant. There is no clear reason to think that the development time should vary between future migratory behaviours (phenotype). The development time might vary with climate change because any increase in temperature should lead to faster development (B. Jonsson and N. Jonsson, 2009). To facilitate the implementation of the model we made the choice not to study the evolution of t_0, because we hypothesize that climate change should shift the development time in the same manner on the expanding front (space and time).

Other biological assumptions could have been made on the influence of time and space on the parameter estimates (accordingly to the preliminary studies). For computational reasons, these models would have been hardly interpretable because of convergence problems. Although we did use vBGF model to study the evolution of freshwater growth, we did not consider maturation, which could be considered as a misuse of vBGF for indeterminate growth (Day and Taylor, 1997). Numerous other improvements of the vBGF model could be made, such as yearly and seasonal vbGF growth (Pitcher and Macdonald, 1973), or a correction for the correlation between vBGF parameters (Sainsbury, 1980). Other biological assumptions have been omitted in this model such as the sex ratio (Grayson and Wilbur, 2009; Guezi et al., 2017; Jarry et al., 2018). Models remain tools that allow us to analyze data. In the case of this study, the data are not homogeneous in time and space, but have the advantage of processing a large spatial and temporal dataset, on populations made up of both residents and migrants.

Evolution of growth in time

The general pattern observed in our study is a decrease in growth rate according to time since colonization. Results of decrease in body size at age is significant for the youngest individuals (1 and 2 years old), whereas more variability is observed for older age classes. The negative density-dependence of growth (increase in competition for resources, *e.g.* food or mates) has already been proven in numerous studies (in fish: Imre et al., 2005; Vincenzi, 2014, in mammals: Loe et al., 2009; Mysterud et al., 2011, in amphibians: Grayson and Wilbur, 2009). To validate this assertion, a study on the evolution of densities could be envisaged. In fact, during long-term monitoring, many samplings have been carried out using electro-fishing to estimate densities (either Peterson or De Lury methods, **Box 1**). Density is probably one of the factors explaining the decrease of growth and confirms the theoretical expectations. There is a strong decrease during the 20 first years after colonization (on average by a factor of 2). After 20 years of colonization, not all rivers are represented, which may partly explain the fluctuation in the temporal growth parameter (ε_t). Another explanation could come from the increase in temperature, even more important at the poles than at the equator. This climate change has an impact on the temperature of waters, which in turn affects growth capacities (accessibility of the resource in particular) (Thompson and Beauchamp, 2016). Further work would be needed to validate this hypothesis.

Individual growth is linked to access to the resource, which may be limited by increased competition (through the effect of density) but also by extrinsic factors, such as environmental conditions (temperature, flow rate, habitat diversity) (Iwama and Tautz, 1981; Nilsson et al., 2006). Theoretical expectations are often in favour of differentiated growth according to the habitat in which individuals live. This is particularly the case for the differentiation of growth in freshwater and marine growth in the brown trout (Pakkasmaa, 2001; Thorstad et al., 2016). At finer scales, as inter-river conditions are not the same, the individual growths observed should vary. However, our model does not allow us to establish a significant difference in growths between the Kerguelen Islands rivers, either for resident trout or for future migrants. Local variability is still observed, but with our imbalanced dataset, it is difficult to conclude clearly on local adaptation.

Differential growth between the future migratory behaviour

It is often demonstrated that individuals with the highest energy demand are those who grow fastest and are the fastest to migrate (Bohlin, Dellefors et al., 1996). Equally, once migration is chosen by some individuals, they might start to allocate more to growth to reach larger size necessary to survive the early marine period. The higher average growth rate for migrant trout seems to suggest that migrant are faster growers, but growth differences may either drive migration decisions or follow from migration decision. The choice of the migratory strategy is often biased in favour of females, who benefit more from migrating than males (Alonso et al., 2009). Indeed, at the expense of the costs associated with migration (loss of energy, risk of mortality), females can generally acquire more energy that they can reinvest in reproduction. The sexing of individuals is not carried out systematically as part of this long-term monitoring. The only effective way to know the sex at present is to carry out mixture models, sharing known information with the entire dataset containing individuals for whom the sex is unknown. Applying such methodology, developed in Jarry et al. (2018), we found that migration was favoured for females (60% of females among migrant), whatever the age at first migration.

Our dataset shows a general differentiation between the growth of resident and future migrant trout, but this pattern is variable depending on the river. Significant differences in growth are observed on Rivers Château, Manchots, Nord, and Port-Kirk, whereas on Rivers Acœna, Norvégienne, and Rohan this result is not evident. In the present manuscript, we have considered two main migratory tactics. The brown trout is a species that presents phenotypic plasticity such that sometimes the morphological diversity of individuals living in the same habitat surpasses the expected genetic differentiation between the migratory tactics (Pakkasmaa, 2001). As an example, the presence of the lagoon at the estuary of the River Manchots, offers growth advantages to migratory individuals because they may benefit from the increase in food supply in the estuary without the costly need for smoltification. On the other hand, if salinities fluctuate a lot through time in the lagoon, this might be quite stressful from an osmoregulatory perspectives

The evolution of growth on the expanding front

Estimated body sizes at age according to time since colonization are similar on every considered rivers whatever the future phenotype except for River Port-Kirk (**Appendix C.3**). This result may seem surprising given the environmental differences observed in these different rivers (see *Chapter 3*, *Table. 3.4*). The local conditions met on the different rivers varies greatly, as for example the length of the mainstream (3.6 km for River Rohan, to 22.2 km for River Château), the catchment area (13 $^km2$ for River Port-Kirk, to 115 $^km2$ for River Château), the estuarine transitions (presence or absence of protected areas at the estuary, or oceanic conditions such as the presence of a bay). Non-significant variations are observed, except on River Port-Kirk where resident trout are the smallest recorded (future migrant trout does not appear to be bigger-at-age). At the margin of the expanding front, this river may open avenues for strong selection against faster growth, or it may simply reflect the small number of fish caught. The reduction of growth rate at the margin could also come from the increase in kin competition in populations principally made of young individuals (Imre et al., 2005). On the different rivers, the brown trout is in sympatry with brook trout (*Salvelinus fontinalis*) on Rivers Norvégienne and Château, and in allopatry in the other studied rivers (see *Chapter 3*, *Fig. 3.1*). The presence of competing species does not seem to affect the growth of individuals. The brown trout is indeed a highly competitive species for resources (Berg, Bremset et al., 2014; Houde et al., 2015; McHugh and Budy, 2006; Zwol et al., 2012), and the effects of competition are minor in the Kerguelen Islands. The lack of effect on individual growth because of interspecific competition has already been demonstrated in Vincenzi, Crivelli, Jeseňsek et al. (2019). Nevertheless, inter-species competition affects other life-history traits and lead to earlier reproduction in lifespan or higher mortality.

No strain effect is detected on the growth patterns. If there was a founder effect through the introduction of different strains (strain from Poland in the Acœna river (Ayllon et al., 2006; Lecomte et al., 2013) and Pyrenean strains in other introduced rivers), we would have expected to observe differences in growth. Two hypotheses may explain the similar growth rate of the two strains. First, individual growth is constrained by the novel environment, which is (at least during the first years after colonization) eutrophic in the Kerguelen Islands. Secondly, under the effect of genetic mixing, the two strains might be observed in the studied populations (Fayard et al., 2009; Glémin, 2005; Wagner et al., 2017). The genetic mixing seems to be validated when comparing human-induced introduced rivers to naturally colonized ones. The individuals who grow fastest are the most likely to migrate. Among migrants, the individuals being in poorer body conditions, negatively correlated to length, might become dispersers (Bordeleau et al., 2018). If dispersers carry genes that induce better growth (Ferguson et al., 2019; Nevoux et al., 2019) then we might have expected to observe better growth in naturally colonized systems if selection favoured these individuals. This phenomenon is not observed. From an alternative migratory perspective, the environment might simply trigger differential gene expression (differential growth observed in space) but the two strains growth pattern does not differ. The early environmental factors may influence greatly the life-history decisions and the phenotypic plasticity in the brown trout.

Conclusion

In the present work, we demonstrated that growth decreases over time since colonization, on every river along the colonization front, possibly through the main effect of negative density dependence of growth. Future migrants presented various growth rate according to the rivers but were among the faster-growing individuals in the Kerguelen Islands. Finally, various growth rates were observed according to the location on the colonization front but no clear conclusion could be made whether the selection operates against the biggest individuals. Overall, the brown trout has been demonstrated to display a great plasticity in their growing pattern. The evolution of growth takes place rapidly after the colonization event. The decrease in growth rate value seems to particularly affect estimates of body sizes at age for the youngest individuals (age classes 1 and 2). For the older age-classes, a decrease in body size at age is observable but is offset for by high variability. Body size at age is a life-history trait involved in the decision to migrate (Bohlin, Dellefors et al., 1996). Individuals need to reach a certain size to be able to migrate because migration is a conditional strategy in partial migratory populations. Further study on the evolution of body size at age, especially for the youngest age classes (early life of fish) is of paramount importance (Cucherousset et al., 2005). Therefore, we decided to study the evolution of body size along a colonization front in the next section of this work.

5.3 The evolution of body size of partial migratory population on shifting expanding range

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The present section is a work in preparation for publication.

Introduction

The evolution of body size is one of the most common trends studied in evolutionary biology. Body size is a fundamental trait known to be linked with metabolic rate, physiology, life history (reproduction, competition, survival), and consequently fitness (Stearns, 1992). According to general rules, the body can evolve either towards larger or smaller sizes. Cope's rule suggests that size should evolve towards larger values according to evolutionary times, because it should confer fitness advantages to larger individuals, by means of reduced predation risks, higher competitive ability for resources and mates. Nevertheless, such an increase in body size implies longer development time, higher food intake requirements, and possibly lower fecundity, what is usually referred to as a shift from a r- towards a K-strategy (Hunt and Roy, 2006). Other models however factor the effects of environmental variation on body size evolution explicitly. The Bergman's rule for instance predicts that within a clade, or within a species, body size will be positively correlated with latitude, and thus negatively correlated to temperature (Meiri and Dayan, 2003). Alternatively, the island rule states that small animals will evolve towards gigantism (through relaxation of predation and competition for instance) and large animals towards dwarfism (through food limitation) (Benítez-López et al., 2020). Body size seems to change adaptively regarding both social environment (*e.g.* competition) and biotic (*e.g.* predation) or abiotic (*e.g.* temperature) non-social environment. It does so at macro-evolutionary levels (Hunt and Roy, 2006; Velasco et al., 2020), but it is also observable at micro-evolutionary scale (D'Amico et al., 2001; Maurer et al., 1992).

The current pace and magnitude of environmental change (McCarty, 2001; Walther et al., 2002) are therefore likely to have a strong impact on body size evolution (Blanckenhorn, 2015; Caruso et al., 2014; Millien, 2004). Shifting population ranges are both a consequence of global change (through local environment variation or through biological invasions) but are also an adequate context to study body size evolution: in particular, they present strong density gradients from the core to the edge of the distribution area. Resource competition at the core is strong, directly affecting individual growth opportunities. To escape a harsh environment (competition, density) (Phillips, 2009), individuals that can disperse may expand the population range. By dispersing, they tend to encounter novel environmental conditions and may be exposed to a different set of selection pressures. As new populations are established, density is low. Under the competitive release hypothesis, growth opportunities are expected to increase. The general expectation is that body size at age should be greater on the expansion range than in the core area according to plasticity, but also due to evolution if spatial sorting of genotypes occurs on shifting expansion range. On the other hand, there are several reasons to expect that body size at age will be smaller under lower densities. First, because there are several costs that individuals should pay to achieve a larger body size (Stamps, 2007). Individuals that must grow for a longer time or develop faster (reduced development time) are prone to higher mortality risks (Abrams et al., 1996). Moreover, the reproductive advantage of being large could be counterbalanced by sneaking tactics favouring smaller individuals. The advantage of being large under high density may not apply at low density. Secondly, the demonstrated negative relationship between average body size and density is expected to be stronger at low density (non-linear relationship between body size and density) especially when most of the population is made up of young individuals (Imre et al., 2005).
However, as the expansion range continues to shift, spatial sorting may happen (Burton et al., 2010). The population expansion rate results from an interplay between dispersal and growth (Deforet et al., 2019). Therefore, the possible evolutionary strategies are dispersing faster or growing faster. Of course, the simultaneous improvement of both traits is even better. Dispersers could also be the largest individuals under the fasting endurance hypothesis (Lindstedt and Boyce, 1985). In both cases, if dispersers traits are selected for along the expanding front, one can expect body size to evolve over time towards smaller or larger value, through spatial sorting, drift and local-adaptation post-colonisation (Graciá et al., 2013; Phillips et al., 2010). This could allow to observe a contrast in body size between the core area and the expansion range. In short, the initial relationship between body size and density among populations in a recently founded metapopulation should gradually evolve to be steeper generation after generation as new populations are founded and the expansion range makes progress. Granted, such a relationship can be substantially obscured by environmental contrasts among the populations.

To test the above hypothesis, we turn to a partial migratory species, the brown trout (*Salmo trutta*) whose body size is a proxy of dispersal propensity while being involved in fitness (Acolas et al., 2012). Benefiting from 60-year long-term monitoring (1956-2019), distributed over 11 populations in the sub-Antarctic Kerguelen Islands where the species was introduced (Lecomte et al., 2013), we investigate the evolution of body size on two independent datasets amounting to more than 27000 individuals.

Material and methods

The Kerguelen Islands is a French sub-Antarctic territory originally free from freshwater fish. Lecomte et al. (2013) record the history and purpose of salmonids introduction. As partial migratory salmonids, the brown trout naturally colonized new rivers, and the species is still expanding (Labonne, Vignon et al., 2013).

We investigated specifically the body size at the age of one-year-old (body size at age-1), when fish are still living in fresh water, so growth reflects the local environment. Over the long-term monitoring, all captured fish were measured (total length, mm), and the day of capture noted. We used two different approaches: in the first one, we aimed at sampling individuals in the database that were older than one year but younger than two years. However, because growth can be very variable in time and space, to ensure the age of the fish, we used Neural Network Learning (knn function of class R package, *ver.* 7.3-14) applied on 46241 fish between 50 and 249 mm long. 6191 were already aged (13%) using scale reading. Based on body size and day of capture (considering July 1^{st} as the anniversary date), we train the neural network using these individuals to predict the likely age of all individuals. On average, the percentage of accurate assignation to an age class was 97% (**Appendix C.4**), and we were able to distinguish 22160 one-year-old fish in 44 rivers. Less than a hundred individuals represented some rivers, so we chose to focus this study on 12 rivers, keeping 19974 one-year-old fish (ranging from 383 to 639 days old). This first dataset (D1) therefore may include a variation of one-year-old fish that has not yet been fully exposed to selection. The second approach relied on a more diverse sample of fish (4556) caught in 8 different rivers (common as the rivers recorded in D1) which age was known through scale reading (1 to 11 years old at capture, median = 4, mean = 4.3, ratio migrant-resident = 0.9). This second dataset (D2) includes information about selective mortality. Using back-calculation, we were able to estimate the body size at age on both datasets (see **Appendix C.4** for D1 and *Chapter 4, Section 4.3* for D2). Body size at ages superior to 1, ranging from 2 to 6, were investigated only through the analysis of D2.

To determine whether body size evolved through space (shifting expansion range) and time, we performed a random forest analysis based on Breiman and Cutler's original code (randomForest *ver.* 4.6-14 in R). We used partial dependence in our two datasets to explore the relationship between the marginal effect of our predictive variables and body size. Predictive variables were time, cohort, river, state and for the D2 dataset only, we included a variable reader, to include for a possible change in scale reading methodology between readers. Time corresponds to the time since colonization where t=0 stands for the first reproductive event recorded in a river (Labonne, Vignon et al., 2013). As time passes, intra-river density increases. Time was therefore taken as a proxy of the density increase, reflecting local level for competition (Davaine and Beall, 1997). We used the cohort (year of birth) as a proxy for homogenous (environmental or evolutionary) change among rivers (populations) over time. The interactive effect of time and cohort records any intra-river variation in terms of population density, temperature shift, or food deprivation, and is the best proxy of phenotypic changes. We also included the river variable to reflect environmental contrasts at a local scale, as well as a state variable, to distinguish between introduced and naturally colonized rivers. We determined the variables importance effect measuring node purity (NP, measured by Gini Index), and mean squared error (MSE). This approach allowed to disentangle local environment effects from the general replicated trends (effect of density gradient and spatial sorting) that we sought to uncover at the metapopulation scale.

Results

Body size varies through the joint effects of space and time. Given the node purity value, the three main variables affecting body size were time, cohort, and river in both D1 and D2, meaning that there was a strong inequality in body size represented by those variables. Readers (D2 only) and state (D1 and D2) variables had no clear effect on body size (*Table 5.1*). Given the MSE index, variables affecting the most body size remain the same on D1, but the spatial effect (river) is the strongest (any change in this variable will increase the MSE by 80.4%), meaning that body size varies more in space than in time (42 rivers). On D2, the MSE index gives that body size varies equally according to space and time (8 rivers). On D2, Reader variable explains most of the change in body size (any change in this variable will increase the MSE by 39.4%), probably because of the change in scale readings methodology during the long-term monitoring.

Table 5.1: Variables' importance effect on body size estimation using two methods: mean squared error (MSE) and node purity (NP) on D1 and D2.

D1				D2			
MSE		**NP**		**MSE**		**NP**	
river	80.4%	time	29564	reader	39.4%	cohort	39605
time	32.3%	river	24978	cohort	19.9%	time	36946
cohort	29.4%	cohort	20239	time	16.9%	river	18765
state	13.2%	state	1552	river	16.3%	reader	5721
				state	13.1%	state	3973

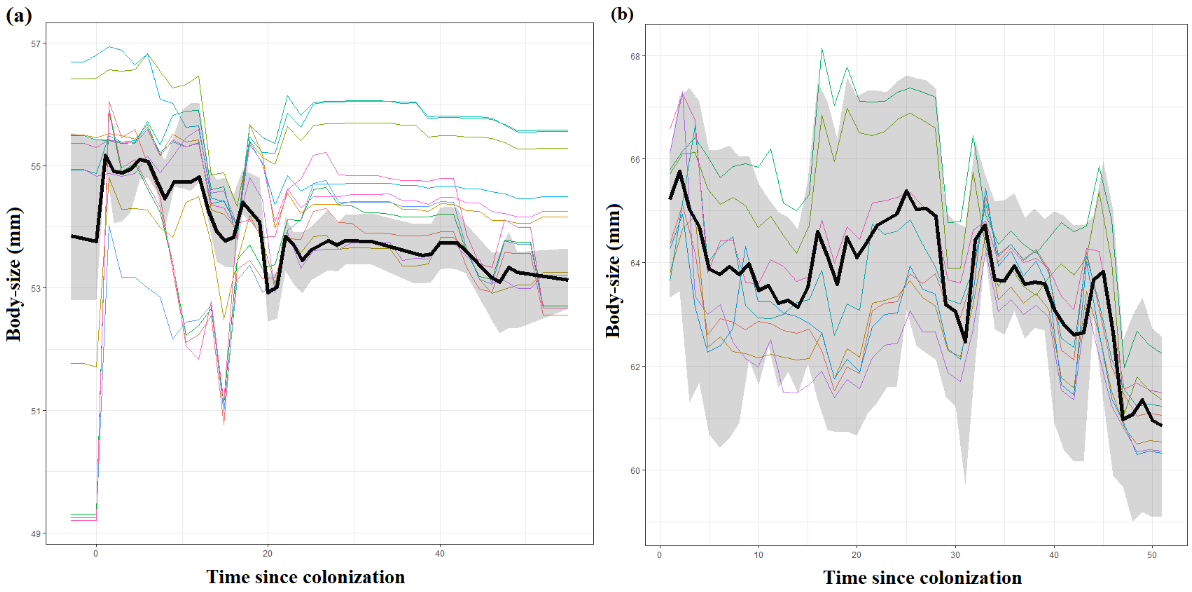

Figure **5.7**: Estimation of the evolution of body size according to time since colonization, for D1 (a) and D2 (b).

The average pattern is given with the bold line and its confidence interval at 75% (grey area). Each coloured lines represents the average pattern observed on each river separately.

The body size is decreasing over time relative to the river, with variation in the estimation of body size from one system to another (*Fig. 5.7*). On D1, the estimated body size is decreasing during the 10 to 20 years post-colonization after an increase in some systems at colonization (time = 0). Then the estimated body size increases again to stabilize. On average, the same pattern is observed on D2, but body size does not seem to have stabilized yet. The between river variation in body size never exceed 8 mm at the age of one.

Body size (D1, *Fig. 5.8a* and D2, *Fig. 5.8b*) decreases over time (density effect), to a greater or lesser extent depending on the cohort (diagonal evolution along the abscissa axis). Changes in body size on D1 are inferior to 6 mm whereas on D2 changes reach 15 mm over time. Along the ordinate axis, which is a proxy of the evolution of body size along the colonization front, no change in body size is observed on D1. On D2, it seems that the body size at first colonization has increased, if we consider the cohort prior to 1976 where fish were smaller. The estimation of body size differs between D1 and D2, and fish are estimated to be bigger on D2.

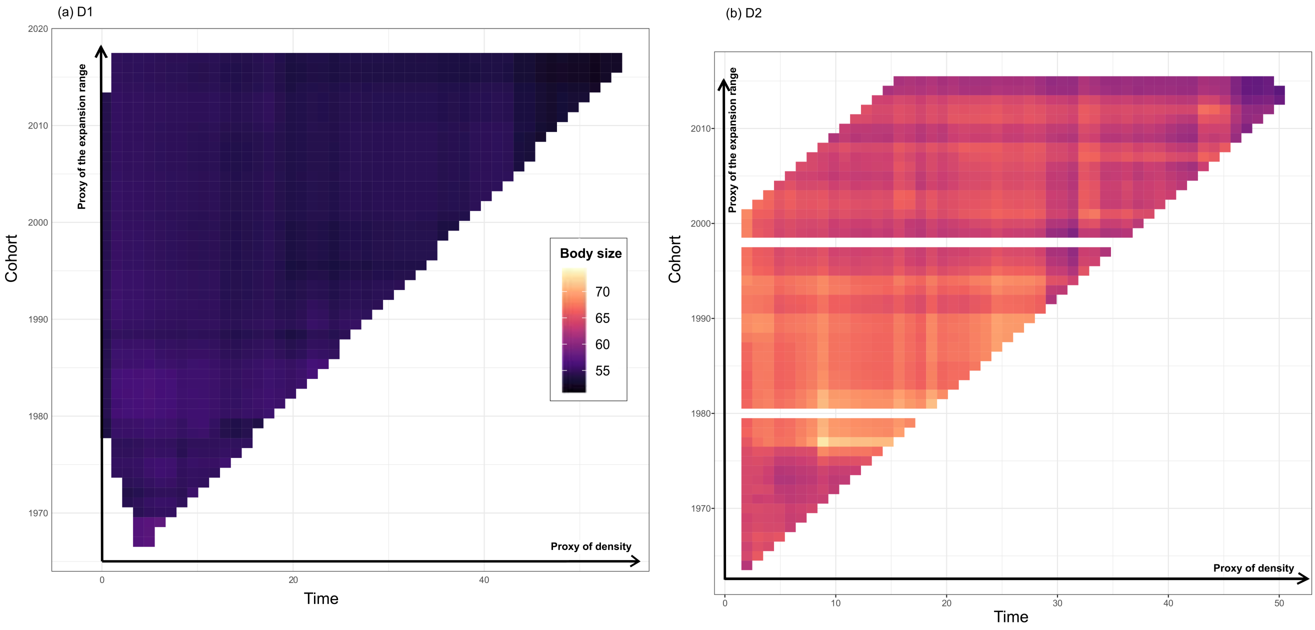

Figure **5.8**: Partial dependence of body size and the interaction of time since colonization and cohort for D1 (a) and for D2 (b).

The scale colour gives the average body size at age; value being higher when lighter and lower when darker.

The analysis of the evolution of body size on D2 for ages 2 to 6 (*Fig. 5.9*), shows the same pattern of a decrease in average body size at age according to time (density). According to the cohort (a proxy of the expansion range), a slight decrease in body size is observable for ages 2 and 3, whereas the change in body size is greater at older ages, meaning either the condition of growth have changed (through space and time) or bigger individuals are being counter-selected. The increase in density affects in the same manner the resident trout and the future migrant trout in fresh water. Moreover, the future migrant trouts are bigger than the resident trout in fresh water at least until the age of 3. Caution must be paid for migrant trout at ages 5 and 6. First because the number of data is scarce. Second, it may be that some already migrating trout are counted among those individuals.

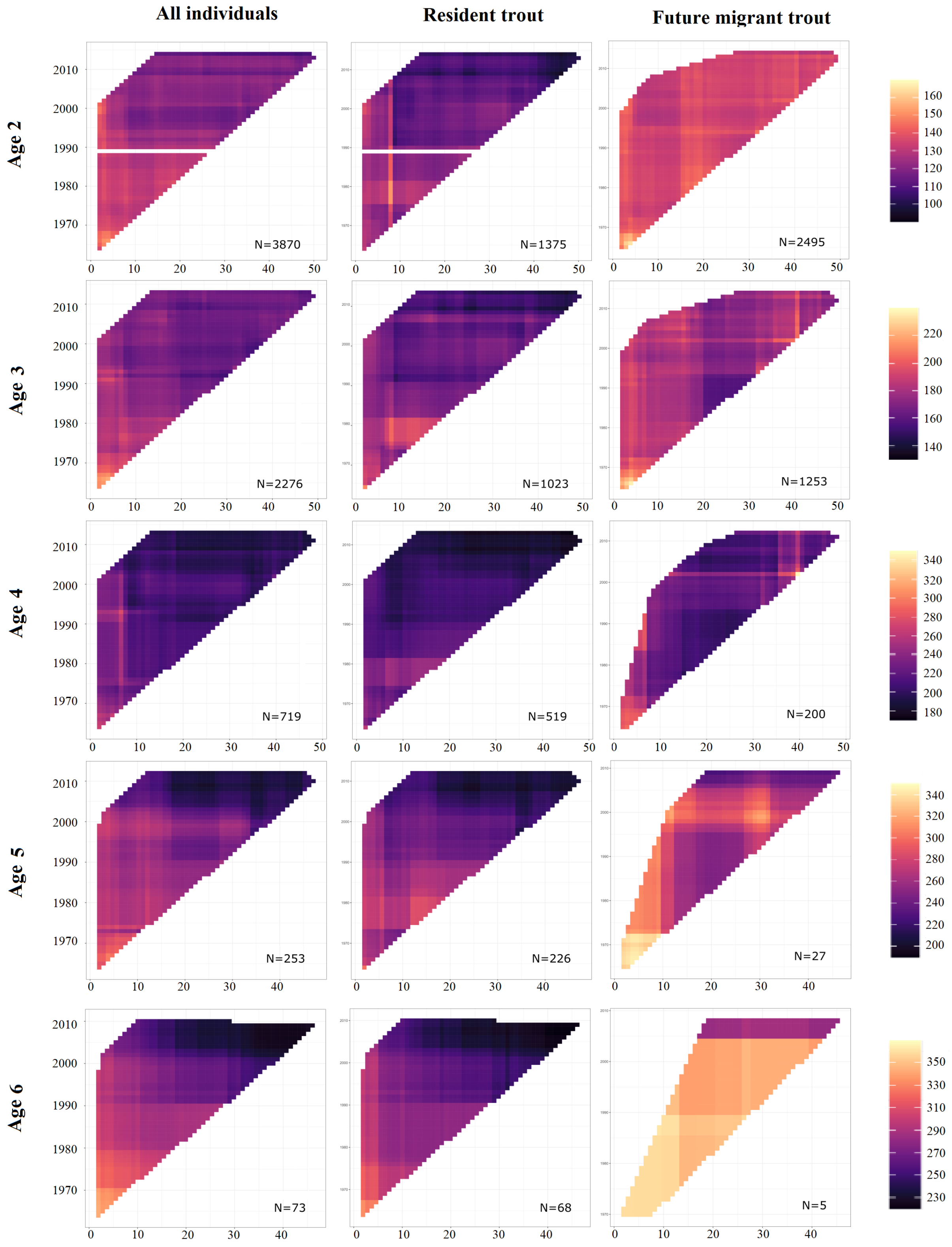

Figure **5.9**: Evolution of body size during freshwater life according to time since colonization and cohort, for the different age classes from 2 to 6.

The same analysis was performed on all the dataset D2 (left column), resident trout only (central column) and future migrant trout only (right column). The scale color gives the average body size at age; value being higher when lighter and lower when darker. Each scale is valid for its age class line. N gives the number of fish considered to fit the random forest.

According to the change in slope observed on D1 (*Fig. 5.10*), the initial relationship between body size and time since colonization (as a proxy of density) in a recently founded meta-population changed gradually to be steeper generation after generation as new populations are founded and the expansion range makes progress. Linear trends are null to negative. Body size tends mostly to decrease with time and density. Nearly all types of populations appear to have declining trends, irrespective of their colonization age. However, in D2, it is not changing in the same direction between rivers: some show little change (despite increased density), some show positive changes (especially rivers colonized in the 80's), some show negative changes. What is happening at the edge is potentially monotonic. It suggests that the driving forces behind body size evolution for this dataset is relatively homogenous. Studying D2, the relationship between body size and density is not linear nor monotonous along the shift of the expansion range. It suggests that the driving forces behind body size evolution have themselves changed.

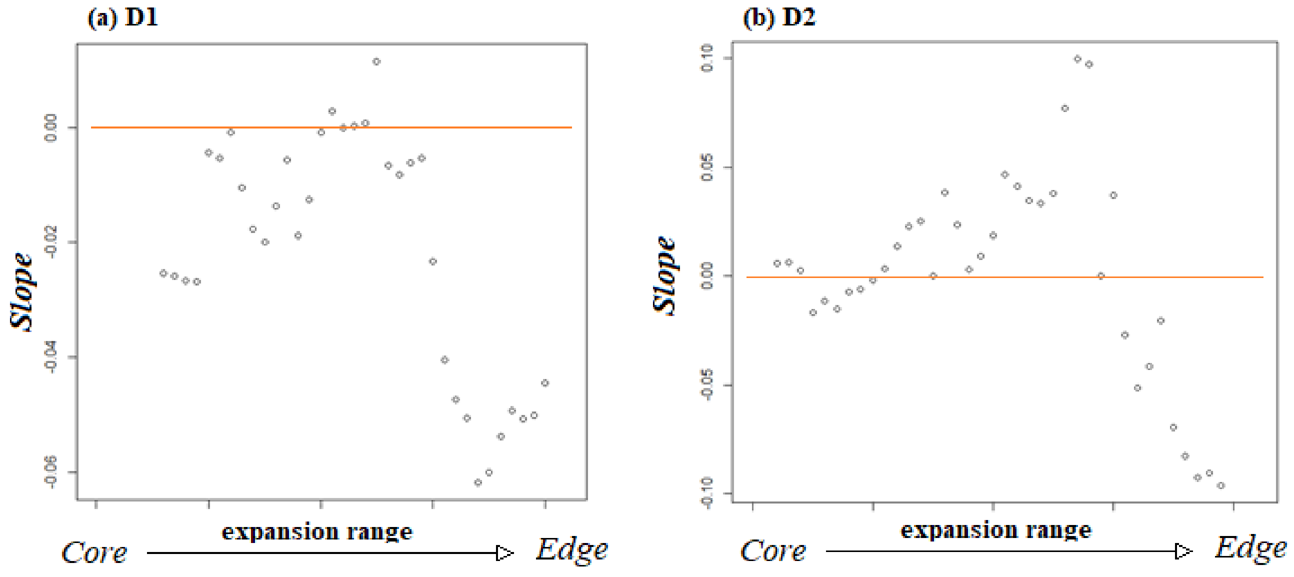

Figure **5.10**: Evolution of the relationship between body size and time (slope) along the colonization front, on D1 (a) and D2 (b).

Discussion

We re-demonstrate the negative relationship between density and body size (Imre et al., 2005). Its validity before and after differential mortality has operated could be observed when comparing results on D1 and D2. The biggest individuals at one year of age (or in the upper classes) are the ones who survive. For reasons of sample sizes, but also because of the errors induced in the back-calculation of the sizes on the D2 dataset (methodology, Reader effect (Aulus-Giacosa et al., 2019)) and misestimation of body size at age (see *Chapter 4*, *Fig. 4.9*), some cautions must be taken when interpreting the results of this dataset. Moreover, while the use of random forest is a good tool to study large and imbalanced data, it is also sensitive to the sampling design.

Density is one of the main drivers explaining the evolution of body size. Other life-history traits such as survival and reproduction could be impacted. We, therefore, expect that in the course of time reproduction or the decision to migrate will be delayed, since both phenomena are linked to body size (Kaitala et al., 1993; Matthysen, 2005; Reznick et al., 2019). Other topics that warrant further investigation are the differential size among sex and its effect on density-dependent emigration (Loe et al., 2009). In salmonids, sex-ratio at migration is often favoured in females (Jarry et al., 2018). The early growth of Brown trout (particularly first and second-year growth) has been demonstrated to play a role in the future migratory behaviour of individuals (Cucherousset et al., 2005) and to depend on the life-history and reproductive investment of females (Taborsky, 2006). Bigger sizes for females induce higher fertility (number of eggs and size (Ojanguren et al., 1996) of the progeny (Carlson and Seamons, 2008). Egg size influences survival and growth, explaining most variation among the populations through maternal effect (Thorn and Morbey, 2018).

We compare the body size of individuals and its evolution on a shifting expansion range on two complementary datasets, obtained through long-term monitoring, and demonstrate that there is no particular selection for bigger body size on the border of the expansion range. The non-significant effect of the initial state of the river (naturally colonized versus introduced) makes it difficult to believe in the complete heritability of the migratory behaviour. In fact, selection seems to act against bigger individuals (Ulaski et al., 2020). Invasive species are often used to explore the impact of range expansion on life-history traits. Traits related to dispersal are expected to be spatially distributed along a colonization front, because of genetic drift and founder effects (Fayard et al., 2009; Labonne, Kaeuffer et al., 2016). In our case, the temporal evolution of body size was consistent across all the studied rivers, and we concluded that smaller body sizes were selected for along the colonization front. D1 and D2 gave different signal shapes concerning the evolution of the relation between body size and density (slope). The signal seemed quite monotonous on D1, being steeper and steeper along the colonization front. It was not the case on D2. Again, caution must be taken while looking at D2 but what can be said is also that density dependence-relationship could take complex varying forms (Harman et al., 2020) according to the local environment.

Under climate change, habitats variability and fragmentation are a source of environmental pressure, linked to body sizes declines in many species (Oke et al., 2020). Spatially structured environments have been demonstrated to favour dispersal at the cost of growth (Deforet et al., 2019). Habitat fragmentation can be argued to explain why bigger is better to ensure longer dispersal distance (Hillaert et al., 2018). In our case, we did not find bigger individuals in the evolution course, neither with time nor along the expansion range. This result supports the hypothesis that coastal dispersion may be less risky (Labonne, Vignon et al., 2013). The case of pristine habitats is not common in the literature making it hardly comparable to other studies of expansion range. However, as the body size is a liability trait to migration, this is a good illustration of the possible evolution of dispersal in areas offering new colonizable habitats.

5.4 Conclusion

In this chapter, we demonstrate that both growth rate and body size at age decrease over time since colonization, along the colonization front. Both phenotypes (future migratory tactics) were affected in the same manner, possibly through the main effect of negative density dependence of growth. The growth rate of individuals during the freshwater phase appears inked to the future migratory behaviour of individuals, with faster-growing fish getting more chance to become future migrants. Among those migrants some may be dispersers.

Along the colonization front, a new population that might have been founded by dispersers does not seem to record bigger individuals at age. On the contrary, we demonstrate that individuals are getting smaller in time and space and that the relationship between body size at age (in fresh water) and density is getting steeper and steeper as the populations are expanding. Selection against bigger individuals seems to operate along the colonization front in a monotonous way.

However, in salmonids, the decision to migrate is often conditioned by the growth of the individuals and their size at age. If the fish are getting smaller and smaller, it is expected that the invasion of new systems will slow down. Environmental induction is an adaptative norm of reaction making possible evolution of threshold trait (Pulido, 2011). If the threshold value for the decision to migrate were stable, we would expect that any evolution of body size at age would lead to a shift in the age at migration. Earlier migration should occur while growth abilities increase and the opposite when growth slows down. However, if body size is stable (environmentally influenced cue), an evolution in the age at migration might also be expected if the threshold value for the decision to migrate changes in time. The evolution of migratory behaviour depends not only on the evolution of the size of individuals at a given age, but also on intrinsic factors governing migratory decisions (genetic or environmental), which opens up research perspectives on the notion of the evolution of the threshold to migration (Phillis et al., 2016).

6 Towards an evolution of the migratory pattern?

6.1 The link between growth and migration, the reaction norm principle

Migration is a widespread phenomenon occurring in numerous taxa, including insects, fish, birds, and mammals. A threshold determines the migration tendency and the liability trait that governs the decision to migrate is often correlated to body size at age (Hillaert et al., 2018; B. Jonsson, M. Jonsson et al., 2016). Individuals with poorer conditions and lower growth have been demonstrated to have a higher propensity to migrate (Peiman, Birnie-Gauvin, Midwood et al., 2017). The opposite being also true in salmonids (Abrams et al., 1996; Acolas et al., 2012), making the question of size as a liability trait quite a controversial question. In partially migratory species, alternative migratory tactics co-exist within the population, and all individuals may adopt any of the alternative phenotypes. Alternative migratory tactics (AMT) are considered as threshold traits because of their polygenic nature (Dodson et al., 2013). The environmental threshold model links the environment to alternative phenotypes through a genetically determined threshold. It involves two components, a normally distributed trait (liability trait) under polygenic and environmental influence such as body size or weight, and a genetically and environmentally determined threshold that will determine the limit value of the liability trait under which a certain tactic is chosen and above the other (Fisher, 1919; Lepais et al., 2017; Wright, 1932; Wright, 1931).

The estimation of a probabilistic reaction norm (Heino et al., 2002) is a particularly suitable tool to disentangle phenotypic plasticity and evolutionary changes. It was first described to study the probability to mature and is still used towards this purpose (Dieckmann and Heino, 2007; Gíslason et al., 2019; Lepais et al., 2017; Siegel et al., 2018). The principle is quite simple. It comes from the fact that the probability of being mature is a function of age and/or size (maturity ogives) and the probability of maturing is a function of age and size (the maturation reaction norm) (Barot et al., 2005). Recently, the concept of reaction norms has been applied to AMT (Pulido, 2011; Sahashi and Morita, 2018; Thibault et al., 2010), body size often assumed as being the liability trait to migration. Any change either in the liability trait (*e.g* body size, weight) or the threshold value may explain the variation in the probability to migrate and the size at migration.

In the case of salmonids, a decrease in the number of migrants has been observed in several populations (Ferguson et al., 2019; Syrjänen et al., 2017). This trend is also being observed in the Kerguelen Islands (*Fig. 6.1*). On Rivers Norvégienne and Château, this number has been divided by four in only ten years. There are two possible reasons for this. First, at the beginning of the monitoring, a very high fishing effort on migrant trout may have increased in the number of migrants caught. The other explanation would be that there is indeed an underlying biological phenomenon, and that the migratory tactic is disadvantaged as time passes. According to the other rivers, the decrease in the number of migrant trout seems to be an artefact linked to fishing effort. Nevertheless, the oldest populations record more migrants than the newly colonized ones (Rivers Port-Kirk and Rohan).

Figure **6.1**: Number of migrant trout caught by rivers during the long-term monitoring and evolution of the age at first migration according to the time since colonization.

Date in the right corner remind the date at first colonization by rivers.

Alternative explanations have been put forward concerning the decrease in the number of migrants. First, this trend could be a response to pure phenotypic plasticity (Stearns, 1989). Second, age at migration could have changed through space and time under the interplay of evolutionary forces (Hargreaves and Eckert, 2014; Pigot and Tobias, 2013; Pruett-Jones and Lewis, 1990; Ulaski et al., 2020). Distinguishing the role of phenotypic plasticity and evolution is a difficult task. An increase in population size (density) is likely to strengthen density-dependent negative effects, for example through a decrease in the access of food per capita. This could in turn result in a decrease in growth rate and potential body size at age of individuals, which in turn leads to delayed age at first migration. In the particular case of the Kerguelen Islands, this increase in age at first migration is an observed trend (*Fig. 6.2*). The average

age at first migration is calculated on a variable number of individuals according to space and time, so caution must be paid while interpreting this graph. Except River Manchots (where the average age at first migration decrease), Rivers Rohan and Port-kirk (where too few migrant trout have been caught), there is an average increase of 1 year in the age at first migration.

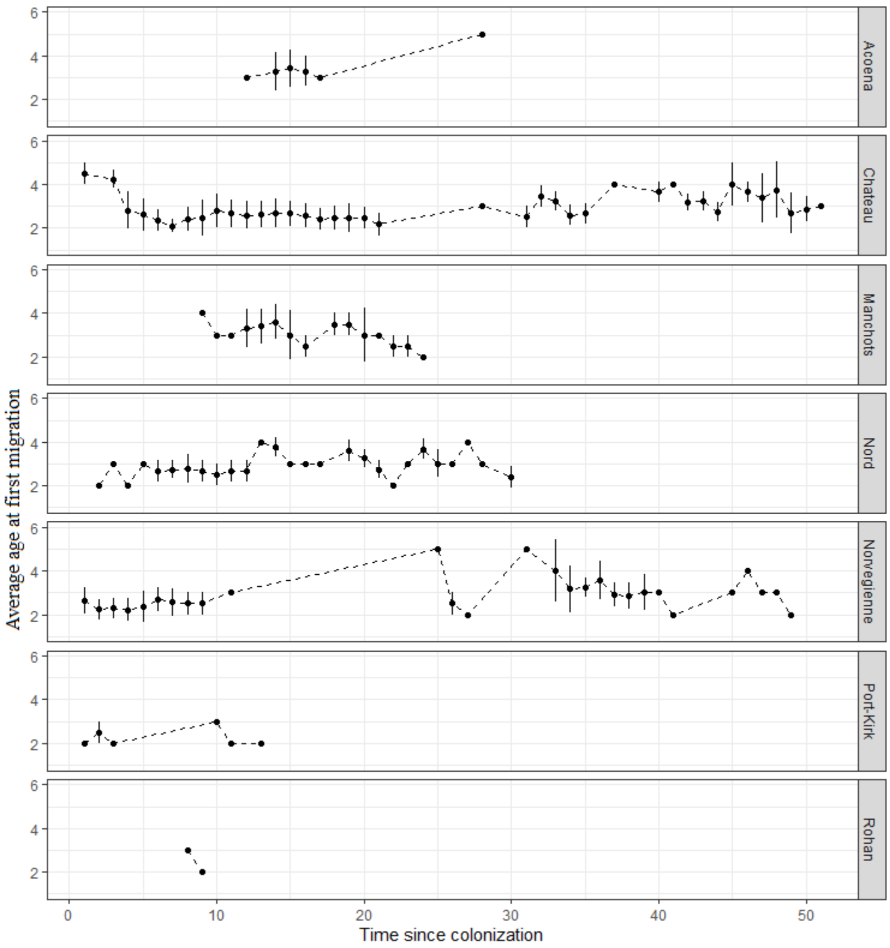

Figure **6.2**: Evolution of the average-age at first migration through time according to the different studied rivers.

Results are given with the standard errors (thin lines). The absence of data records either that no migrant trout were caught or no fishing campaign was led in this particular year.

Partial migration in salmonids relies on an environmentally influenced cue (body size) and a threshold value governing the decision to migrate. Under environmental changes, the average value of the threshold trait may vary while phenotypic plasticity can be stable or evolve. The evolution of phenotypic plasticity is recorded as the evolution of the slope of the reaction norm in the simplest cases. In the case of salmonids, the threshold trait to migration is the optimal size at seaward migration (B. Jonsson, M. Jonsson et al., 2016). As already mentioned, through strong environmental induction (such as mortality induced by fisheries), the threshold may evolve towards either a smaller or larger value. This is a perfect example of a fitness trade-off that individuals could pay (Roff, 1996). Threshold may also be maintained through time. In that case, delayed migration could be observed because individuals are smaller at a given age (change in growth or bdy size at age). In the previous chapter, we emphasized the evolution of the liability trait (growth rate and body size) in time and along the colonization front in the Kerguelen

Islands. If the threshold value at migration does not evolve, we expect delayed age at first migration according to time since colonization. Moreover, on a spatial scale, the relax in competition on the margins seem to favour smaller individuals. It may be that the migrant tactic is less and less favoured and that the shift in the expansion range may be reduced on the colonization borders.

The aim of this chapter is first to look at whether migration reaction norms change over time and space. The comparison of these results with the findings on growth and size of individuals is the second purpose. Cross-referencing these results should enable us to discuss the evolution of partial migration in salmonids along a colonization front.

6.2 Towards the evolution of the threshold size at migration

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The present section is a work in preparation for publication.

Introduction

Migration evokes the movement of individuals at different spatial (within or beyond the individual home range) and temporal scales (seasonal, irruptive) and is observed across a wide range of taxa (Dingle, 2006; Dingle and Drake, 2007). There are plenty of reasons for migration but the most important is the access to resources including access to conspecific for reproduction or access to feeding grounds (Wysujack et al., 2009). Migration helps to fulfil the individual requirements for breeding or maintenance (or both) and is prone to happen when the home range habitat is deteriorating. Any disturbance, such as habitat fragmentation (Cayuela et al., 2019; Gyllenberg, Kisdi and Weigang, 2016; Kuno, 1981) or climate change (Travis and Dytham, 2002), may change the propensity to migrate. There are several forms of migration, the most common being partial migration where only a fraction of the population migrates. Why some individuals migrate while others stay resident is a fundamental question as natural selection occurs at the individual level. Many studies focus on differences in physiological, morphological, and behavioural traits to provide valuable insight into the migration clues. The intra-population variability in migratory tactics depends upon the individual conditions, such as basal metabolic rate (blue tits) or body size (Gyllenberg, Kisdi and Utz, 2008; Jahn et al., 2010). A review of studies shows that no morphotype has a universally higher fitness, and that the relative fitness of two morphotypes is contingent with the environment conditions (Roff, 1996). The expression of one or the other morphotypes is the result of individual trade-off. For example, wing dimorphic insects can migrate, thereby able to escape inclement conditions. This advantage is obtained at the cost of a reduced rate of reproduction (decrease in fecundity, increase in development time). The maintenance of partial migration assumes that in stabilized systems, fitness pay-offs to migrant and resident should be the same or a result of conditional strategies (Chapman et al., 2011).

The conditional strategy is a theoretical framework that explains the existence within populations of individuals that express alternative tactics (Repka and Gross, 1995). From a life history perspective, a life-history strategy is genetically determined and has evolved to maximize fitness under frequency-dependent intraspecific competition. It means that the fitness from an individual life history depends upon other individuals' decisions within populations. For example, the competition to access to territory may depend upon the individual size. The individual success to obtain the territory is dependent upon the size distribution of individuals within the population. Strategies are composed of tactics. For example, the maturation strategy may be composed of early and delayed maturity tactics, where the delay in maturity is an individual decision to mature later at a larger size compared to other members of the population. Within the population, migration is a strategy, and being a resident or migrant are individuals' tactics. In a conditional strategy framework, the concept of threshold traits is often used to explain the expression of alternative migratory tactics (AMT)(Tomkins and Hazel, 2007); whether an individual status exceeds the threshold value for the liability trait will condition its alternative phenotype. The migratory status can arise from genetic polymorphism or phenotypic plasticity. Because of the presence of additive genetic variance in both the liability trait and the threshold-value, migration is prone to changes under evolutionary pressures (Myers and Hutchings, 1986; Páez et al., 2011). As a trait of species that decide to exploit one or several ranges, partial migration makes individuals extremely sensitive to contrast variation (in space and time). One way to study the AMT is the theoretical approach of the probabilistic migration reaction norm (PmRN), allowing disentangling whether the shift in migration age or size is a plastic or an evolutionary response.

The context of expansion range is an ideal situation to assess whether partial migration evolution is likely to occur or not. It is so because density gradients between range core and edges are prominent. Range edges may show different demography than core populations, exhibiting lower density (Fagan et al., 1999). Under positive density dependence, they may be prone to demographic Allee effect. Under this hypothesis, a reduction in individual fitness is expected, explained partly by reduced individuals' cooperation, reduced facilitation, increased predation risks, and increased costs of parental care (Chuang and Peterson, 2016). Under negative density-dependence, individual fitness at low density should be higher, decreasing competition which might mean less need for migration. On another hand, range edges are thought to promote higher dispersal capabilities because of spatial sorting (Travis and Dytham, 2002). Either we believe partial migration is a general trait with a homogenous driver behind, or we believe there are several drivers (ecosystem and potentially dispersal), expansion range studies may be helpful. In such a case, again, expansion range allows contrasting the benefits of dispersers much more than any other situation.

Salmonids are well known for their diversity in life-history forms, and their life-history tactics have been widely studied (Buoro et al., 2010; Dodson et al., 2013). Many salmonids display partial migration, such as within the population both anadromous (seaward migrant that migrate out of the reproductive period) and resident (that fulfil their entire life cycle in fresh water) live in sympatry (B. Jonsson and N. Jonsson, 2011). Salmonids are a good biological species to study conditional life-history strategies such as the particular case of migration. The migration decision rules involve energy thresholds and various components of individual energetic states (Bohlin, Hamrin et al., 1989; Thorpe et al., 1990). In salmonids, AMTs is often expressed as a function of size, weight, or growth rate (Dodson et al., 2013; Hutchings, 2011). Among the population, there are noticeable variation in age and size at migration (as well as variations in others life-history characteristics) that may be explained by the high capacity of both the liability trait and the threshold to respond to selective processes (Hutchings and Myers, 1994; Páez et al., 2011; Piché et al., 2008) or by plasticity. Spatial variations are observed, but temporal variations could also be expected.

Among salmonids, we chose the brown trout (*Salmo trutta* L.) introduced in the Kerguelen Islands, a French sub-Antarctic territory, to study the evolution of partial migration according to both space and time during a colonization process. The dataset used, resulting from long-term field campaigns, records the whole colonization history from introduction/natural colonization up to now (Lecomte et al., 2013) and includes more than 50 years of fishing data. The exclusivity of this dataset makes it possible to test for the temporal evolution of partial migration as well as its spatial evolution along a shifting expanding front. The size of the dataset also allows for replicated analysis, both in space and in time. Based on this dataset, we sought to determine whether age-at-first migration evolved during colonization, studying the first seaward migration occurring during fish life. For this, we used the theoretical framework of PmRN. In this study, the PmRN was calculated for body size at different ages of first seaward migration, using an age-state dependent model. The fact that we look at the decision to migrate of individuals at different stages of their life enables us to avoid a singular conclusion on a single age. To evolve, migration must maximize fitness (reproductive success x survivorship). Migration is expected to occur when the gain in fitness for migrant minus the migration costs exceed the fitness of the resident strategy. Therefore, any increase in the migration costs or increase in the river's productivity (in terms of access to resources: either food or mates) would favour the resident strategy. On the contrary, any deterioration of the freshwater conditions (*e.g.* increase in competition through density effect) at the cost of reproduction would benefit the migrmust face.

Material and Methods

The brown trout is a facultative anadromous salmonid, meaning that within populations both anadromous (seaward migrants) and resident individuals may be found. The anadromous (hereafter referred as migrants) perform a seaward migration out of the reproductive period. For reproduction, both migrant and resident are found in fresh waters, where resident spend their entire life cycle (Klemetsen et al., 2003). The native range of brown trout encompasses Europe, North Africa, and Western Asia (MacCrimmon et al., 1970). Throughout this range, migrants are not found everywhere (Klemetsen et al., 2003). After multiple introductions, the brown trout have now a worldwide distribution (Cucherousset et al., 2005; Závorka et al., 2018). The reason for this is the ability of the species to spread and colonize new. The sub-Antarctic Kerguelen Islands (49°S, 70°E), where the brown trout was introduced in the 50's (complete history of the introductions recorded in Lecomte et al., 2013), is no exception to this colonization success.

Brown trout were sampled during a long-term monitoring in the Kerguelen Islands from 1952 until now in more than 68 locations (rivers and ponds). For this study, we focused on 4044 fish caught in 5 rivers: Château (1962), Norvégienne (1968), Acœna (1983), Nord (1986), and Manchots (1990). The above-mentioned dates in parenthesis record the first realized reproduction and stands for what we will call later the colonization date. Rivers Château and Acœna were human-assisted introduced rivers, while the other rivers were colonized naturally. Mainly caught in spring and summer, through electro-fishing, the fish size (total length, L_T) was measured to the nearest millimetre (mm), its weight was taken (g) and scales were removed in the optimal zone (second rank below the dorsal fin and above the lateral line (Elliott and Chambers, 1996) for later life-history traits determination in laboratory. The phenotype at capture was also a priori determined (migrant *vs.* resident) based on appearance criterion (length–weight relationship (B. Jonsson, 1985) and colouration (Quigley et al., 2006)).

To determine the different life history traits of interest (age, back-calculated size at ages prior to capture (*i.e.* body size), and migratory status), we used scale readings. For the oldest samples, readings were performed using retro-projected images. For the most recent samples, scales were photographed under transmitted light (using a stereomicroscope (Olympus SZX-16) and attached camera (Olympus DP72). Photographs were processed and saved using CellSens Entry micro-imaging software. For this work, and because most of the variability arises at the fish-level, we determined age reading several scales and considered measures of growth taken on one scale per fish only (Aulus-Giacosa et al., 2019). The periodic growth of scales (circuli deposition) is used as a proxy of the somatic growth of fish. During the winter period, fish strongly reduce their growth, and this results in the formation of a visible ring on the scale called the annuli (tightening zone of circuli deposition). The number of annuli formed on the scale is therefore equal to the number of winter the fish went through (*i.e.* its age). The distance between two consecutive annulus records the yearly scale growth and is thought to be proportional to somatic growth (Casselman, 1990; Kipling, 1962). An increase in the inter-circuli spacing indicates that the fish grow faster and is a good indicator of seaward migration. Distinguish migrants from residents based on morphological criterion is possible, but it does not give the age at which the individual made the decision to migrate. We used scales reading to validate phenotype at capture, determine age at migration and migratory status at each read age (resident *vs.* migrant). The total age of fish was recorded by counting the total numbers of annulus. For migrants, age at first migration was determined as the age at which an annulus was formed prior to an increase in inter-circuli spacing. Measurements of growth scales were made along a longitudinal axis (from the core (center of a scale) to its border (total radius, R_T). Each measurement is called a radius, and $R_{i,j}$ stands for the radius measures of the individual i at age j. Finally, to determine body size at each age, we did use a back-calculation model which links the scalimteric growth to the somatic one. We assumed that body size, $L_{i,j}$ length of individual i at age j, is normally distributed, with a certain mean $\mu_{l_{i,j}}$ and variance σ (uniformly distributed). We adapted the Fraser-Lee model (Beall et al., 1992; Ogle, 2013; Vigliola and Meekan, 2009) on $\mu_{l_{i,j}}$ as in the equation (6.1).

$$\begin{aligned} L_{i,j} &\sim N(\mu_{l_{i,j}}, \sigma) \\ \sigma &\sim U(0, 50) \\ \mu_{l_{i,j}} &= 28 + (L_{T_i} - 28)\frac{R_{i,j}}{R_{T_i}} \end{aligned} \tag{6.1}$$

We defined the migratory status (M) as a binary trait based on physical appearance (Nichols et al., 2008; Thrower et al., 2004). M is either zero, meaning the fish has not yet migrated, or one meaning it has achieved seaward migration. Let $p_{i,j}$ be the probability of migrating and $m_{i,j}$ the probability of first migration. A state-dependence relation (6.2) links the two probabilities. It results that the two probabilities are equal if the fish has not migrated the previous year.

$$\begin{aligned} M_{i,j} &\sim B(p_{i,j}) \\ p_{i,j} &= (1 - M_{i,j-1})m_{i,j} + M_{i,j-1} \end{aligned} \tag{6.2}$$

To study the evolution of partial migration, we developed a model describing the probability of first migration ($m_{i,j}$) as a logistic function of age (j) and size ($L_{i,j}$) (6.3). Intercept ($\delta_{r_i,j}$) and slope ($\alpha_{r_i,j}$) of the reaction norm were defined at the population level (spatial effect), depending on the river (r) and age of the individual i. The slope of the probabilistic migration reaction norm was implemented to evolve through time since colonization. An additive spatial and temporal parameter ($\eta_{r_i,j}$) was added in the model to account for any temporal evolution of the threshold at first migration. The variable t records the time since colonization, and varies from 0 (the date at colonization of the river) to 30 for the newly colonized river (River Manchots) or 57 for the oldest one (River Château).

$$logit(m_{i,j}) = \delta_{r_i,j} + (\alpha_{r_i,j} + \eta_{r_i,j}(t_i - 1))L_{i,j} \tag{6.3}$$

We used a Bayesian approach using Markov Chain Monte Carlo algorithms (MCMC) (Bentivegna et al., 2014; Brooks and Gelman, 1998; Hastings, 1970; Hornik et al., 2003; Plummer, 2003) to fit the model. With this method, the likelihood is contained in the data and it allows the description of prior distribution (based on available knowledge). The prior distributions of the parameters (α, η, and δ) were hierarchized by population. It means that individuals at age j in different populations are supposed to share common features in their probabilistic reaction norm. The prior distributions are given in *Table 6.1*.

Table 6.1: Prior distribution of the PmRN parameters (6.3)

PmRN				
Intercept	$\delta_{r_i,j} \sim N(\mu_{1_j}, \sigma_{1_j})$	$\mu_{1_j} \sim N(0,100)$	$\sigma_{1_j} = \sqrt{\frac{1}{\tau_{1_j}}}$	$\tau_{1_j} \sim G(0.1,0.1)$
Slope	$\alpha_{r_i,j} \sim N(\mu_{2_j}, \sigma_{2_j})$	$\mu_{2_j} \sim N(0,100)$	$\sigma_{2_j} = \sqrt{\frac{1}{\tau_{2_j}}}$	$\tau_{2_j} \sim G(0.1,0.1)$
	$\eta_{r_i,j} \sim N(\mu_{3_j}, \sigma_{3_j})$	$\mu_{3_j} \sim N(0,100)$	$\sigma_{3_j} = \sqrt{\frac{1}{\tau_{3_j}}}$	$\tau_{3_j} \sim G(0.1,0.1)$

The joint posterior distribution was derived by means of MCMC sampling. We used the Nimble R package (*ver.* 0.8.0) in R (*ver.* 3.5.3) for implementing the model. We ran two parallel MCMC chains and retained 500 000 iterations (with a thinning at 20 and a burning phase of 5000 iterations). The convergence of the chains was assessed using the Brooks-Gelman Rubin diagnostic (Brooks and Gelman, 1998).

To characterize the effect of time since colonization on the evolution of the PmRN, we focused on the estimated value of η by rivers and age classes. Age classes at first migration range from 2 to 4 in this study, and are respectively denoted 2^+, 3^+ and 4^+. We gave the median and the confidence interval at 50% ($CI_{50\%}$, [25% - 75%]) and 95% ($CI_{95\%}$, [2.5%-97.5%]). We characterized the PmRN at different arbitrarily chosen times since colonization (5, 15 and 30 years) for each studied using age-specific estimates of body size with 50% probability to achieve migration for the first time (m_{50}).

Results

The time since colonization affects the estimation of the PmRN slope in a different manner according to the rivers (*Fig. 6.3*). In the oldest colonized population (Rivers Château and Norvégienne), there is a positive effect of time on the slope value. This trend is not significant for two rivers (Rivers Acœna and Manchots), whatever the age class considered. For the last river (River Nord), there is no temporal evolution of the slope for the age classes 2^+ and 3^+, but the effect is positively significant for the 4^+.

The expression of one or either phenotype (resident/migrant) varies according to time since colonization and on the expansion range, as a result of ongoing interactions between genes and environment. In our model, the positive evolution of the slope could mean that the migratory decision window (in term of body size at age) sharpen as time passes (increasing density). On the contrary, when the slope decreases in time, it could mean that greater plasticity, or at least more variability in the migratory response, is observed. In our case, none of the negative slopes are significant (Acœna and Manchots). Slope values are constant on range edges, suggesting constant plasticity.

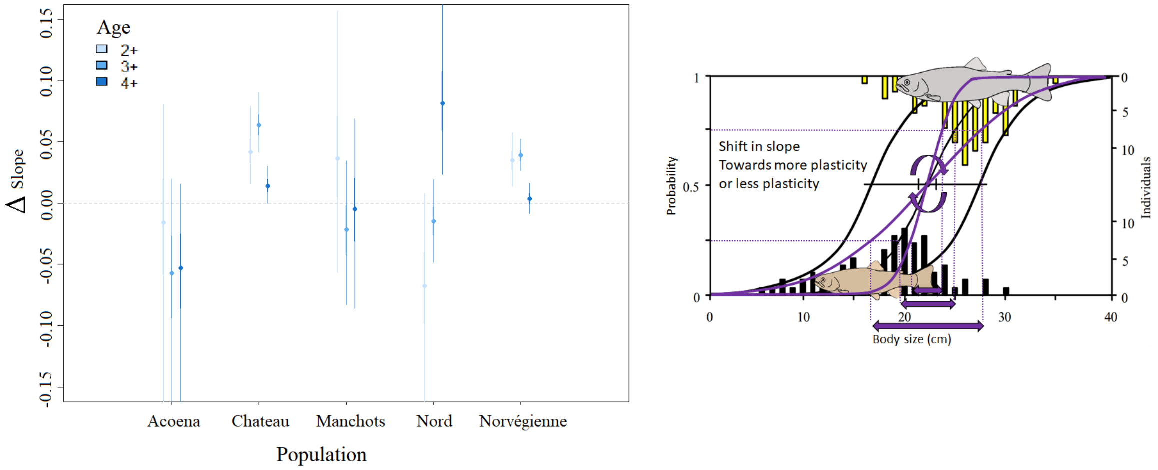

Figure **6.3**: Rate of change of the PmRN slope estimates (η) over time since colonization, according to the age classes at first migration (2 to 4) and rivers.

The size at first migration seems to be conserved through time and space (*Fig. 6.4*), with a minimum average body size value around 200 mm. This means that any individual below this threshold size has very little chance to become a migrant at that age. There is one exception to this main result, observed on Manchots, where the estimation of probable body size at first reaches smaller values at age 3^+. The estimates of body size with 50% probability to achieve migration (m_{50}) increases as age increases on some rivers (Rivers Acœna, Norvégienne) but is relatively stable on other rivers (River Château).

The evolution of the PmRN according to the age classes at first migration varies according to the location of the rivers on the expanding front as well as with time since colonization. There is no clear general pattern towards a migration threshold shift in one direction or the other, i.e. towards smaller or bigger body size at a given age (*Fig. 6.4*). On the two oldest core rivers (Rivers Château and Norvégienne), we observe a decrease in m_{50} over the time since colonization. The threshold value of body size to first migration does not change through time at the age 4^+. On Manchots, the western studied river, there is no evolution according to time since the colonization of the threshold body size at first migration. Rather a huge variability in the threshold body size is observed at 3^+ and 4^+. Any individuals reaching a size of 200 mm got a 50% chance to become migrant at 3^+ and 25% chance at 4^+. On the two border rivers (Rivers Acœna and Nord), the estimates of body size with 50% probability to achieve migration increases with time since colonization for age classes 2^+ and 3^+, in a significant way at 2^+ on River Nord and at 3^+ on River Acœna. At 4^+, the two rivers show different patterns in the evolution of the threshold at migration. On River Nord the evolution of the threshold, favour the migration of smaller body size individuals whereas the opposite is observed on River Acœna.

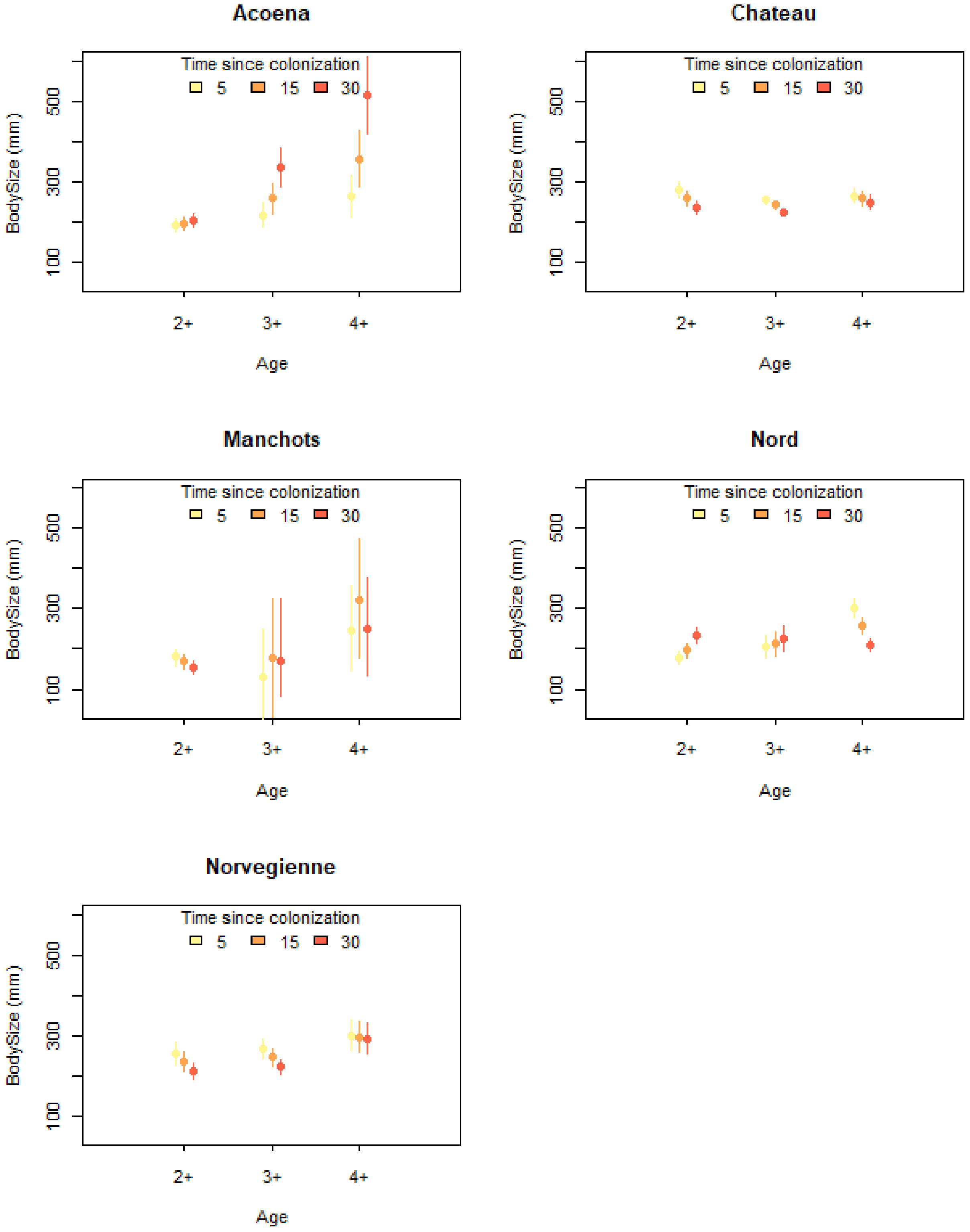

Figure **6.4**: PmRN for each studied rivers at the different age at possible first migration. *Main dot point gives the specific estimates of body size with 50% probability to achieve migration* (m_{50})*, and segment represent the probability to achieve migration at respectively 25%* (m_{25}) *and 75%* (m_{75})*.*

Discussion

To study the PmRN and its evolution through space and time, we use a large longitudinal dataset of rebuilt body size (through back-calculation) as B. Jonsson, M. Jonsson et al. (2016). Contrary to most studies based on capture-mark-recapture, it allows us to rebuilt life histories at different ages of first migration, from a long-term monitoring survey lead in the Kerguelen Islands, in the particular context of expanding colonization front. There are several major findings in the present study. First, the core populations evolved towards less variability in body size response around the threshold value (slope), that could mean less plasticity compared to range edge populations. Second, great variation exists in the estimated threshold body size at a given age over space and time. In early times after the population are being founded, it seems that the core population have threshold value to migration with higher body size values than in the range edges, especially for the younger age (2^+). As time passes (a proxy of density), the threshold evolves towards lower values in the core population whereas the opposite is observed on range edges. Advantages to the migratory tactics are given to bigger individuals on the front wherein the core population there are advantages to migrate smaller after time since colonization. This result suggests that different trade-off acts along a colonization front. Nevertheless, a required bare minimum size of about 200 mm seems to be conserved along the colonization front to migrate. Finally, when populations are being newly founded, the expansion front favours smaller body size migrants. Rapidly, as the population establishes, the shift in the threshold value indicates that larger body sizes are favoured to achieve migration on the edge, whereas the opposite is observed in the core population. Overall, the great diversity of responses along the colonization front over time suggests that selection pressures differ greatly.

Less variable response in body size around the threshold value is observed over time in the core populations and no significant change in plastic response is observed on the edge of the expansion front. Adaptive plasticity seems to change, and there might be different costs for maintaining plasticity along the expanding front. Pigliucci (2005) explains that in some cases, costs are found only in some geographical areas, presumably because of local selective pressures. King and Hadfield (2019), explored the evolution of plasticity in both space and time, and concluded that when the relationship between the environment and selection pressures evolves in space and time, so does plastic response. Plastic phenotypic responses are important for population persistence in changing environments (Beaman et al., 2016; Reed et al., 2010). Traits means (threshold body size at migration) is also evolving according to our spatial and temporal gradient, and responses are geographically different (*Fig. 6.5*). Both traits mean and plasticity can contribute to adaptive responses in the context of expanding range (Kingsolver and Buckley, 2017). The varying pattern between core and edges population also illustrates the local adaptations of the species, in varying environments. The three edges rivers, Acœna, Nord, and Manchots, display great environmental diversity. The presence of the lagoon on Manchots is probably one of the major reasons why individuals in a wide range of body sizes can migrate. As for Acœna, it was founded by a different strain than the other system (Ayllon et al., 2006) and was expected to show a higher propensity to migrate. The fact that the migratory tactic seems defavoured on the range edge could be discussed with regards on the expansion range theory. The expected accelerated invasion rate promoted by spatial sorting (Travis and Dytham, 2002) seems to be highly compensated by other phenomenon such as the demographic Allee effect (Chuang and Peterson, 2016).

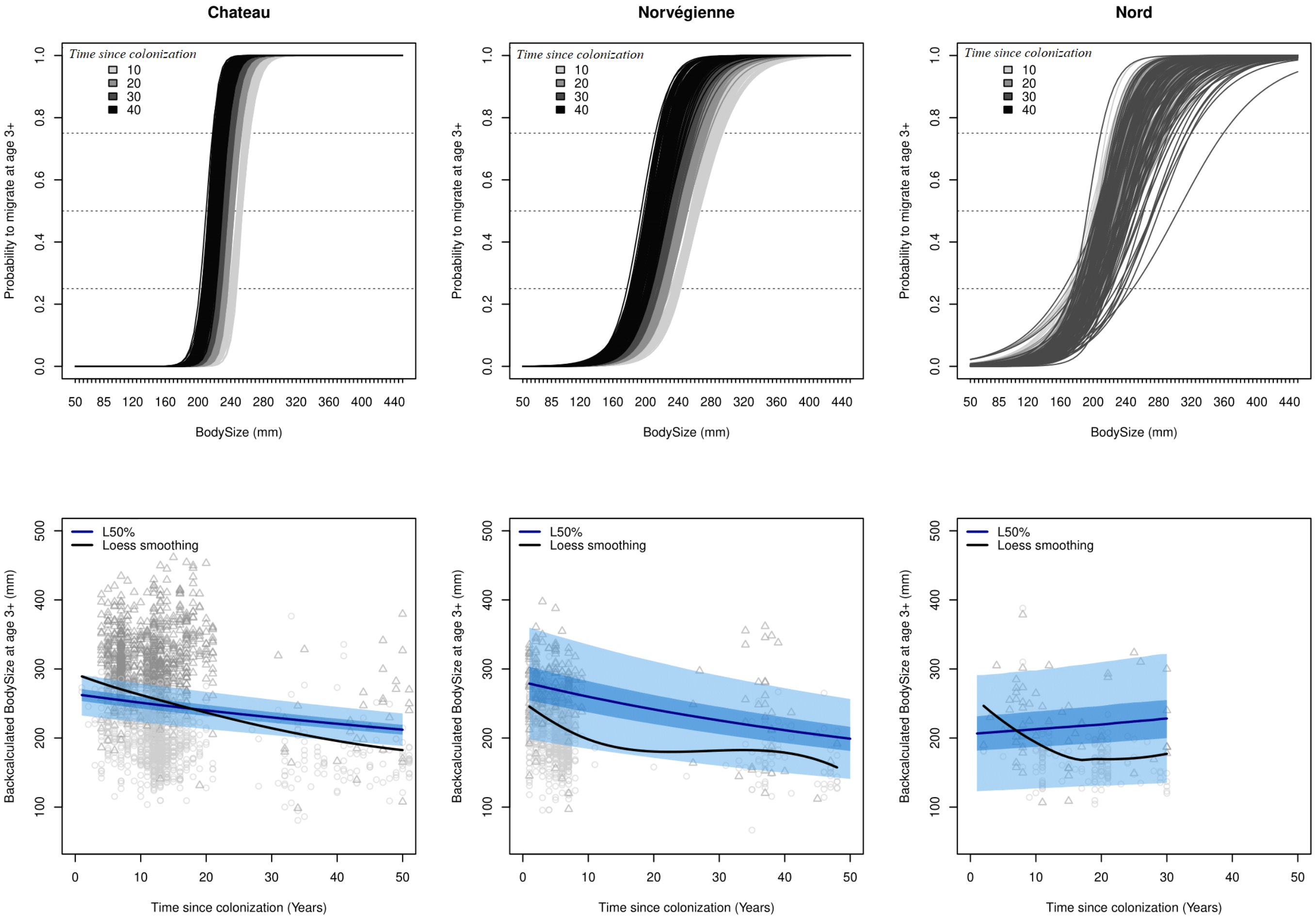

Figure **6.5**: PmRN (above) and body size (below) change in time for three of the studied rivers at the age of 3+.

Triangles stand for migrants and circles stand for residents on the below graph representing the change in body size according to time since colonization.

The evolution of both plasticity and estimated body size at 50% chance to migration are to be compared to body size distributions of the two morphotypes, in the same spatial and temporal frame. In the Kerguelen Islands, we already demonstrated that body size at age decreases over time, according to the increase in density (Aulus-Giacosa et al. in prep, see *Chapter 5, section 5.3*). The evolution of the PmRN in the core population (lower plasticity, lower threshold value at first migration) facilitates the maintenance of partial migration. The average age at migration in those populations seems for now quite stable. Populations on the margins suffer the full extent of a counter-selection against the largest individuals. The negative density dependence of growth is steeper and steeper as the range expands. If the PmRN evolves towards higher threshold values, the dispersive capacity on the fronts is bound to diminish. No such conclusion could be affirmed, but a tendency towards a diminution of the dispersal abilities on the front is expected, leading to a decrease in the invasion rate (Labonne, Vignon et al., 2013). How do stress-related slower growing individuals alter their age at migration to keep fitness as high as possible despite the constraints imposed by slower growth? Combined adaptative microevolution (PmRN) and size-selective exploitation in fish have already been demonstrated to produce the observed pattern of delayed maturation (Gíslason et al., 2019; Kendall et al., 2014).

PmRN helps to disentangle, to some degree, the phenotypic plasticity of life-history traits caused by environmental or temporal change, to evolutionary responses. Nevertheless, PmRN have some shortcomings, especially its sensitivity in the distribution of the sampled individuals and their size distribution at migration (Heino et al., 2002). This is the reason why we removed two recently colonized rivers initially planned to be in our analysis. In the model, we did implement a temporal effect only on the slope of the PmRN. One may want to investigate whether the intercept of the logistic relation will evolve with time. We did not perform these analyses. First because we aimed at comparing population plasticity in a simple way. Secondly, because our dataset probably would not have allowed us to test for such hypothesis, because of convergence challenges. In this study, we present the evolution of PmRN through the glass of the evolution of body size and age. Although this may be erroneously identified if the plastic response is determined by multiple cues (Chevin and Lande, 2015). An investigation of traits along a range expansion is not complete without consideration of associated trade-offs, as they may suggest constraints, mechanisms, and strategies underlying energetic allocations to traits (Chuang and Peterson, 2016). A complete study on evolutionary trade-off, as Buoro et al. did in 2010, in shifting expanding range wild population would be a great topic of future research.

Expanding population range allowed us to demonstrate the evolution of traits related to migration. Contrary to theoretical predictions (Chevin and Lande, 2011), we found that greater plasticity and mean traits evolved in core populations to facilitate migration and thus dispersal. On the edge, no such plasticity was determined and great variations in mean trait were associated to the population. The PmRN should not only be analysed through the study of one driver but several and should aim at analysing trade-off. In our case, trade-offs may be particularly dependent on local conditions on the expanding front. Rapid changes in life history and dispersal ability raise the question of whether continual selection for certain traits can continue indefinitely or if it will eventually be constrained by life-history trade-offs (Chuang and Peterson, 2016).

Discussion on the evolution of migratory tactics and dispersal

Growth rate evolves according to time since colonization on every studied river. One of the drivers of such a decrease in growth rate is thought to be the negative density dependence of growth (Imre et al., 2005). Fitting vBGF according to the future individual tactics helped us to explore the differential growth rate between future migrants and residents. Future migrants show a higher growth rate before migration (B. Jonsson, 1985), the physiological basis of migration being demonstrated (Boel et al., 2014). The growth rate is correlated with higher individual physiological needs. Seaward migration is itself condition-dependent (Bordeleau et al., 2018), conditioning distance, duration (Berg and B. Jonsson, 1990), and marine habitat use. Thus, correlated to migration propensity, the growth rate is also a trigger for maturation, with faster-growing individuals getting more chance to mature earlier (Chapman et al., 2011). Fast-growing individuals in salmonids may thus invest their effort into early reproduction or early migration (and delayed first reproduction) (Bull and Shine, 1979).
Body size at age evolved according to both time and space along the colonization front. Involved in survival (Acolas et al., 2012), body size at age is often used as the liability trait to migration in salmonids (Bohlin, Dellefors et al., 1996). Bigger size is theoretically used as a proxy of dispersal probability (positive correlation) and distance (Gyllenberg, Kisdi and Utz, 2008). Dispersal is a set of mechanisms (departure, migration, settlement) at the origin of the colonization of new habitats by a species. From the core to the edge of an expansion range, spatial sorting may happen (Chuang and Peterson, 2016; Ochocki and Miller, 2017). Dispersers, which are migrants that reproduce elsewhere than in their breeding site, were probably among the fastest growing and the bigger individuals. If the growth rate or the body size at age are transmissible characteristics (Carlson and Seamons, 2008), one may expect better-growing individuals on the edge. Both the decrease in density along the expansion range and the spatial sorting hypothesis, lead us to think that individuals within the newest population might record better growth rate, bigger body size at age, and a higher propensity to migrate. An increase in dispersal during range expansion is expected (Lombaert et al., 2014; Weiss-Lehman et al., 2017). On the contrary, we demonstrate that body size at age is getting smaller in time and space, and that the relationship between body size (in fresh water) and density is getting steeper and steeper as the populations expand. This means that any increase in density on the edge will affect in a stronger manner the body size of individuals compared to core populations. This phenomenon might be explained by food availability that is supposed to be less important on the edge (currently opening habitat) compared to core rivers. Selection against bigger individuals seems to operate along the colonization front. As the range of the population shifts, larger individuals are counter-selected, presuming that being large is no longer an advantage on the edges, probably because of differential geographical trade-offs. Especially, Ulaski et al. (2020), demonstrated that selection on body size for fish migrating to sea was positive or negative according to age-classes.

In salmonids, the decision to migrate is often conditioned by the growth and body size of individuals that are considered as liability traits to migration. If the body size at age evolves towards a smaller value over time and space, we could expect that fewer individuals will be able to migrate to sea. Hence, there will be less scope for dispersal among rivers and we would expect the expansion speed to slow down.

The environmental induction is an adaptative norm of reaction making possible evolution of threshold trait (Gienapp et al., 2014; Oke et al., 2020; Sahashi and Morita, 2018). Migration is an alternative migratory tactic, where the expression of one or the other tactic (residency *vs.* migration) relies upon a threshold trait, often characterized by a threshold value of body size at age under which the resident tactic is expressed and above which the migratory tactic. If the threshold value for the decision to migrate does not evolve, we would expect that any evolution of body size at age would lead to a shift in the age at migration and even could impact the proportion of migrants found within populations (Heino et al., 2002). The evolution of migratory behaviour depends not only on the evolution of the size of individuals at a given age, but also on intrinsic factors governing migratory decisions (genetic or environmental), which opens research perspectives on the notion of the evolution of the threshold to migration (Phillis et al., 2016). We looked at the temporal and spatial phenotypic variation of the threshold body size at first migration. The threshold value was demonstrated to both vary in space and time, presuming the action of evolutionary forces (selection, local adaptation, gene surfing). Moreover, phenotypic plasticity evolved towards greater plastic responses in the core population compared to the edges, facilitating the maintenance of migration. Under the hypothesis of negative density dependence emigration (Harman et al., 2020; Loe et al., 2009), the highest densities found in the core populations would cause a decrease in body size at age, and therefore delay migration or limit the number of migrants. The opposite being in action on the edge. In such cases, and because of spatial sorting (Travis and Dytham, 2002), an increase in invasion rate is hypothesized on the range edges (Weiss-Lehman et al., 2017). On the contrary, spatial sorting may lead to demographic Allee effect, causing a decrease in migration capability on the range edges (Chuang and Peterson, 2016). Not all migrants are dispersers, but some are. We can easily hypothesize that if there are fewer migrants there will be less chance to find dispersers (Harts et al., 2016; Masson et al., 2017). The combination of these demographic effects and its fluctuation in space would lead to the evolution of dispersal on the expansion range.

The simultaneous evolution of the growth rate, body size at age, and the reaction norm (genotype x environment interactions) allows us to conclude that age at first migration will be delayed over time since colonization (as population settle down and grow) and space (along the colonization front) (*Fig. 6.6*). At age-2, even though threshold size values vary according to rivers, the distribution of body size for both residents and future migrants are wider at the beginning of the colonization of the rivers than after a longer time since colonization. After 30 years of post-colonization, no more migrants are caught at age-2. Even though the threshold value at migration evolves towards a lower value, it seems that as time passes, migration at age-2 becomes unfavourable at smaller sizes. For the age-3 and age-4, a decrease in body size is observed as well as a decrease in the threshold size. The joint evolution of these components makes it possible to preserve the migration pattern at these ages, by changing the likely average size of the first migration. This general result is true to a greater or lesser extent whatever the river, except for River Acœna, where the migration seems greatly to be disfavoured at younger ages. Unfortunately, because of a lack of data, it was not possible to decline this study for the most recent populations (Rivers Port-Kirk and Rohan). Colonized naturally around 20 years ago, very few migrants are being caught on those rivers. It could confirm that range edges are unfavourable to the production of migrants (and possibly dispersers), or it presumes bias in our analyses. Among these biases, we could mention the differential fishing effort or sampling design. Sampling biases could come from the chosen sites, or from the lack of scalimetric data to be analysed, problems which can be easily solved before publication. Another bias, which may be more likely for River Rohan, would be that the conditions at the site would not allow the efficient return of migrants (in case these sites produce migrants). Particularly in River Rohan, given the structure of the estuary, it could be that homing, which is predominant in the brown trout (Masson et al., 2017), is not an effective strategy.

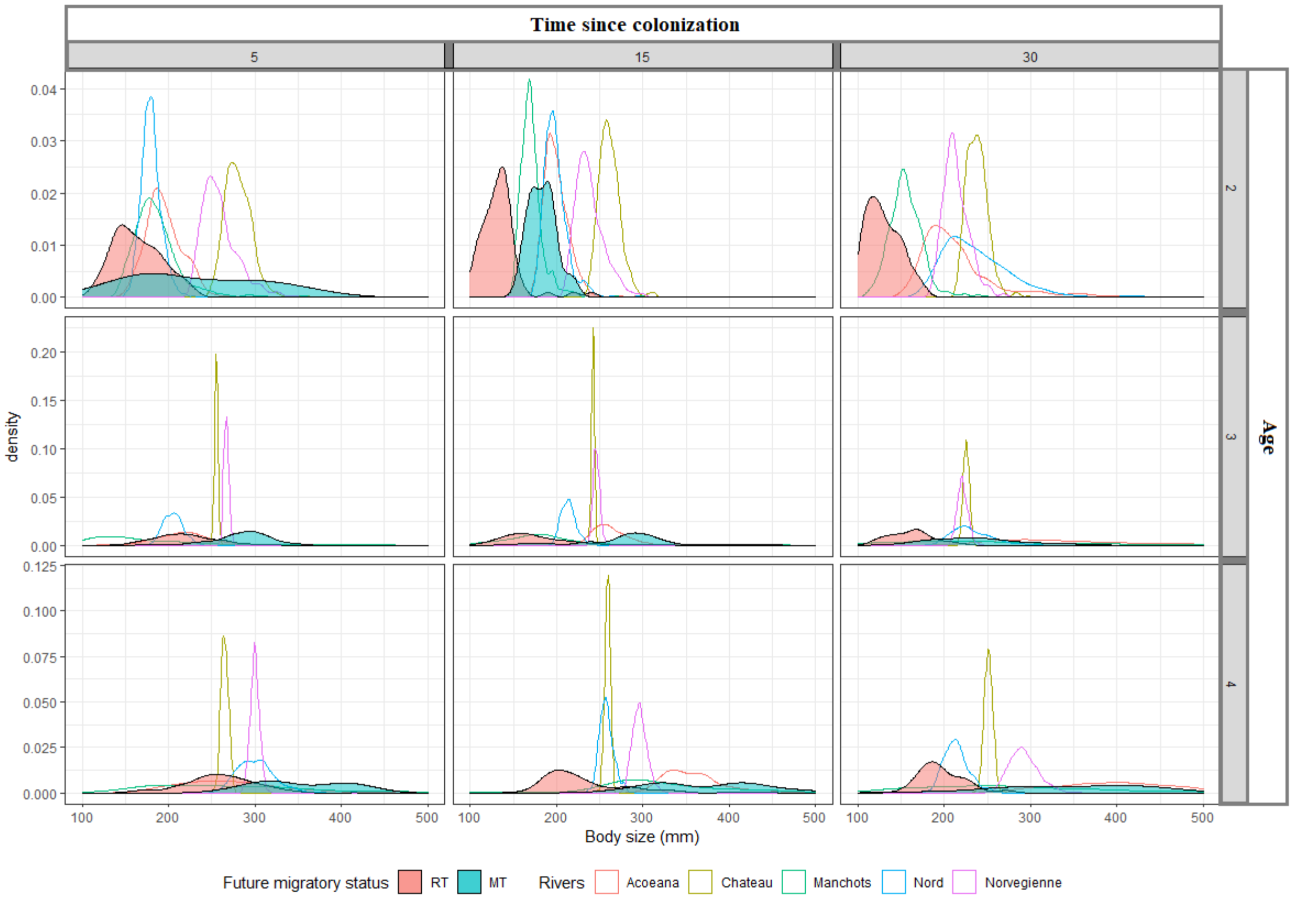

Figure **6.6**: Distribution of body size at age according to future migratory status (plain densities) and distribution of first migration threshold (bell shaped curves) by rivers.

Each age at first migration are represent in lines, and columns represents three different arbitrarily chosen time since colonization, respectively 5, 15 and 30 years.

These migrants, unable to reproduce on their birth site, are forced to disperse, confronted with wandering at sea for no longer, thus either dying, integrating neighbour populations, or founding a new population (if the dispersers find new reproduction sites and are not alone). In the end, it seems that migration is delayed over time, and is sometimes a less favourable tactic on the edges of the colonization front.

A part of the diversity of responses comes from spatial variations. Spatial variations favour the evolution of threshold trait if there is a cue associated with the environment in which individuals finds itself. For protective and trophic polymorphisms, spatial variation may be more important than temporal variation, but for life cycle polymorphisms, temporal or spatio-temporal variation may be critical (Chapman et al., 2011). Dispersal, as a life-cycle polymorphism, is spatially dependent and its form depends on habitat patches (Gyllenberg, Kisdi and Weigang, 2016) and connectivity between different patches (Karisto and Kisdi, 2017). Moreover, patch persistence plays a critical role in the ability to disperse, with a structured environment prone to favour dispersal in amphibians (Cayuela et al., 2019).

In the Kerguelen Islands, theoretical models have proven that the brown trout had a higher chance to display a coastal dispersal (Labonne, Vignon et al., 2013). Spatial variations may also arise from demographic conditions reached in a particular habitat, such as population density. In most studies, density acts as a driver of dispersal, emigration being positively correlated to density (Matthysen, 2005). The most likely hypotheses are the avoidance of competition (Mysterud et al., 2011), interacting with different fitness traits (*e.g.* the accessibility of food, release in the competition for mates). In the case of the Kerguelen Islands, such positive density-dependent migration is observed. Populations from the core, recording the highest densities, display the highest number of migrants caught, even if the migration has been delayed by one year on average. On the range edges, where the density is increasing as time passes, such a phenomenon does not seem to be observed yet, presuming that positive density dependence is not the unique driver of partial migration and that range expansion speed is mitigated by other demographic effects (Travis and Dytham, 2002). The diversity of rivers, in their habitat characteristics, presented in that manuscript may explain the spatial diversity in migratory tactics (age and size at first migration). It possibly either highlights the importance of local adaptation or plasticity. The relative similarities in the growth pattern, and geography met on Rivers Château and Norvégienne may explain that the threshold value, as well as the liability trait to migration, evolves towards the same plastic response. Fish from these rivers enters a wide and protected oceanic Bay, that may be favourable for short-distance migration. The migration fluxes between the two rivers are thought to be important since the two estuaries are close to each other. On some sites, such as River Manchots, the migration is favoured at smaller sizes. It might be that the presence of an intermediate habitat in the estuary (lagoon) changes the migratory fate of the individuals. However, it is difficult to judge the biological explanation for this result. Another explanation is the misclassification of migrants on this river, due to the presence of this lagoon which induces very particular growth trajectories and scalimetric patterns like growth at sea. Concerning Rivers Nord and Acœna, age-2 and age-3 individuals have to be bigger over time to attend migration (early migration is unfavourable). At age-4, the same pattern is observed on Acœna, whereas on Nord, age-4 migration is favoured for a larger range of body size. The migration tendency results from not only the age of the fish but also on local conditions met by the individual.

Another part of the diversity of responses probably represents genetically based local adaptation rather than variation along a norm of reaction. Populations that are geographically different may vary markedly in their life histories, because of their phylogeographic origin (McKeown et al., 2010) or either because of varying environmental conditions such as food availability, or temperature (B. Jonsson and N. Jonsson, 2019; B. Jonsson and Ruud-Hansen, 1985). Multiple introductions can result in populations with equal or greater genetic diversity compared to native populations. Investigations of evolutionary aspects of biological invasions must consider the introduction dynamics (Novak, 2007). In the case of the Kerguelen Islands, several stocks of different origins were introduced (wild polish and domestic commercial). The complete history of introduction and stages of development of the introduced individuals (from eggs to adults) is recorded in Lecomte et al., 2013. Genetic mixtures and multiple introductions are thought to accelerate the range expansion (Wagner et al., 2017). The antagonistic interplay of the propagule pressure and the course of colonization along the expanding front of the Kerguelen Islands, results in an initial rapid invasion phase, followed by a strong decrease in the invasion rate (Labonne, Vignon et al., 2013). Ayllon et al. (2006), studied the genetic structures of populations that came into secondary contact and found different colonization strategy of the naturalized stocks, related to differential performance. They also found a greater proportion of individuals belonging to the lineage of the polish strains within rivers of the Morbihan Gulf. Those individuals displayed higher reproductive success. This might be in concordance with the present results because migrants originated from that population are expected to be older and/or bigger fish (because delayed migration is favoured in that river). This migration at a larger body size might be necessary to survive longer dispersal distance in the gulf (Bordeleau et al., 2018; Eldøy et al., 2015; Sahashi and Morita, 2013). The genetic structure of the freshwater population is probably shaped by the spatial arrangement and quality of the marine habitat itself (trade-offs), which promote or not the migratory tactic and therefore the gene flow (Quéméré et al., 2016). Nevertheless, the phenotypic model presented in this work does not allow to distinguish a single phenotypically plastic genotype from a genetic polymorphism (Roff, 1996). Experiments on salmonids have been led to examine the presence of genetic variations in the threshold trait. The genetic basis of migration is still an ongoing research topic.

The present work is based on a huge collection of data, principally based on scalimetry. Several biases may have been introduced in the study of body size at age because of the choice of our back-calculation model, which is conservative for young individuals but overestimate body size when fish are older than 4 (application of Fraser-Lee, see *Chapter 4, section 4.3*). When comparing to the back-calculated body size of the fish selected via the neural network (knn), the estimation of body size at the age of one is different between the two datasets. This back-calculation model probably will have to be improved, using logistic yearly growth for example. As the same back-calculation model was applied in both growth and reaction norm studies, it allowed us to compare and confront the two complementary approaches. Sampling in the field is not always as simple as we expect. Sampling design may suffer from a selective type of fishing, environmental conditions met on the day of fishing or limitation in the spendable time on a river to fish. All those field limitations explain that during the long-term monitoring, it was not possible to catch fish in every river. This partly explains the unbalance scalimetric dataset we did use in the growth section (see *Chapter 5*) and the reaction norm (see *Chapter 6*). The database used in the present work is still under actualization with older data that were not implemented electronically. It turns that more than **151000 fish are now available in the long-term monitoring database**, among which 90500 are brown trouts. The present work would benefit from such increase in the available data, which will allow the models to be refined and the first results to be confirmed.

Finally, the purpose of this research section was to study traits related to dispersal. If age at migration, freshwater growth, and size are prerequisites for the study of migration, many other traits remain to be studied, such as reproduction (age at reproduction, number of reproductions), or mortality that may also differ in space and time. This study focused on the freshwater phase before migration. Even if freshwater conditions may evolve in time (*e.g.* temperature, food availability) and space (diversity of rivers, *e.g.* water flow, micro-habitat), seaward migration involves another environment which is the sea, where the conditions may evolve as well. Since migration is an individual balance between costs and benefits met in those two environments, any change of one or the other will lead to the evolution of migration itself. The combination of those traits and environments would allow future research on the trade-off driving the alternative migratory tactic along the colonization front.

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Part IV

Conclusive part

7

General discussion

7.1 Quantifying the variation in life-history traits

The objective of this thesis was to investigate the evolution of life-history traits related to dispersal based on the uniquely large and complete database obtained thanks to the long-term monitoring led since the 50's in the Kerguelen Islands. We mainly focused this work on the evolution of migration as a prerequisite to dispersal.

Among all collected data, otoliths and scales provide valuable insights into historical variability in individual growth rate and migratory pattern. In the present work, I focused on how to accurately rebuilt the age and growth of fish based on scales readings, in order to study the evolution of migration. It has been proven that seaward migration makes it difficult to read scales structures, causing an increase in variance both in age and scale size at first migration, thus affecting the estimation of growth and probabilistic migration reaction norms. Nevertheless, since the same dataset was used to perform both analyses, the same biases have been considered. A major part of variance arises from the individual fish level, highlighting the importance of individual variability to be taken into account in statistical modelling aiming at understanding the evolution of traits. By combining several complementary datasets and models, we bring some key insight proving that individual variability is one of the determinants in growth trajectories and migratory strategies.

A rapid shift towards a lower growth rate according to time since colonization was observed, probably through the main effect of negative density dependence. During the 20 first years after colonization, the growth rate is divided by two. Moreover, this decrease seems to affect particularly the estimation of body size at age for the youngest individual (1 and 2 years old). In salmonids, early life has been proven to be of particular importance in the migratory fate of individuals (Cucherousset et al., 2005). Growth abilities vary from one river to another, but the result of our model does not prove significant differences in growth according to the location on the expansion range. I demonstrated that freshwater body size at age (ages 1 to 6) decreases according to the time since colonization. The comparison of two datasets on the evolution of body size at the age of one year old, showed a difference comprised between one and two centimetres. Because back-calculations performed on both datasets were different, a conclusion on selective mortality is difficult.

Delayed migration is congruent with the evolution of body size towards smaller value over time. On average, a one-year delay is observed in the oldest founded rivers (core populations). In rivers located on the edges, the pattern is not as simple and varies in space, highlighting the importance of local adaptations. The joint evolution of the liability trait (body size at age) and threshold value at first migration, allows us to observe the maintenance of migration in core populations, whereas the migratory tactic seems to be disadvantage for the youngest individuals located on the edges. It is difficult to conclude on the evolution of the proportion of migrants within populations along the colonization front. However, our first observations show that more migrants are caught in the core populations. In all cases, our results presume a probable evolution of the brown trout dispersal capacity in a context of shifting expansion range, and these results could confirm the predicted decrease in invasion rate (Labonne, Vignon et al., 2013).

7.2 Mechanisms promoting dispersal

The differences in growth rate prior to migration have been shown in a variety of species. In this work, we re-demonstrated such evidence in growth rate abilities according to the future migratory phenotype. Using vBGF approach, we did not decompose the signal in a year-to-year response, which may be of particular interest. because the migratory fate of an individual may depend on yearly growth. For example, Jonsson (1985) demonstrated that parr that become migrant at age 2 grow faster than parr that become migrant at age 4. In a preliminary approach[1], we determined that the growth was quite conservative during the lifespan of the fish (Spearman correlation test), except for the first year of life, reminding that a great deal of the migratory fate is at stake from an early age. Other studies demonstrated that body size rank is maintained through life (Vincenzi, Crivelli et al., 2019; Vincenzi, Mangel et al., 2014). Nevertheless, this study also showed the results demonstrated by Jonsson (1985) where early migrants were among the better growing individuals within the population during the first year of life, whereas late migrants were among the slower growing ones. Much work on compensation in growth has to be undertaken (Ali et al., 2003; Dobson and Holmes, 1984).

The shift in the probabilistic migration reaction norm highlights the adaptative microevolution. The differential evolution of the slope along the colonization front raises the question of the evolution of plastic responses. Phenotypic plasticity refers to the changes in organisms' characteristics in response to environmental change. The evolution towards greater plasticity is hypothesized when species are introduced out of their native ranges (Richards et al., 2006). Differential plasticit responses are observed along the Kerguelen Islands expansion range, where plasticity is lower in the core populations. On the edges, no such evolution of phenotypic plasticity is observed, highlighting the differences in response magnitude over populations (Kendall, Dieckmann et al., 2014; Kendall, McMillan et al., 2015). Reduced phenotypic plasticity on the core may mean smaller decision window in term of body size (selection for an optimized migratory phenotype at that age) or may simply mean that the species is now responding to another environmental variable (Chevin and Lande, 2015). The difference in plastic response along the colonization front probably highlights other evolutionary forces at work, such as spatial sorting, assortative mating, or genetic drift (Gienapp et al., 2013). In fluctuating environments, that are less predictable, the evolutionary theory predicts that phenotypic plasticity should evolve to lower levels, because it could induce mismatches between plastic responses and selective pressures (Leung et al., 2020).

Interestingly, the relation between time (a proxy of density) and body size becomes steeper and steeper as the population is located on the edges of the expansion range. This result highlights that the environment may be a great source and inducer of phenotypic and genotypic variability and that natural selection may fix this variation giving the rise to a novel ecological pattern (Abouheif et al., 2014). With the evolution of populations, and particularly their density, being large may no longer be an advantage (Ulaski et al., 2020).

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[1] Work developped by Paul Gouzou (intern under my co-supervision). This work is not presented in this manuscript.

7.3 The context of expanding populations

Understand migration a pre-requisite to dispersal, though all migrants are not dispersers but all dispersers are migrants (Hatch and Jiao, 2016; Masson et al., 2017), is of paramount importance in an invasion context, because it gives clues to population management and conservation (Martin et al., 2015). The invasion process can be viewed as a series of steps that are initiated when propagules of a species (such as seeds, eggs, larvae, vegetative material, or mature individuals) are moving out of their native range and established in a new area. However, little research has focused on the evolutionary aspects of biological invasions and addressed how evolutionary mechanisms may contribute to the success of an invasion (Novak, 2007). Some theoretical work has highlighted the persistence of population in an unstable environment, where dispersal has allowed converting habitat instability into profitable conditions (Copp et al., 2005; Kuno, 1981). The novel climatic conditions, and the global change which is the strongest at the poles (Bergstrom and Chown, 1999; Turner and Overland, 2009), are predicted to strongly affect the fate of both native and invasive species. The context of salmonids expanding populations in the Kerguelen Islands provides a perfect and unique occasion to study the evolutionary mechanisms that may contribute to the success of an invasion.

The shape of the dispersal kernel is critical for the genetic structure of diversity along an expanding front (Fayard et al., 2009). Invasions initiated with several genetic mixtures have been demonstrated to boost local demography (survival and population growth) during the initial stages of invasion (Labonne, Vignon et al., 2013; Wagner et al., 2017). Several genetic mixtures were introduced in the Kerguelen Islands, and we tried to study introduced versus naturally colonized rivers, to observe whether the initial state of the population (founder effect) affect the fate of migration along the colonization front (Labonne, Vignon et al., 2013). However, this first approach does not make it possible to distinguish genetic effects from other evolutionary forces. On the other hand, such genetic mixtures do not always affect the dispersal ability. Theory suggests that spatial sorting may favour the dispersal ability on the edges thus allowing accelerated expansion range (Ochocki and Miller, 2017; Weiss-Lehman et al., 2017). Where natural selection selects for genotype through time, spatial sorting operates through space (Phillips and Perkins). The importance of parental contribution to offspring migratory behaviour is demonstrated in salmonids, and the genetic basis of migration, either direct (Nichols et al., 2008) or indirect (McLennan et al., 2017), is greatly discussed (Debowski and Dobosz, 2016; Ojanguren et al., 1996; Rosenfeld et al., 2015; Taborsky, 2006). If dispersal is under genetic control, one may expect to observe a genetic structuration along the colonization front. Nevertheless, the local demographics process can mitigate this general result (Travis and Dytham, 2002). Shifting expansion range have to be studied as a combination of trade-off to accurately predict the fate of a population. Dispersal refers to an entire cycle from the decision to migrate (departure) followed by transience (migration) to finally end in the settlement of the organisms in a new population (Berthold and Terrill, 1991). These three steps necessary for dispersal are all based on cost-benefit balances, both in terms of reproduction and survival. On an expansion range, and in any context of environmental or temporal change, traits related to reproduction and survival (fitness) are also expected to evolve.

8

Conclusion and perspectives

It is an ongoing issue to better understand colonization process, adaptation potential to new environments, and invasiveness of a species (Lecomte et al., 2013). It is useful to analyse such process that happened in the past to be able to do more reliable modelling about future fish dynamics (Piou and Prévost, 2012). Invasion ability of a species depends on several factors: number of propagules, survival, variability of life-history traits among species, competition, anthropic pressure, climatic conditions among other things. To be able to model population dynamics in an invasion context, sub Antarctic Kerguelen Islands are a perfect model. This unique dataset, of long-term monitoring fishing data from the 50's until now give valuable insight on the possible evolution of migration in salmonids in a context of expansion range. The full potential of this dataset could not be exploited in this manuscript, but it opens many new avenues of research. These include changes in population density, genetic structures, and the evolution of other life-history traits such as reproduction and survival. Scales are valuable materials, and many data is still to be exploited. Other biological materials can also be used to answer many other questions, such as otoliths (habitat use, growth, ageing), fins (sequencing) or other samples such as stomach contents (resource use).

The approach taken in this manuscript focuses on the evolution of one of the prerequisites to dispersal, which is migration. The major advantages to dispersal are the release of density-dependence, which imply that the growth and the energy acquisition increase. The individuals may therefore invest this energy acquired at sea in the next freshwater reproduction. Migration also implies costs, the most famous being mortality (*e.g.* predation risks). The balance between costs and benefits of migration may also vary in space and time. The demonstrated evolution of migration does not prevent from deeper studies on other life-history traits, to understand underlying trade-off in the decision to migrate. Further studies on differential freshwater mortality and reproductive capacity (age at reproduction, number of breeding attempt, and number of offspring) are needed to fully exploit this unique dataset. A few lines of thought and studies to be carried out are evoked.

If natal conditions, migration route, or destination conditions evolved so will the benefits and costs of migration. The evolution of the oceanic conditions in the Kerguelen Islands may be one key to migratory tendency. If the benefits (increase in growth at sea) diminish over time or are counter-balanced by increased costs (higher mortality), the fitness of the migratory tactic could decrease. One may thus be interested in studying the evolution of growth at sea (Jarry et al., 2018). Numerous studies are being led on the link between body size at migration and marine residency (Bordeleau et al., 2018; Eldøy et al., 2015). Among migrant individuals, the sex balance could be studied, to understand the link between migration and reproductive abilities (Ayer et al., 2018; Jonsson, 1985; Rundio et al., 2012; Wysujack et al., 2009). Moreover, one may want to study if the advantages at sea are equal whatever the age at first migration or if the balance costs-benefices depend on the age-class. Finally, numerous studies are being led on the implication in oceanic conditions changes on individuals' survival and recruitment (Friedland, 2000; Thorstad et al., 2016). The capture-mark-recapture campaign (CMR) conducted on River Norvégienne in the 1980's may well be a workable dataset to answer many of these questions.

In addition, new research on seaward migration in the Kerguelen Islands is being carried out through acoustic-tracking monitoring (in which I was fortunate enough to participate). The monitoring of these acoustic-tracked fish should teach us more about the use of the marine environment (**Appendix A.2**).

The term evolution refers to heritable characteristics. Evolution might therefore be understood through the study of genes. Many studies are interested in the genetic character of migration, in particular by demonstrating the heritability of size or even the dispersive capacities themselves (Nevoux et al., 2019; Roff, 1996). The fate of genes in expanding population range are of particular interest to study founder effects and genetics bottlenecks involved in the establishment success of invasive population (Labonne, Kaeuffer et al., 2016). The recent development of molecular tools could be one of the major issues to pursue on (Blanchet, 2012). Beyond genetics, indirect links also seem to exist between the dispersive capacity of individuals and that of their parent. Recent studies conducted on the isotopic tracers contained in the otoliths of trout show that the juvenile period to free oneself from the maternal signal is more or less long[1]. Parental influence and the role of epigenetics are two other avenues not to be neglected.

All these studies at individual, populational and metapopulational scales can also have consequences on trophic dynamics (Brodersen et al., 2011) and communities. Partial migration may be a vector of freshwater enrichment. The presence of trout in originally pristine streams also has consequences for local species, especially in the trophic chains. Indeed, it would seem that the presence of trout in the Kerguelen Islands could be the vector of change of niches and habitats of two tern species, the arctic tern (*Sterna paradisaea*) and Kerguelen tern (*Sterna virgate*). This track may be developed for the next field campaign.

Biological invasions have reached an unprecedented level and the number of introduced species is still increasing worldwide (Chabrerie et al., 2019). The brown trout colonization success in the Kerguelen Islands still offers many research perspectives to understand the evolution of dispersal in a changing world.

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[1] Work developed by Hervé Rogissart (intern under my co-supervision). This work is not presented in this manuscript.

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Part V

APPENDICES

A Supportive information to Chapter 3. Individual selection in a spatio-temporal framework

A.1 Status of knowledge in 2019 on presence of salmonids in streams and waterbodies of the Kerguelen Islands

The following table records all the information about the presence/absence of salmonids in the different streams and ponds in the Kerguelen Islands. Names follow the 1/100 000 IGN (French Geographic Institute) map nomenclature of the Kerguelen Islands To understand the number, the associated Map was extracted from the paper of Lecomte et al. (2013). Most of names are from the repertoire of the Commission Territoriale de Toponomie (1973). For some unnamed streams,we gave temporary names or numbers according to geographic or topographic features. Holding ponds are shown by *. NV: not visited; NS: not sampled. Code in the first column refer to previous works of Labonne et al. (2013).

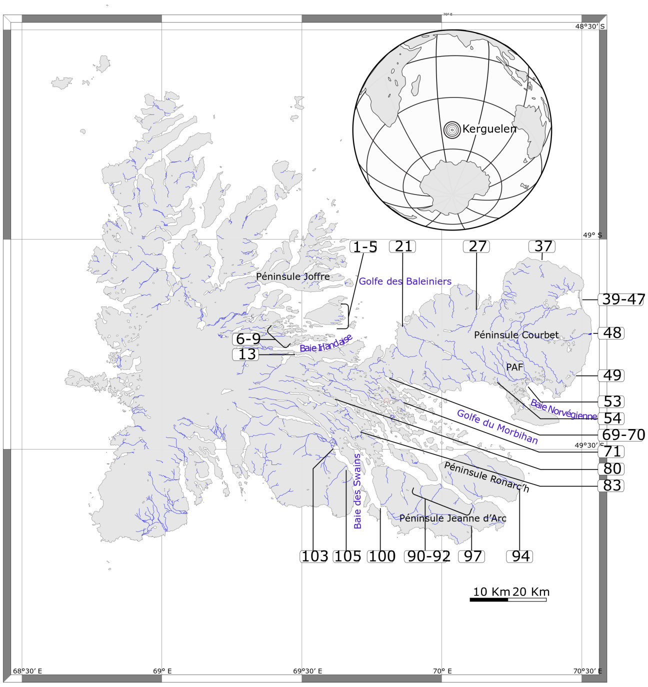


Figure A.1: Map of the Kerguelen Islands showing rivers surveyed, and their referring numbers.

Code	Site	GPS position of estuary	Estimated 1rst repro *Salmo trutta*	Date last sampling	Species present at last sampling	Strayers (date seen)	Possible colonization	Comments. For human introduction, year of the1rst successful
NORTHERN Is. & PENINSULAS								
190	Peninsula Loranchet, Anse Excursion (river?)	48°52'58''S 68°57'51E	?	2018		*Salmo trutta* (2018)	Yes (several rivers)	Rod fishing, 11 sea trouts
191	Peninsula Loranchet, Anse du Jardin (river?)	48°51'13''S 69°00'49''E		2018			Yes (several rivers)	Rod fishing
192	Peninsula Loranchet, Port Léontine (V. Rapides)	48°59'08''S 68°59'46''E		2018			Yes	Rod fishing
193	Peninsula Loranchet, Anse du Ring (V. du Ring)	49°05'25''S 68°58'36''E		2018			Yes (several rivers)	Rod fishing
194	Baie Française, Anse du Cartographe (river?)	49°07'47''S 69°12'44''E		2018			Yes	Rod fishing
195	Cascade de la Lozère (outlet Lac d'Astée)	49°05'00''S 69°36'30E	? - 2017	2019	*Salmo trutta*		Yes	
196	La Bastille R.	49°02'18''S 69°33'35E		NV			Unknown	
199	Sinaï R.	49°09'16''S 69°19'52''E		NV			Unknown	
200	Mont Ventoux R.	49°09'58''S 69°18'39''E		NV			Unknown	
1	Val des Entrelacs	49°10'50''S 69°18'22''E		2019			Yes	
2	Inlet Bassin Victoria	49°12'17''S 69°19'02''E		2019			Yes	
3	Outlet of Croix du Sud Lake	49°13'13''S 69°24'51''E		2019			Yes	
4	Outlet of Lake Euphrosine	49°14'14''S 69°25'50''E		2019			Yes	
5	Ballon R.	49°14'41''S 69°26'27''E		2011			Yes	
6	Sannom R.	49°14'52''S 69°26'26''E		2011			Yes	
7	S Brook Ile aux Skuas	49°14'55''S 69°35'32''E		2011			Yes	
7a	E Brook Ile aux Skuas	49°14'46''S 69°35'01''E		*NS*			No	Low discharge
8	Brook 1 S Ile du Port	49°12'36''S 69°37'17''E		2011			Yes	
9	Brook 2 Ile du Port	49°12'10''S 69°37'59''E		2011			Yes	
10	Brook 3 Ile du Port	49°11'10''S 69°38'37''E		2011			Yes	
11	Brook 4 Ile du Port	49°10'36''S 69°38'10''E		NS			No	Low discharge
11a	Brook 5 N Ile du Port	49°09'28''S 69°38'17''E		NV			Unknown	
12	Valfroide R.	49°16'11''S 69°24'03''E	1998-2015	2017	*Salmo trutta*	*Salmo trutta* (2011)	Yes	
CENTRAL PLATEAU NORTH								
13	Val Travers R. & Bontemps estuary	49°16'48''S 69°28'38''E	1993	2019	*Salmo trutta*		Yes	human introduction (*S. trutta*, 1992)
14	Brook N of Port-Couvreux	49°16'49''S 69°41'26''E		2012			Yes	
15	Brook S of Port-Couvreux cabin	49°17'05''S 69°41'41''E		2012			No	
16	Brook W end of Havre du Beau Temps	49°18'10''S 69°34'05''E		2011			Yes	
17	Bassin de la Gazelle Brook	49°18'48''S 69°40'16''E		2011			No	
17a	Anse Sablonneuse Brook	49°18'50''S 69°42'05''E		2011			Yes	

Code	**Site**	**GPS position of estuary**	**Estimated 1rst repro *Salmo trutta***	**Date last sampling**	**Species present at last sampling**	**Strayers (date seen)**	**Possible colonization**	**Comments. For human introduction, year of the1rst successful**
COURBET NORTH								
18	Port Kirk R.	49°17'28''S 69°47'19''E	1997	2019	*Salmo trutta*		Yes	
19	Val de l'Ouest R.	49°16'02''S 69°50'50''E	1987	2002	*Salmo trutta*		Yes	
20	Studer Basin	49°12'48''S 69°52'12''E	1962	2018	*Salmo trutta / Salvelinus fontinalis*		Yes	human introduction (*S. trutta*, 1959 ; *S fontinalis*, 1962)
20a	Port-Elizabeth Brook	49°12'39''S 69°53'31''E		1973		*Salmo trutta* (1973)	Yes	
21	Doute R.	49°11'44''S 69°55'34''E	1985	2002	*Salmo trutta*		Yes	
22	Vallée du Charbon R.	49°11'39''S 69°55'53''E	1986-1992	2002	*Salmo trutta*		Yes	
23	Sérail R.	49°11'39''S 69°55'53''E	1988-1992	2002	*Salmo trutta*		Yes	
24	Chasseurs R.	49°08'31''S 70°02'35''E	1986	2002	*Salmo trutta*		Yes	
25	Nord R.	49°10'27''S 70°08'13''E	1985	2019	*Salmo trutta*		Yes	human introduction (*S. trutta*, 1981)
26	Pépins R.	49°09'57''S 70°11'31''E	1989	2001	*Salmo trutta*		Yes	
27	Cataractes R.	49°09'01''S 70°13'36''E	1985-1989	2011	*Salmo trutta*		Yes	
28	Hautes Mares South Brook (Gorfous 1)	49°08'10''S 70°14'06''E	2000	2011	*Salmo trutta*		Yes	
29	Hautes Mares North Brook (Gorfous 2)	49°07'57''S 70°14'08''E	1991-2000	2011	*Salmo trutta*		Yes	
29a	Gorfous 3	49°07'15''S 70°13'52''E		2011			Uncertain	
30	Pointe des Cabanes Brook (Gorfous 4)	49°06'11''S 70°14'05''E	1998-2000	2011	*Salmo trutta*		Uncertain	
31	Cap Rouge Brook S (Gorfous 5)	49°04'47''S 70°16'09''E	1997-2000	2011	*Salmo trutta*		Uncertain	
32	Cap Rouge Brook N (Gorfous 6)	49°04'18''S 70°16'45''E		2011			Uncertain	
32a	Gorfous 7	49°03'50''S 70°17'09''E		2011	NS		No	
COURBET EAST								
33	Cap de Rohan R.	49°03'28''S 70°22'24"E	1995-1999	2019	*Salmo trutta*		Yes	
33a	Cap Digby Brook	49°06'23''S 70°31'25"E			NS		Yes	
34a	Lac Marville north tributary 1 (West)	49°08'43''S 70°25'39"E	1982-1989	1992	*Salmo trutta*		Yes	
34b	Lac Marville north tributary 2	49°08'40''S 70°25'42"E	1982-1989	1992	*Salmo trutta*		Yes	
34c	Lac Marville north tributary 3	49°07'41''S 70°26'58"E	1982-1989	2001	*Salmo trutta*		Yes	
34d	Lac Marville north tributary 4	49°07'24''S 70°28'05"E			NV		Unknown	
34e	Lac Marville north tributary 5 (East)	49°07'23''S 70°28'11"E			NV		Unknown	
34	Lac Marville Outlet	49°09'04''S 70°30'41"E	1982-1989	2011	*Salmo trutta*		Yes	
34f	Est R.	49°10'12''S 70°30'24"E	1982-1989	2001	*Salmo trutta*		Yes	
34g	Volcan R.	49°10'10''S 70°25'58"E	1982-1989	2001	*Salmo trutta*		Yes	
34h	Lac Marville south tributary	49°10'30''S 70°30'02"E	1982-1989	2001	*Salmo trutta*		Yes	
35	Manchots R.	49°13'43''S 70°33'12"E	1982-1989	2010	*Salmo trutta*		Yes	
36	Pointe des Calcédoines R.	49°19'45''S 70°29'45"E	2003-2006	2011	*Salmo trutta*		Yes	
37	Bungay R.	49°21'27''S 70°28'11"E	1984-1988	2001	*Salmo trutta*		Yes	

Code	Site	GPS position of estuary	Estimated 1rst repro *Salmo trutta*	Date last sampling	Species present at last sampling	Strayers (date seen)	Possible colonization	Comments. For human introduction, year of the1rst successful
38	Albatros R.	49°21'03''S 70°22'31"E	1968	2010	*Salmo trutta / Salvelinus fontinalis*		Yes	
39	Norvégienne R.	49°20'51''S 70°21'05"E	1968	2018	*Salmo trutta / Salvelinus fontinalis*		Yes	
40	Château R.	49°21'10''S 70°19'35"E	1962	2018	*Salmo trutta / Salvelinus fontinalis*		Yes	human introduction (*S. trutta*, 1962 ; *S. fontinalis*, 1962)
MORBIHAN NORTH								
41	PAF Ferme R.	49°21'03''S 70°13'21"E	1962	2018	*Salmo trutta / Salvelinus fontinalis*		Yes	human introduction (*S. trutta*, 1962 ; *S. fontinalis*, 1963)
41a	*PAF Sablière Pond	49°20'25"S 70°12'03" E	?	2005	*Salmo trutta / Salvelinus fontinalis*		?	human introduction, year unknown (*S. trutta* & *S fontinalis*)
41b	*PAF Magnétisme Pond	49°20'58"S 70°12'23" E	?	2001	*Salmo trutta / Salvelinus fontinalis*		?	human introduction (*S. trutta*, 1970 ; *S. fontinalis*, unknown)
41c	*PAF Décharge Pond	49°20'46"S 70°12'39" E	1970	2005	*Salmo trutta / Salvelinus fontinalis*		1/2 isolated site	human introduction (*S. trutta*, 1970 ; *S fontinalis*, unknown)
41d	*PAF Collets Pond	49°20'41"S 70°12'51" E	1970	2009	*Salmo trutta / Salvelinus fontinalis*		1/2 isolated site	human introduction (*S. trutta*, 1970 ; *S. fontinalis*, unknown)
41e	*Iono Pond	49°20'57"S 70°15'14" E	1960	2010	Information not available		1/2 isolated site	Information not available
41f	*Béliers Pond	49°20'46"S 70°13'57" E			Information not available		No	Information not available
42	Borgne R.	49°20'44''S 70°10'13"E	1973	2016	*Salmo trutta / Salvelinus fontinalis*		Yes	human introduction (*S. trutta*, 1973 ; *S. fontinalis*, 1972)
42a	Otarie R.	49°20'45''S 70°09'55"E		2016			No	Falls
43	Sud R.	49°20'47''S 70°07'54"E	1979	2018	*Salmo trutta / Salvelinus fontinalis*		Yes	human introduction (*S. fontinalis*, 1962)
44	Pointe de l'Epave Brook	49°20'36''S 70°06'56"E	1991	2016	*Salmo trutta / Salvelinus fontinalis*		Yes	
45	Américains R.	49°21'07''S 70°04'48"E	1978-80	2016	*Salmo trutta / Salvelinus fontinalis*		Yes	
46	3 Lacs R.	49°22'01''S 70°00'40"E	1988	2016	*Salmo trutta*		Yes	
46a	Lac Christiane outlet	49°20'25''S 69°51'18"E		2016			No	Falls
47	Val d'Auge R.	49°20'25''S 69°51'18"E	1994-98	2016	*Salmo trutta*		Yes	
48a	Lac des Trois Enseignes outlet	49°20'23''S 69°49'17"E		2002			No	Falls
48	Anse de St Malo R. = Port Raymond R.	49°20'11''S 69°48'48"E	2003-2014	2016	*Salmo trutta*	*O. kisutch* (smolts 2016)	Yes	
MORBIHAN WEST								
49	Basin downstream of Korrigans Lake	49°23'32''S 69°51'32"E	1975-1979	2016	*Salmo trutta*	*Oncorhynchus kisutch* (2009)	Yes	human introduction (*S. salar*, 1975)
50	Baie de l'Observatoire R.	49°23'55''S 69°52'38"E	2003-2014	2016	*Salmo trutta*	*Salmo trutta* (2002)	Yes	
51	East Brook on Bras Jules Laboureur	49°23'58''S 69°48'57"E		2016	*Oncorhynchus kisutch*	*O. kisutch, Salmo trutta* (2010)	Yes	
51a	Lac Saturne outlet	49°23'23''S 69°47'38"E		2016			Yes	Low discharge

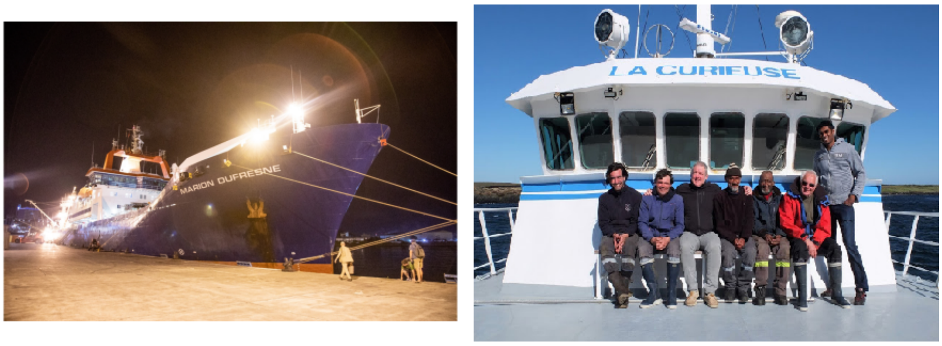
Code	**Site**	**GPS position of estuary**	**Estimated 1^{rst} repro *Salmo trutta***	**Date last sampling**	**Species present at last sampling**	**Strayers (date seen)**	**Possible colonization**	**Comments. For human introduction, year of the1rst successful**
51b	SW Brook on Bras Jules Laboureur	49°24'42''S 69°48'37"E		2011	possible intro. (*species unknown*)	*Oncorhynchus kisutch* (2001)	Yes	Low discharge
51c	S Brook on Bras Jules Laboureur	49°25'20''S 69°48'12"E		1977			Yes	Low discharge
51d	East Brook on Bras Baudissin	49°23'53''S 69°45'41"E		2011			Yes	Low discharge
51e	Gave de l'Azorella	49°23'35''S 69°45'02"E		2011			No	Falls
52f	Valdotaine R.	49°23'03''S 69°36'26"E	2003-2007	2012	*S. trutta / O. kisutch*		yes	Falls 200m from sea
52	Grisanche R.	49°23'13''S 69°36'27"E	2003-2007	2012	*S trutta / O. kisutch / S. alpinus*		Yes	human introduction (*O. kisutch*, 1978)
52	Alster R.	49°24'17''S 69°38'18"E			NS		No	
53	Lac des Fougères + outlet	49°24'43''S 69°39'39"E		2019	*Salvelinus alpinus*	*Salmo trutta* (2012)	Yes	human introduction (*S. alpinus*, 1991)
54	Lac d'Armor Basin	49°27'59''S 69°43'44"E	*1994*	2012	*S. trutta / S. salar / S. fontinalis*	*Oncorhynchus kisutch* (2012)	Yes	human introduction (S. salar, 1977 ; *S. trutta*, 1991 ; *S. fontinalis*, 1992)
55	Anse J. Bourcart Brook	49°29'17''S 69°46'02"E		2003		*Oncorhynchus kisutch* (1989)	Yes	
MORBIHAN SOUTH								
55a	*Port Bizet Pond (Ile Longue)	49°31'30''S 69°54'18"E	1969	2010	*Salvelinus fontinalis*		No	
55b	*NW Ponds (Ile Longue)	49°31'12''S 69°53'25"E	1975	2009	*Salvelinus fontinalis*		No	human introduction (*S. fontinalis*, 1975)
55c	*Ile du Cimetière Pond	49°29'38''S 70°04'33"E	2001	2009	*Salmo trutta*		No	
56	Ravin du Charbon R.	49°33'01''S 69°49'08"E		2016		*Salmo trutta-Salmo salar* (2003)	Yes	
57	Vallée des Neiges Basin	49°33'51''S 69°52'55"E	?-2003	2003	*Salmo trutta*		Yes	
58	Acaena R.	49°35'49''S 69°56'38"E	1979	2019	*Salmo trutta*	*Salvelinus fontinalis* (1984)	Yes	human introduction (*S. trutta*, 1979)
59	Vallée de la Planchette R.	49°35'49''S 70°01'11"E	1984	2003	*Salmo trutta*		Yes	
60	Val Raide Brook	49°38'09''S 70°07'50"E	1987	2003	*Salmo trutta*		Yes	
61	Mouettes R.	49°35'36''S 70°03'17"E	1987	2003	*Salmo trutta*		Yes	
SOUTH COAST (Jeanne d'Arc & Ronarc'h peninsulas)								
62	Macaronis R.	49°35'54''S 70°18'13"E	1995-99	2016	*Salmo trutta*			
63	Vallée Phonolite Basin	49°37'16''S 70°10'01"E		2016	*Salvelinus fontinalis*			human introduction (*S. fontinalis*, 1993)
64a	Albéric R.	49°40'57''S 70°14'29"E		1992	NS		No	Falls
64	Val du Levant R.	49°41'24''S 70°07'28"E	1993	2003	*Salmo trutta*			human introduction (*S. trutta*, 1992)
64b	Cap du Challenger R.	49°43'49''S 70°04'55"E			NV		No	Falls
65	Anse de la Canicule R.	49°39'27''S 69°49'47"E			NV		probably no	Falls low discharge
66	Crête des Laves R.	49°38'17''S 69°47'49"E		1992	NS		Yes	
67	Halage des Swains R.	49°33'02''S 69°46'33"E		2016	NS		Yes	
68	Northern arm of Anse aux Ecueils Brook	49°29'14''S 69°39'26"E		2012	NS		Yes	

Code	Site	GPS position of estuary	Estimated 1^rst^ repro *Salmo trutta*	Date last sampling	Species present at last sampling	Strayers (date seen)	Possible colonization	Comments. For human introduction, year of the1rst successful
SOUTH COAST (Gallieni Mountains & Audierne Bay)								
69	La Clarée Basin: Hermance Lake & Galets R.	49°30'01''S 69°37'37''E	1993	2018	*S. trutta / S.fontinalis X alpinus*		Yes	human intro. (*S. trutta*, 1993 ; *S. fontinalis X alpinus*, 1993)
70	Olsen R.	49°31'29''S 69°40'18''E	2014-2016	2018	*S. trutta / S.fontinalis X alpinus*		Yes	
71	Vallée du Radioleine R.	49°33'00''S 69°40'18''E	?-2016	2018	*Salmo trutta*		Yes	
72	Val des Skuas	49°38'29''S 69°35'20''E		2018	NS		No	Glacier near beach
73	River between Le Peigne& Doigt Sainte Anne	49°35'07''S 69°22'31''E		2018	NV		Possible	high slope + pinguins
74	Plaine de Dante R,	49°34'17''S 69°21'26''E	? - 2015	2018	*Salmo truta*		Yes	
75	Torrent des cristaux (outlet Marioz lake)	49°27'49''S 69°17'31''E			NS		Unknown	
80	Plaine Ampère Bassin	49°29'10''S 69°12'46''E		2018	NS	Smolts *unknown sp* (2018)	Yes	
83	Portes Noires R.	49°29'06''S 69°05'30''E			NV		Unknown	
90	Des Contacts Valley	49°32'24''S 69°05'01''E			NV		Unknown	
98	Vallée de La Mouche Bassin	49°35'01''S 69°03'36''E		2018	NS	*Salmo trutta* (2018)	Yes	1 sea trout hand caught
100	Larmor R.	49°39'49''S 69°05'15''E			NV		Unknown	
103	Plage jaune R.	49°43'18''S 68°55'16''E			NV		Unknown	
105	Des Sables R.	49°42'28''S 69°00'50''E			NV		Unknown	

A.2 Campagne de terrain 2018-2019 dans les Terres Australes et Antarctiques Françaises

Préparation de la campagne

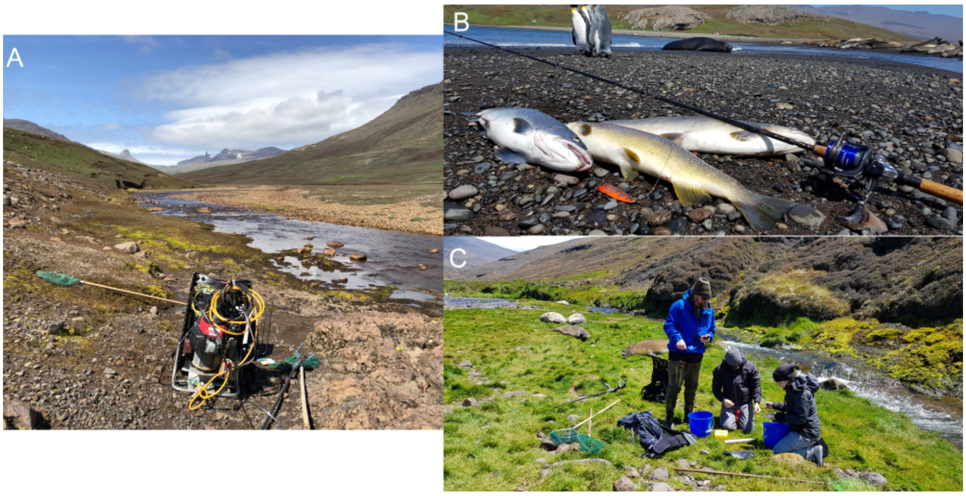
En amont de la campagne de terrain, un programme est établi ainsi que les demandes d'autorisations de capture. Quelques tâches administratives sont remplies pour s'assurer notamment d'un bon état de santé avant son départ. Finalement après un trajet en train vers Paris, un vol vers la Réunion, nous sommes prêts à embarquer sur l'emblématique Marion Dufresnes. Le retour se fera avec la Curieuse.



Réalisation de la campagne de terrain

Les sondages (PE) correspondent à des échantillonnages ciblés sur certaines catégories de poissons ou d'habitat. Les pêches d'inventaire correspondent à des pêches en 2 passages ou plus pour estimer une densité (De Lury (DL)). La surface pêchée doit permettre de capturer au moins un total de 60-100 individus sur les 2 passages, des compléments par sondage ou pêche à la ligne (PL) hors zone ou en zone (post-inventaire) peuvent permettre de compléter l'échantillonnage pour des classes de taille peu représentées dans la pêche d'inventaire prévue dans le plan d'échantillonnage (par exemple au moins 30 alevins et 20 individus d'une certaine taille).

Matériel de pêche électrique (A), pêche à la ligne (B) et récupération des données (matériel biologiques et mesures) (C).



Lors des pêches, les poissons sont mesurés (longueur fourche, mm), peser (g) et des écailles sont prélevées. Le prélèvement des écailles est réalisé dans la zone optimale, et les écailles sont stockées dans des pochettes prévues à cet effet. Pour certaines des pêches, prévues dans le protocole, des prélèvements de tissus des différentes espèces ont également été réalisé sur une trentaine d'individus, les prélèvements étant stockés dans de l'alcool. En complément, sur certains sites (Norvégienne et déversoir du lac Bontemps par exemple) des contenus stomacaux ont été prélevés. Lorsque des smolts ou truites de mer sont pêchées, elles sont euthanasiées pour prélevement de leurs otolithes.

Les opérations sont présentées dans un ordre chronologique, et ont été adapté aux contraintes locales météorologiques et logistiques (dont les dates de mise à disposition de la Curieuse) par rapport au programme prévisionnel(*Table A.1*).

Table A.1: Echantillonnages détaillés par site, types d'échantillon, types de pêche et espèces.

Les abréviations pour les types de pêche correspondent à: pêche à l'électricité (sondage, PE), pêche de densité (DL) et pêche à la ligne (PL). Pour les espèces, ST signifie Salmo trutta, SF Salvelinus fontinalis.

Sites et dates		Prélèvements				Type de pêche			Espèces		
		Ecailles	Otolithes	Tissus	Entier	PE	DL	PL	ST	SF	autres
Crozet											
Camp	11/12/2018	X	X	X	X	X	X		18	16	0
Kerguelen											
Ferme	18/12/2018	X	X			X			5	0	0
Chateau	20/12/2018 22/12/2018	X	X		X	X	X		184	0	0
Acœna	25/12/2018 Au 27/12/2018	X	X		X	X	X	X	258	0	0
Norvégienne	30/12/2018 Et 19/01/2019	X	X				X	X	129	1	0
Bontemps	11/01/2019	X	X			X		X	24	0	0
Lozere	12/01/2019	X	X	X	X	X			9	0	0
Nord	14/01/2019	X	X	X		X	X	X	68	0	0
Rohan	15/01/2019	X					X		39	0	0

Participation à des travaux de recherche pour le programme Immunitoxker

Des prélèvements sanguins et de mucus ont été réalisés sur certains des poissons prélevés afin de tester de nouvelles techniques de séquençage.

Participation à la campagne de capture de l'omble chevalier (Salvelinus alpinus) dans le Lac Fougères

Afin d'étudier la biologie et le régime alimentaire de l'espèce introduite dans le Lac des Fougères, nous avons procéder à 3 jours de terrain. Les poissons ont été capturés à l'aide de filets déposés à plsieurs profondeurs et endroits afin d'étudier les différentiations d'utilisation de l'habitat. Les poissons capturés ont été sexés. Des échantillons de tissus, les contenus stomacaux ainsi que les pièces calcifiées ont été prélevé. Les analyses isotopiques montrent qu'à Kerguelen l'utilisation de l'habitat dépend de la taille des individus. Ces travaux font l'objet d'une publication :

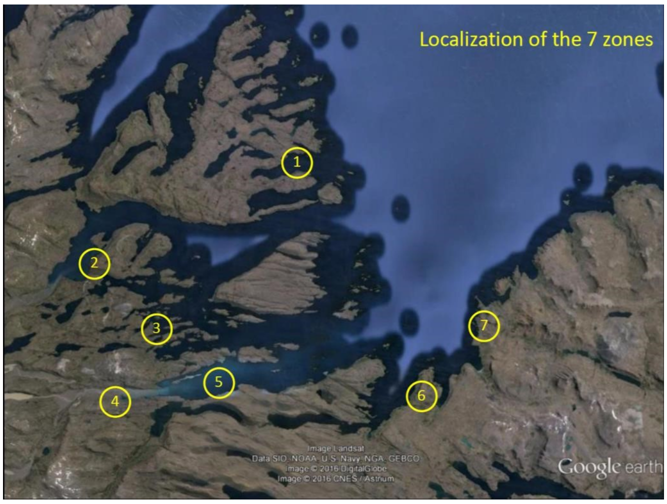
Eldøy, SH, Davidsen, JG, Vignon, M, Power, M. *The biology and feeding ecology of Arctic charr in the Kerguelen Islands.* **J Fish Biol.** 2020; 1– 11. https://doi.org/10.1111/jfb.14596

Télémétrie acoustique à Kerguelen

La pose de récepteurs acoustiques a été réalisé pendant la campagne 2017-2018 pour permettre le suivi des tuites marines marquées à cet effet. Des récepteurs ont été placés en eau douce et en mer, dans 7 zones des îles Kerguelen.

Localisation des récépteurs acoustiques

DEPLOY_DATE_TIME (yyyy-mm-ddThh:mm:ss)	DEPLOY_LAT	DEPLOY_LONG	BOTTOM_DEPTH	RISER_LENGTH	INSTRUMENT_DEPTH	INS_MODEL_NO	INS_SERIAL_NO	TRANSMITTER
2018-01-23T23:37:00	-49,305919	69,695264	26	5	21	VR2AR	546358	A69-1601-60822
2018-01-23T23:47:00	-49,301466	69,720178	20	5	15	VR2AR	546338	A69-1601-60802
2018-01-24T01:07:00	-49,284113	69,801083	15	3	12	VR2AR	546371	A69-1601-60835
2018-01-24T01:27:00	-49,285604	69,805078	15	3	12	VR2AR	546361	A69-1601-60825
2018-01-24T02:00:00	-49,261651	69,841472	15	3	12	VR2AR	546340	A69-1601-60804
2018-01-24T02:15:00	-49,259946	69,845420	15	3	12	VR2AR	546377	A69-1601-60841
2018-01-24T02:25:00	-49,258076	69,849025	13	2	11	VR2AR	546363	A69-1601-60827
2018-01-24T03:25:00	-49,209356	69,859602	20	5	15	VR2AR	546352	A69-1601-60816
2018-01-24T03:40:00	-49,205263	69,873513	15	3	12	VR2AR	546357	A69-1601-60821
2018-01-24T03:50:00	-49,206567	69,868970	16	3	13	VR2AR	546341	A69-1601-60805
2018-01-24T04:00:00	-49,208010	69,864577	19	5	14	VR2AR	546356	A69-1601-60820
2018-01-24T04:30:00	-49,217726	69,874320	NA	NA	NA	VR2AR	546366	NA
2018-01-24T01:45:00	-49,289583	69,791944	NA	NA	NA	VR2AR	546344	NA
2018-01-24T02:30:00	-49,267861	69,848222	NA	NA	NA	VR2AR	546379	NA
2018-01-24T9:45:00	-49,241483	69,544483	37	5	32	VR2AR	546336	A69-1601-60800
2018-01-24T09:50:00	-49,246783	69,543150	29	5	24	VR2AR	546373	A69-1601-60837
2018-01-24T10:05:00	-49,278267	69,483983	29	5	24	VR2AR	546364	A69-1601-60828
2018-01-24T10:15:00	-49,277317	69,480383	25	5	20	VR2AR	546346	A69-1601-60810
2018-01-24T10:25:00	-49,276383	69,476217	30	5	25	VR2AR	546343	A69-1601-60807
2018-01-24T10:50:00	-49,259566	69,477666	13	2	11	VR2AR	546370	A69-1601-60834
2018-01-25T01:30:00	-49,275278	69,338861	NA	NA	NA	VR2W	129967	NA
2018-01-24T23:40:00	-49,275450	69,403067	40	5	35	VR2AR	546353	A69-1601-60817
2018-01-24T23:45:00	-49,272650	69,403383	40	5	35	VR2AR	546372	A69-1601-60836
2018-01-24T23:50:00	-49,270483	69,403683	37	5	32	VR2AR	546339	A69-1601-60803
2018-01-24T23:55:00	-49,268749	69,404000	21	5	16	VR2AR	546991	A69-1601-61455
2018-01-25T01:55:00	-49,267050	69,549149	62	30	32	VR2AR	546365	A69-1601-60829
2018-01-25T02:05:00	-49,262133	69,550083	80	45	35	VR2AR	546367	A69-1601-60831
2018-01-25T02:20:00	-49,257866	69,551033	120	80	40	VR2AR	546354	A69-1601-60818
2018-01-25T02:30:00	-49,253516	69,552266	41	9	32	VR2AR	546369	A69-1601-60833
2018-01-25T02:35:00	-49,253666	69,564133	28	5	23	VR2AR	546347	A69-1601-60811
2018-01-25T02:50:00	-49,257449	69,564233	120	75	45	VR2AR	546355	A69-1601-60819
2018-01-25T02:55:00	-49,261199	69,563766	52	24	28	VR2AR	546374	NA
2018-01-25T03:05:00	-49,264883	69,563150	66	40	26	VR2AR	546376	A69-1601-60840
2018-01-25T03:15:00	-49,268900	69,562933	52	25	27	VR2AR	546342	A69-1601-60806
2018-01-25T05:30:00	-49,237306	69,430278	NA	NA	NA	VR2W	129970	NA
2018-01-25T05:05:00	-49,239216	69,443199	12	2	10	VR2AR	546360	A69-1601-60824
2018-01-25T08:05:00	-49,220716	69,411397	NA	NA	NA	VR2W	129962	NA
2018-01-25T07:30:00	-49,220666	69,420083	12	2	10	VR2AR	546378	A69-1601-60842
2018-01-25T11:20:00	-49,204933	69,312183	NA	NA	NA	VR2W	129971	NA
2018-01-25T12:10:00	-49,193300	69,346766	NA	2	>10	VR2AR	546349	A69-1601-60813
2018-01-25T12:40:00	-49,187899	69,360316	17	5	12	VR2AR	546362	A69-1601-60826
2018-01-26T00:40:00	-49,194183	69,280666	NA	NA	NA	VR2W	129963	NA
2018-01-26T02:20:00	-49,176966	69,312766	12	2	10	VR2AR	546375	A69-1601-60839
2018-01-26T02:30:00	-49,176816	69,309000	37	12	25	VR2AR	546348	A69-1601-60812
2018-01-26T02:35:00	-49,176616	69,306266	12	2	10	VR2AR	546350	A69-1601-60814
2018-01-26T05:50:00	-49,083999	69,611600	37	12	25	VR2AR	546337	A69-1601-60801
2018-01-26T06:30:00	-49,083016	69,607716	1,5	0	1,5	VR2W	129966	NA
2018-01-26T07:00:00	-49,279206	69,479747	3	1	2	VR2AR	546351	NA
2018-01-27T11:10:00	-49,280599	69,475416	2,5	0	2,5	VR2AR	546345	A69-1601-60809
2018-01-27T10:10:00	-49,279850	69,478533	2	0	2	VR2W	129969	NA
2018-01-27T10:45:00	-49,279916	69,477566	2	0	2	VR2W	129968	NA
2018-02-04T04:26:00	-49,309595	69,431182	2	0	2	VR2W	129964	NA



Zones étudiées dans le cadre du suivi acoustique.

Dépose des récepteurs acoustiques lors de la campagne 2017-2018.

Dépose en mer à gauche, dépose en eau douce à droite.

Récupération des récepteurs acoustiques lors de la campagne 2018-2019.

Récupération en mer à gauche, récupération en eau douce à droite.

A.3 Microchemical analysis of Manchots lagoon

Fish growth is known to vary according to environmental conditions such as temperature and habitat selection (Ayllón et al., 2010). Thus, the freshwater growth of brown trout is expected to be different from that in the sea, since environmental conditions differ in particular in terms of accessibility to the food resource. However, the migrant trout which can benefit from life at sea should smoltify prior to migration.

The presence of a lagoon, an intermediate environment between the river estuary and the ocean, poses a problem on Manchots river (*Fig. A.2*). Indeed, the lagoon seems more favourable for better fish growth in terms of temperature but also in terms of accessibility to the resource. The fish caught in the lagoon of river Manchots do indeed have an intermediate phenotype observed, which is transcribed in term of scales reading with a particular intermediate growth patterns. However, the salinity of this lagoon is yet unknown, so whether it is necessary to smoltify for the individuals who take advantage of these growing conditions is unknown.

In this manuscript, we want to study freshwater growth prior to migration. We therefore need to know whether the lagoon is a saline (sea) or non-saline (fresh water) environment. If the lagoon is non-saline, then the fish will be considered as resident trout. If the lagoon is saline, then fish are expected to smoltify, so the fish would be considered as seaward migrants.

To determine the status of this lagoon, we therefore carried out water samplings at different points in the river during the 2019 field campaign. We sampled three areas, the river above the lagoon (R), the lagoon (L) and the sea (S). For each of these areas, three samples (A, B and C) were made, except for the sea where we were only able to recover two samples (SA and SB) (*Fig. A.2* and *Table A.2*). Each of the samples was therefore named by the letter of the zone (R for river, L for lagoon and S for sea), followed by the letter of the sample (A, B or C), the sampling having been carried out from East to West. For each of these samples, three replicates were taken. Therefore a total of 24 water samples were taken.

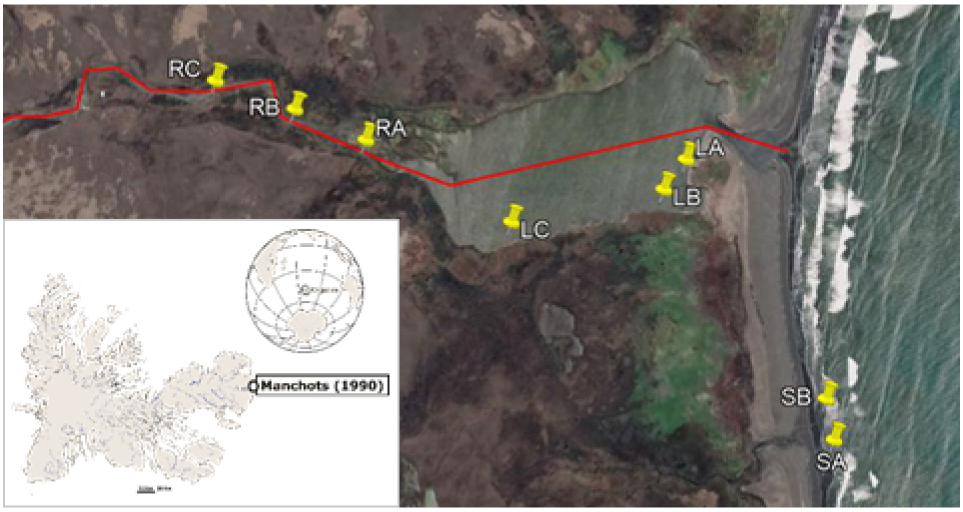


Figure **A.2**: Location of the river Manchots and its lagoon.

The pins stand for the sampled areas.

Table A.2: GPS coordinates of the sampled areas.

RA : S49.22871 E70.53991	LA : S49.22916 E70.55030	SA : S49.23510 E70.55503
RB : S49.22805 E70.53761	LB : S49.22979 E70.54957	SB : S49.23423 E70.55478
RC : S49.22744 E70.53506	LC : S49.23046 E70.54462	

To take the water samples (150 ml), the following protocol was carried out. The water was first taken by a syringe rinsed 3 times with samples to avoid any contamination. Then a final water sample was taken using a syringe equipped with a filter (45 μm). Each sample was isolated from the light and fixed with acid (1ml HNO3/50ml water). The samples were stored (4°C) until their analysis, performed at IPREM in Pau by Gilles Bareille.

Microchemical analyses were carried out to determine the mean composition of the samples in elements as well as the standard deviations were recorded for : Ca (in ppm), Sr (in ppb), Ba (in ppb), K (in ppm), Mg (in ppm), Na (in ppm) and Mn (in ppb). To characterize whether an environment is saline or not, we used the Sr/Ca ratio, which is a good environmental signature (Campbell et al., 2015; Villiers, 1999). We used a pairwise.t.test adjusted with the Bonferroni method to compare the three different areas, river, lagoon and sea (*Fig. A.3* and *Table A.3*).

Table A.3: Results of the pairwise-t-test for the Sr/Ca ratio.

Comparison of paired replicates are given with the p-value of the test. According to the Bonferroni method, differences between replicates are significative if P-value< 0.0018.

	RA	RB	RC	LA	LB	LC	SA
RB	0.049	-	-	-	-	-	-
RC	0.262	0.347	-	-	-	-	-
LA	0.317	0.006	0.043	-	-	-	-
LB	0.449	0.010	0.070	0.799	-	-	-
LC	0.237	0.004	0.029	0.849	0.657	-	-
SA	2.6 e^{-14}	1 .0 e^{-13}	5.5 e^{-14}	1.4 e^{-14}	1.6 e^{-14}	1.3 e^{-14}	-
SB	4.7 e^{-14}	2.0 e^{-13}	1.0 e^{-13}	2.4 e^{-14}	2.9 e^{-14}	2.2 e^{-14}	0.379

According to the results of the pairwise-t-test and the mean ratio Sr/Ca by replicates, it seems obvious that the lagoon in the Manchots river is not saline. Fish do not have to smoltify to live in the lagoon. Those fish are considered as resident trout in the present manuscript. However, life-history traits are studied on an individual basis. For example, the fish in the lagoon of this river may well have different growth patterns from those caught upstream.

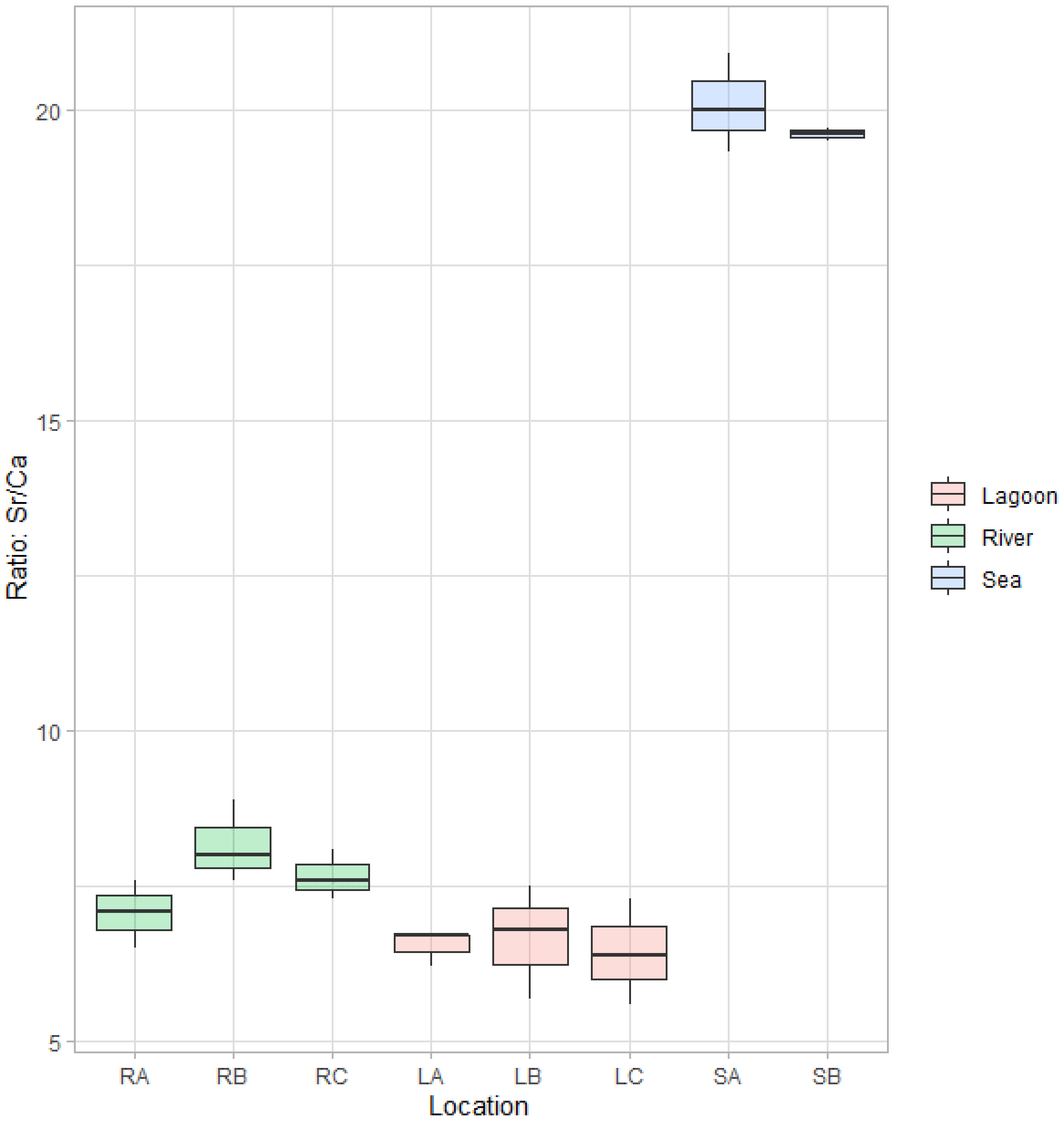
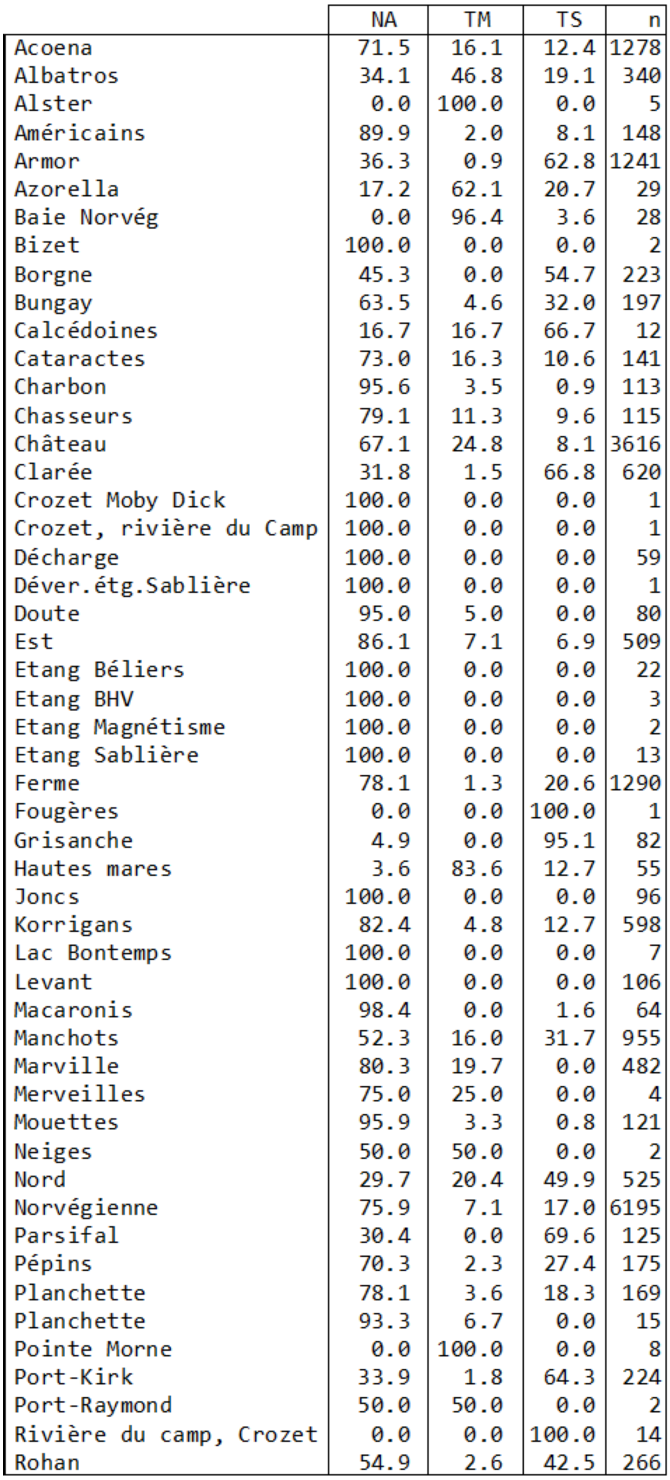


Figure **A.3**: Boxplot of the ratio Sr/Ca by replicates.

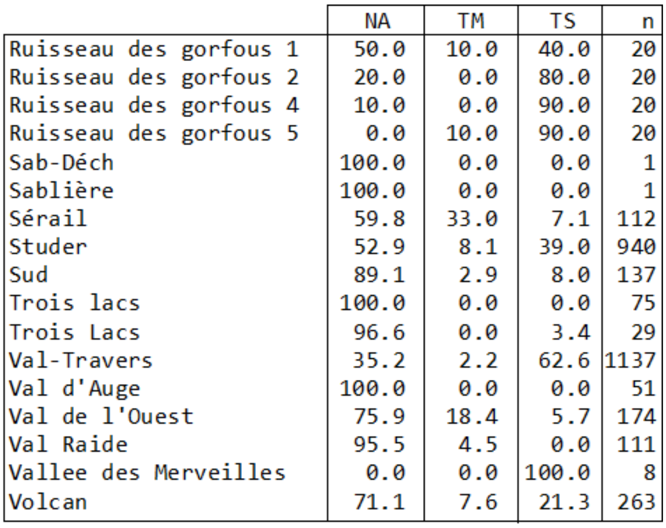
The three different group colours represent the three areas that were sampled.

A.4 Number of samples available in each phenotype category

Details are given by locality. n stands for the total number of fish brown trout caught. Results are given in percent in the table, with NA: phenotype at capture non-identified, TM: migrant trout, TS: resident trout.



	NA	TM	TS	n
Acoena	71.5	16.1	12.4	1278
Albatros	34.1	46.8	19.1	340
Alster	0.0	100.0	0.0	5
Américains	89.9	2.0	8.1	148
Armor	36.3	0.9	62.8	1241
Azorella	17.2	62.1	20.7	29
Baie Norvég	0.0	96.4	3.6	28
Bizet	100.0	0.0	0.0	2
Borgne	45.3	0.0	54.7	223
Bungay	63.5	4.6	32.0	197
Calcédoines	16.7	16.7	66.7	12
Cataractes	73.0	16.3	10.6	141
Charbon	95.6	3.5	0.9	113
Chasseurs	79.1	11.3	9.6	115
Château	67.1	24.8	8.1	3616
Clarée	31.8	1.5	66.8	620
Crozet Moby Dick	100.0	0.0	0.0	1
Crozet, rivière du Camp	100.0	0.0	0.0	1
Décharge	100.0	0.0	0.0	59
Déver.étg.Sablière	100.0	0.0	0.0	1
Doute	95.0	5.0	0.0	80
Est	86.1	7.1	6.9	509
Etang Béliers	100.0	0.0	0.0	22
Etang BHV	100.0	0.0	0.0	3
Etang Magnétisme	100.0	0.0	0.0	2
Etang Sablière	100.0	0.0	0.0	13
Ferme	78.1	1.3	20.6	1290
Fougères	0.0	0.0	100.0	1
Grisanche	4.9	0.0	95.1	82
Hautes mares	3.6	83.6	12.7	55
Joncs	100.0	0.0	0.0	96
Korrigans	82.4	4.8	12.7	598
Lac Bontemps	100.0	0.0	0.0	7
Levant	100.0	0.0	0.0	106
Macaronis	98.4	0.0	1.6	64
Manchots	52.3	16.0	31.7	955
Marville	80.3	19.7	0.0	482
Merveilles	75.0	25.0	0.0	4
Mouettes	95.9	3.3	0.8	121
Neiges	50.0	50.0	0.0	2
Nord	29.7	20.4	49.9	525
Norvégienne	75.9	7.1	17.0	6195
Parsifal	30.4	0.0	69.6	125
Pépins	70.3	2.3	27.4	175
Planchette	78.1	3.6	18.3	169
Planchette	93.3	6.7	0.0	15
Pointe Morne	0.0	100.0	0.0	8
Port-Kirk	33.9	1.8	64.3	224
Port-Raymond	50.0	50.0	0.0	2
Rivière du camp, Crozet	0.0	0.0	100.0	14
Rohan	54.9	2.6	42.5	266



	NA	TM	TS	n
Ruisseau des gorfous 1	50.0	10.0	40.0	20
Ruisseau des gorfous 2	20.0	0.0	80.0	20
Ruisseau des gorfous 4	10.0	0.0	90.0	20
Ruisseau des gorfous 5	0.0	10.0	90.0	20
Sab-Déch	100.0	0.0	0.0	1
Sablière	100.0	0.0	0.0	1
Sérail	59.8	33.0	7.1	112
Studer	52.9	8.1	39.0	940
Sud	89.1	2.9	8.0	137
Trois lacs	100.0	0.0	0.0	75
Trois Lacs	96.6	0.0	3.4	29
Val-Travers	35.2	2.2	62.6	1137
Val d'Auge	100.0	0.0	0.0	51
Val de l'Ouest	75.9	18.4	5.7	174
Val Raide	95.5	4.5	0.0	111
Vallee des Merveilles	0.0	0.0	100.0	8
Volcan	71.1	7.6	21.3	263

B Supportive information to Chapter 4. The use of scales to rebuilt life histories

B.1 Hierarchical variance decomposition of fish scale growth and age to investigate the relative contributions of readers and scales

Supplementary material

Hierarchical variance decomposition of fish scale growth and age to investigate the relative contribution of readers and scales

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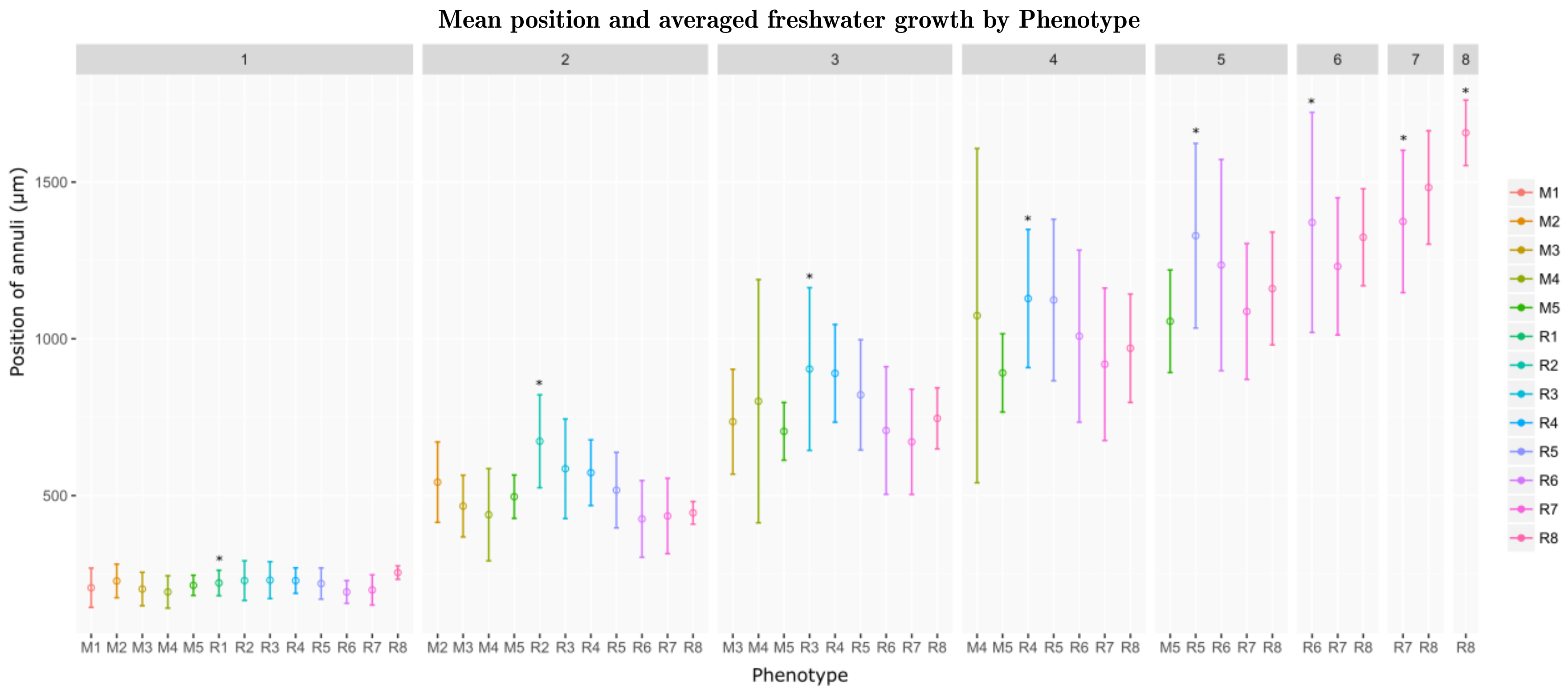


Figure **B.1**: Average position of annuli measured on scales by Phenotype and age for freshwater growth.

Mean position of annuli from age 1 to 8 (maximum age recorded in fresh water for individuals caught) are given with standard error in micrometre (µm). Phenotypes were separated according to the migratory status respectively migrant (M) and resident (R). E.g. M1 stands for anadromous individuals migrating after age 1 but before 2, explaining why M1 disappears in the following average position of annuli 2, because it grows in saltwater after age 1. Annulus position for fish caught at each age is indicated using an asterisk (*). Except for age 1 where the average position seems to be equal whatever the Phenotype, while growing older, migrants and older residents have smaller scales than the reference on average. This could be explained by a methodological bias increasing as fish age as it becomes harder to position annuli. In studies, this phenomenon is often observed for resident individuals and confirmed with capture–mark-recapture datasets. Those differences could also be interpreted as selective mortality acting on resident individuals, with individuals expecting the highest growth rate facing higher mortality probability. Concerning the differences observed between migrants of the year, future migrants and reference, the expected anadromous individuals have on average a lower growth rate than residents. Individuals expecting lower growth rate could adopt another migratory strategy, as a consequence of lower food availability (Wysujack et al., 2009). Because our dataset is limited in term of the number of fish, we cannot conclude for one or another reason.

Hierarchical variance decomposition of fish scale growth and age with Reader as a fixed effect

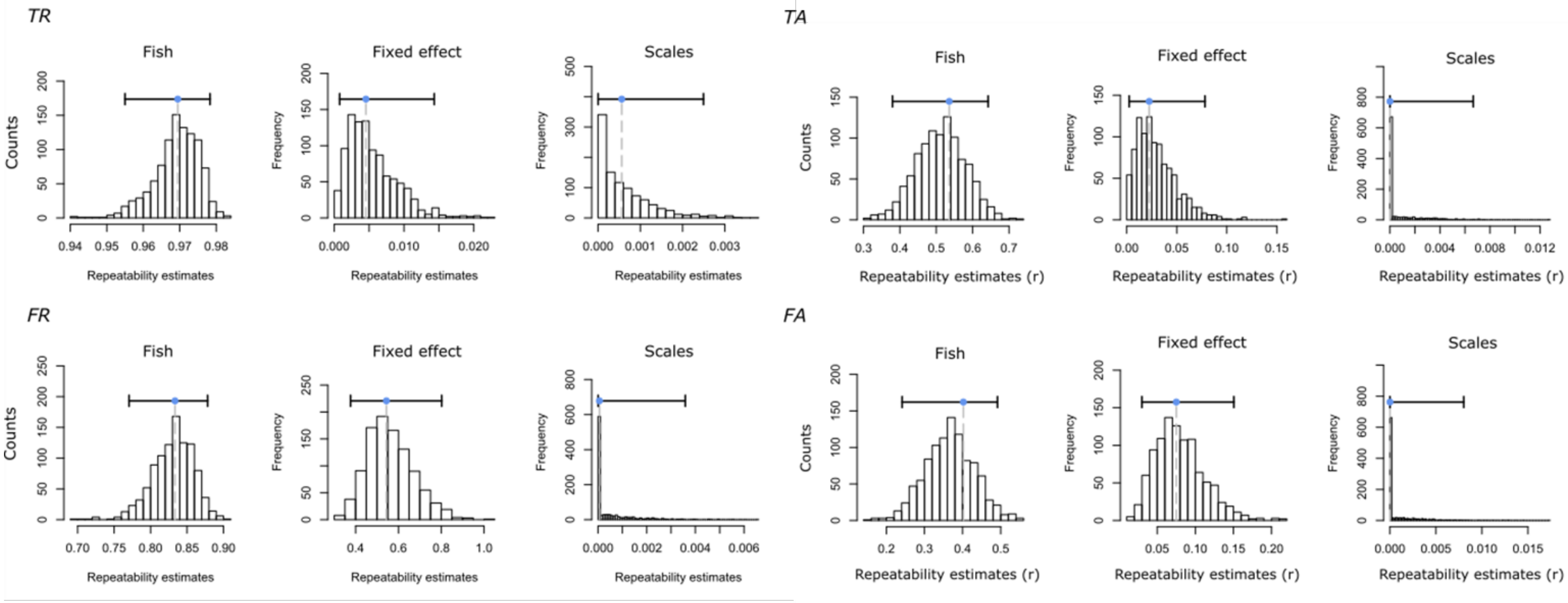


Figure **B.2**: Decomposition of variance considering Reader as a fixed effect. Results are given for measures made on total radius of scales (TR), measures made on freshwater radius (FR), total age (TA) and freshwater age (FA).

Median of the repeatability estimates (r) are given in dashed lines for Fish, fixed effects (Phenotype + Reader) and Scales with uncertainty, i.e. their 95% confidence interval (horizontal interval) obtained over 1000 bootstraps. Compared with results given in the paper where Reader was considered as random, main results for Fish and Scales remains unchanged. Fixed effect record the repeatability for the sum of Phenotype and Reader and their interaction. Only for freshwater growth, the fixed effect repeatability increases, but it is not significantly different from the fixed effect with Reader as random.

Median of the repeatability estimates (r) are given in dashed lines for Fish, fixed effects (Phenotype + Reader) and Scales with uncertainty, *i.e.* their 95% confidence interval (horizontal interval) obtained over 1000 bootstraps.

Compared with results given in the paper where Reader was considered as random, main results for Fish and Scales remains unchanged. Fixed effect record the repeatability for the sum of Phenotype and Reader and their interaction. Only for freshwater growth the fixed effect repeatability increases, but it is not significantly different from the fixed effect with Reader as random.

Going further

Two files are given linked to this paper in order to reproduce the manipulation. A R script, with a description of the models and their output in the file SCRIPT.R. This file is accompanied with a subset of our dataset, with six fish for each stream. Half of the fish are anadromous (M) and the other half are resident (R). The same variables are given in the dataset (data.RData) and can be loaded to run the script.

Parameter estimates of von Bertalanffy growth function

The von Bertalanffy growth function (Von Bertalanffy, 1938, Eqn S1) was implemented in order to clearly lay out the impact of considering individuals as a random effect and the impact of the number of scales reads on the parameter estimates. Modelling of growth was done in a Bayesian framework using Jags.

$$L_t = L_\infty(1 - e^{-k(t-t_0)}) \text{ (S1)}$$

The vBGF model in Eqn S1 has three parameters: L_∞, k, and t_0 which are usually estimated at the population or group (*e.g.* cohort, sex) level. We denote fixed effects by Greek letters (α, β) and random effects (a, b) by roman letters.

$$\begin{gathered} L_{\infty_i} = \alpha + a_i; \alpha \sim U(500, 1000); a_i \sim N(0, \theta_a); \theta_a \sim G(0.001, 0.001) \\ k_i = \beta + b_i; \beta \sim N(0.06, 0.001); b_i \sim N(0, \theta_b); \theta_b \sim G(0.001, 0.001) \\ t_0 \; U(-2, 0.5) \text{ (S2)} \end{gathered}$$

The parameters of the vBGF model were described as in Eqn S2. The indexation i on L_{∞_i} and k_i accounts for the inter-individual variability on the estimation of the parameters. This individual random effect is taken into account when a_i and b_i are not equal to 0. The model was run with or without inter-individual variability on L and k (*i.e.* with and without a_i and b_i). The different distribution of the parameters is given (Eqn S2) with U, N and G corresponding respectively to the uniform, normal and gamma distributions. Additional supporting information may be obtained by contacting the corresponding author. These analyses were based upon the readings made by one reader on four scales of 60 fish.

We first compared the estimates considering or not individuals as a random effect by reading four scales of each fish (*Fig. B.3*, *Table B.1*, two rightmost inserts) and concluded, as in Vincenzi, Crivelli et al., 2016; Vincenzi, Mangel et al., 2014, that not considering individual variability may lead to over or under estimation of parameters.

We then compared the growth curves estimated based on the readings on one to four scales read per fish and concluded the unnecessary need of multiple scales readings (*Fig. B.3*, *Table B.1*.

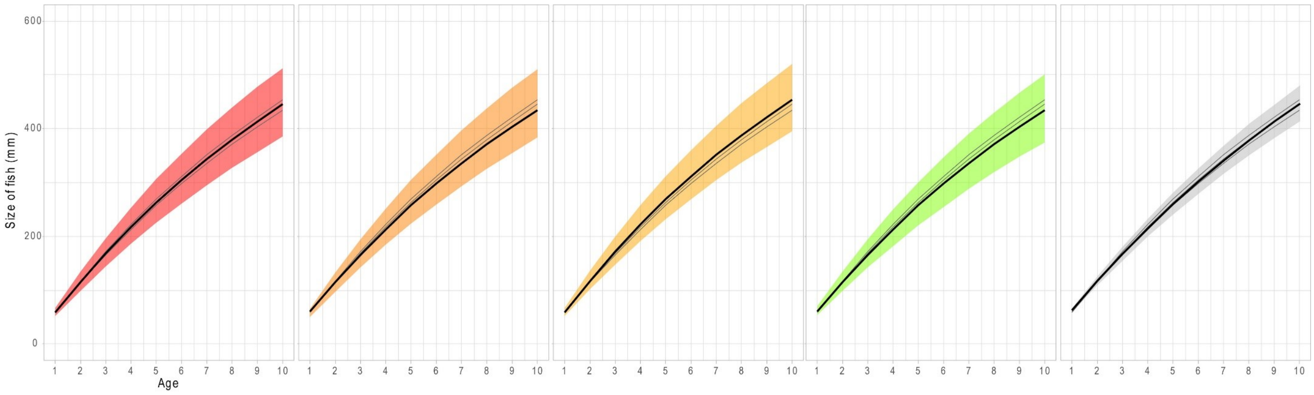


Figure **B.3**: Predicted freshwater growth according to the use of 1 to 4 scales per fish and the consideration of individual as a random effect.

Growth curves are obtained based on the VBGF model described in Eqn S1 and S2. The four leftmost models were approximated considering individuals as random effect and the growth are obtained for one scale (red), 2 scales (dark orange), 3 scales (orange) and 4 scales (green). The rightmost model represents the average growth curve using four scales per fish not considering individuals as random effect. The line represents the 50% prediction, and the polygon around the 25 and 75% quartiles. The grey curves represent the average estimated curve of the other models.

Table B.1: vBGF fixed parameter estimates according to the number of scales read and the consideration of individual as a random effect.

Average estimates of the fixed parameters of Eqn S2 and their standard error are given in line. The number of scales considered per fish is given in row, considering random effects in the parametrization. A comparison of the estimates on 4 scales read per fish is made with and without considering individuals as random effects (two rightmost rows).

	With random effect				Without random effect
Scale	1	2	3	4	4
α	848.7 ± 92.4	832.3 ± 88.1	842.7 ± 86.7	827.7 ± 90.7	931.8 ± 56.1
β	0.076 ± 0.012	0.075 ± 0.011	0.079 ± 0.011	0.075 ± 0.011	0.065 ± 0.005
t_0	0.024 ± 0.065	-0.044 ± 0.059	0.057 ± 0.066	-0.043 ± 0.059	-0.079 ± 0.051

A hierarchical variance decomposition - SCRIPT

Lucie Aulus-Giacosa

1. PACKAGE

```
devtools::install_github("mastoffel/rptR", build_vignettes = TRUE)

library(rptR)
citation("rptR")

##
## To cite rptR in publications please refer to our article:
##
##   Stoffel, M. A., Nakagawa, S. and Schielzeth, H. (2017), rptR:
##   repeatability estimation and variance decomposition by generalized
##   linear mixed-effects models. Methods Ecol Evol, 8: 1639???1644.
##   doi:10.1111/2041-210X.12797
##
## A BibTeX entry for LaTeX users is
##
##   @Article{,
##     title = {rptR: Repeatability estimation and variance decompositio
n by generalized linear mixed-effects models},
##     author = {Martin A. Stoffel and Shinichi Nakagawa and Holger Schi
elzeth},
##     journal = {Methods in Ecology and Evolution},
##     year = {2017},
##     volume = {8},
##     issue = {11},
##     pages = {1639???1644},
##     doi = {10.1111/2041-210X.12797},
##     url = {http://onlinelibrary.wiley.com/doi/10.1111/2041-210X.12797
/full},
##   }
```

2. DATASET

The data are available as Supplementary material of the pusblished article.
https://doi.org/10.1071/MF19059

```
load(file="data.RData")
```

3. REPEATABILITY

1. Model for TR

Phenotype is considered as fixed. Reader, Scales and Fish are random effects. Measures are considered Gaussian. 1000 bootstraps and permutations are made (nboot, npermut) in parallel (parallel = T). Enhanced agreement (adjusted = F) repeatabilities (ratio = T) are calculated.

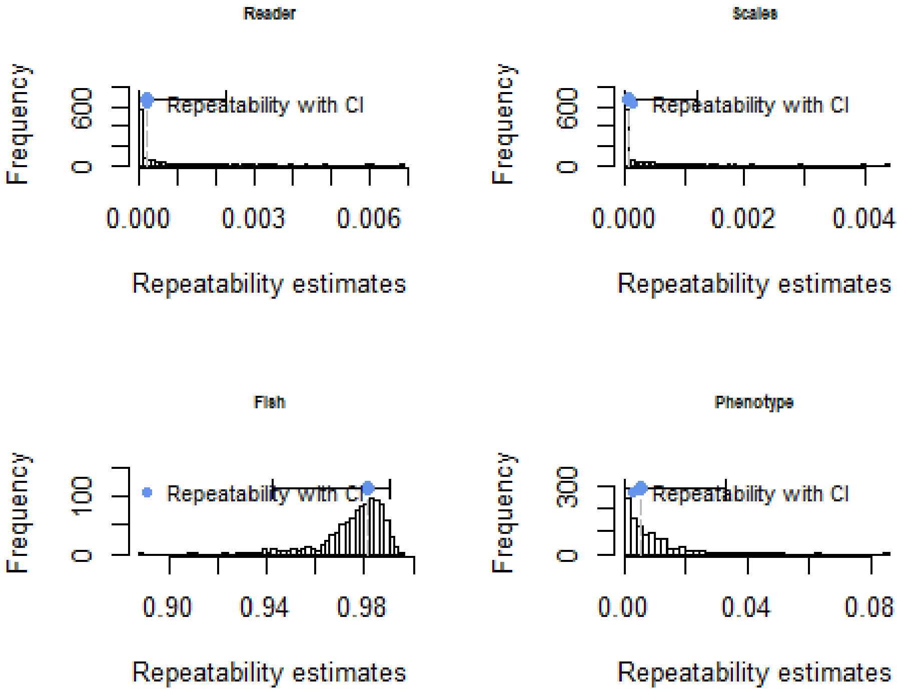
```
model1<-rpt(TR ~ Phenotype + (1|Reader) +  (1 | Scales) + (1 |Fish),
          grname = c("Reader","Scales", "Fish","Fixed"), data = data, da
tatype = "Gaussian",
          nboot = 1000, npermut = 1000, adjusted = F, ratio=T, parallel=
T)

print(model1)

##
##
## Repeatability estimation using the lmm method
##
## Repeatability for Reader
## R  = 0
## SE = 0.001
## CI = [0, 0.002]
## P  = 0.265 [LRT]
##      0.126 [Permutation]
##
## Repeatability for Scales
## R  = 0
## SE = 0
## CI = [0, 0.001]
## P  = 0.433 [LRT]
##      0.345 [Permutation]
##
## Repeatability for Fish
## R  = 0.981
## SE = 0.012
## CI = [0.942, 0.991]
## P  = 1.29e-95 [LRT]
##      0.001 [Permutation]
##
## Repeatability for Fixed
## R  = 0.005
## SE = 0.009
## CI = [0, 0.033]
## P  = NA [LRT]
##      NA [Permutation]

##
## Repeatability estimation using the lmm method
```

```
##
## Call = rpt(formula = TR ~ Phenotype + (1 | Reader) + (1 | Scales) + (
1 | Fish), grname = c("Reader", "Scales", "Fish", "Fixed"), data = data,
datatype = "Gaussian", nboot = 1000, npermut = 1000, parallel = T, ratio
= T, adjusted = F)
##
## Data: 144 observations
## ----------------------------------------
##
## Reader (2 groups)
##
## Repeatability estimation overview:
##         R     SE   2.5%   97.5% P_permut  LRT_P
##  0.000218  7e-04      0 0.00224    0.126  0.265
##
## Bootstrapping and Permutation test:
##             N     Mean   Median   2.5%    97.5%
## boot     1000 3.39e-04 1.91e-07      0 0.002243
## permut   1000 7.92e-05 3.78e-13      0 0.000665
##
## Likelihood ratio test:
## logLik full model = -925.8184
## logLik red. model = -926.0151
## D  = 0.393, df = 1, P = 0.265
##
## ----------------------------------------
##
##
## Scales (4 groups)
##
## Repeatability estimation overview:
##         R       SE   2.5%   97.5% P_permut  LRT_P
##  5.32e-05 0.000377      0 0.00121    0.345  0.433
##
## Bootstrapping and Permutation test:
##             N     Mean   Median   2.5%    97.5%
## boot     1000 0.000189 5.66e-11      0 0.001215
## permut   1000 0.000109 7.19e-12      0 0.000731
##
## Likelihood ratio test:
## logLik full model = -925.8184
## logLik red. model = -925.8326
## D  = 0.0283, df = 1, P = 0.433
##
## ----------------------------------------
##
##
```

```
## Fish (18 groups)
##
## Repeatability estimation overview:
##       R     SE   2.5%  97.5% P_permut   LRT_P
##   0.981 0.0121  0.942  0.991    0.001      0
##
## Bootstrapping and Permutation test:
##             N   Mean   Median   2.5%  97.5%
## boot     1000 0.9765 9.79e-01  0.942 0.9906
## permut   1000 0.0115 6.68e-09  0.000 0.0568
##
## Likelihood ratio test:
## logLik full model = -925.8184
## logLik red. model = -1140.357
## D  = 429, df = 1, P = 1.29e-95
##
## ----------------------------------------
##
##
## Fixed
##
## Repeatability estimation overview:
##        R      SE      2.5%  97.5% P_permut   LRT_P
##  0.00523 0.00894 3.23e-05 0.0329       NA     NA
##
## Bootstrapping and Permutation test:
##             N    Mean Median     2.5%  97.5%
## boot     1000 0.00818 0.0056 3.23e-05 0.0329
## permut   1000      NA     NA       NA     NA
##
## Likelihood ratio test:
## logLik full model = -925.8184
## logLik red. model = NA
## D  = NA, df = NA, P = NA
##
## ----------------------------------------
```

The code below helps plotting the repeatability for TR.

```
par(mfrow=c(2,2))
plot(model1, grname = "Reader", cex.main=0.6,main="Reader", type = "boot
")
plot(model1, grname = "Scales", cex.main=0.6, main="Scales", type = "boo
t")
plot(model1, grname = "Fish", cex.main=0.6,main="Fish", type = "boot")
plot(model1, grname = "Fixed", cex.main=0.6,main="Phenotype", type = "bo
ot")
```



If we want to consider Reader as fixed effect, *e.g.* they are no interactions Scales/Reader, also we can say reader are not influenced by the scales while reading. But it does not change results.

```
model1bis<-rpt(TR ~ Phenotype + Reader +  (1 | Scales) + (1 |Fish),
            grname = c("Scales", "Fish","Fixed"), data = data, datatype
= "Gaussian",
            nboot = 1000, npermut = 1000, adjusted = F, ratio=T, paralle
l=T)
print(model1bis)
```

```
##
##
## Repeatability estimation using the lmm method
##
## Repeatability for Scales
## R  = 0
## SE = 0
## CI = [0, 0.001]
## P  = 0.435 [LRT]
##      0.348 [Permutation]
##
## Repeatability for Fish
## R  = 0.981
## SE = 0.012
## CI = [0.944, 0.991]
## P  = 3.94e-95 [LRT]
##      0.001 [Permutation]
```

```
##
## Repeatability for Fixed
## R  = 0.006
## SE = 0.009
## CI = [0, 0.034]
## P  = NA [LRT]
##      NA [Permutation]
```

Below, you can add the Population effect. Repeatability of Fish decreases and Fixed effect increase. Fish are partly different because they belong to different Population.

```
model2<-rpt(TR ~ Population + Phenotype + (1|Reader) +  (1 | Scales) + (
1 |Fish), grname = c("Reader","Scales", "Fish","Fixed"), data = data, da
tatype = "Gaussian",
            nboot = 1000, npermut = 1000, adjusted = F, ratio=T, paralle
l=T)
print(model2)
```

```
##
##
## Repeatability estimation using the lmm method
##
## Repeatability for Reader
## R  = 0
## SE = 0.001
## CI = [0, 0.002]
## P  = 0.263 [LRT]
##      0.122 [Permutation]
##
## Repeatability for Scales
## R  = 0
## SE = 0
## CI = [0, 0.001]
## P  = 0.434 [LRT]
##      0.316 [Permutation]
##
## Repeatability for Fish
## R  = 0.599
## SE = 0.145
## CI = [0.297, 0.853]
## P  = 1.27e-83 [LRT]
##      0.001 [Permutation]
##
## Repeatability for Fixed
## R  = 0.389
## SE = 0.146
## CI = [0.131, 0.693]
```

```
## P   = NA [LRT]
##        NA [Permutation]
```

2. Model for TA

Phenotype is considered as fixed. Reader, Scales and Fish are random effects. Ages are considered as Poisson distibuted data. 1000 bootstraps are made (nboot). Enhanced agreement (adjusted = F) repeatabilities (ratio = T) are calculated.

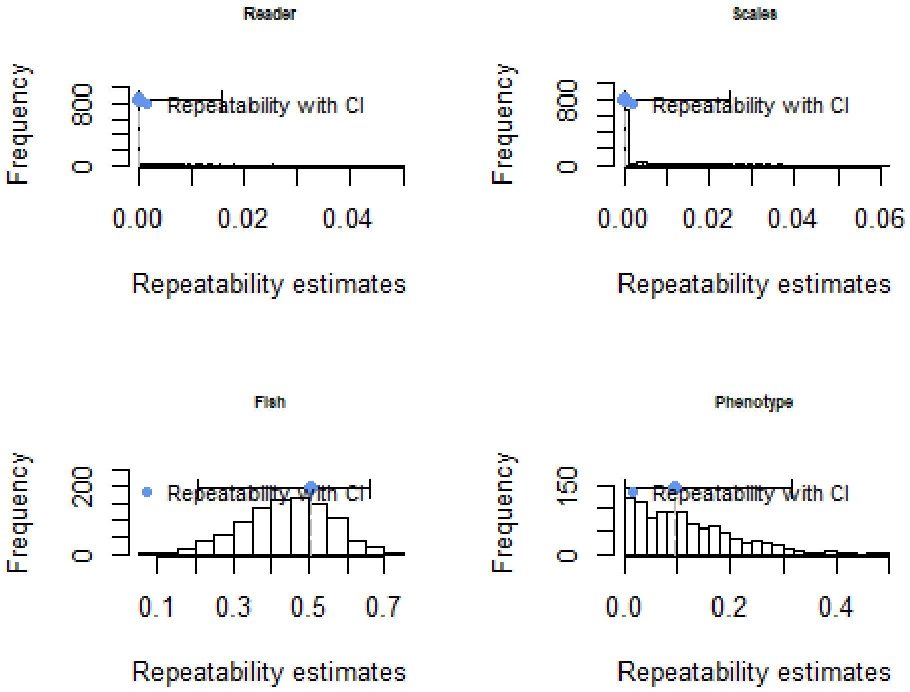
```
model3<-rpt(TA ~ Phenotype + (1|Reader) +  (1 | Scales) + (1 |Fish),
            grname = c("Reader","Scales", "Fish","Fixed"), data = data,
datatype = "Poisson",
            nboot = 1000, adjusted = F, ratio=T)

## Bootstrap Progress:

print(model3)

##
##
## Repeatability estimation using the glmm method and log link
##
## Repeatability for Reader
## --------------------------------
## Link-scale approximation:
## R   = 0
## SE = 0.005
## CI = [0, 0.016]
## P   = 1 [LRT]
##        NA [Permutation]
##
## Original-scale approximation:
## R   = 0
## SE = 0.004
## CI = [0, 0.014]
## P   = 1 [LRT]
##        NA [Permutation]
##
## Repeatability for Scales
## --------------------------------
## Link-scale approximation:
## R   = 0
## SE = 0.007
## CI = [0, 0.025]
## P   = 0.5 [LRT]
##        NA [Permutation]
##
## Original-scale approximation:
```

```
## R  = 0
## SE = 0.006
## CI = [0, 0.022]
## P  = 0.5 [LRT]
##      NA [Permutation]
##
## Repeatability for Fish
## --------------------------------
## Link-scale approximation:
## R  = 0.502
## SE = 0.114
## CI = [0.207, 0.658]
## P  = 1.89e-20 [LRT]
##      NA [Permutation]
##
## Original-scale approximation:
## R  = 0.5
## SE = 0.12
## CI = [0.196, 0.67]
## P  = 1.89e-20 [LRT]
##      NA [Permutation]
##
## Repeatability for Fixed
## --------------------------------
## Link-scale approximation:
## R  = 0.094
## SE = 0.089
## CI = [0.001, 0.319]
## P  = NA [LRT]
##      NA [Permutation]
##
## Original-scale approximation:
## R  = 0.085
## SE = 0.083
## CI = [0.001, 0.3]
## P  = NA [LRT]
##      NA [Permutation]
```

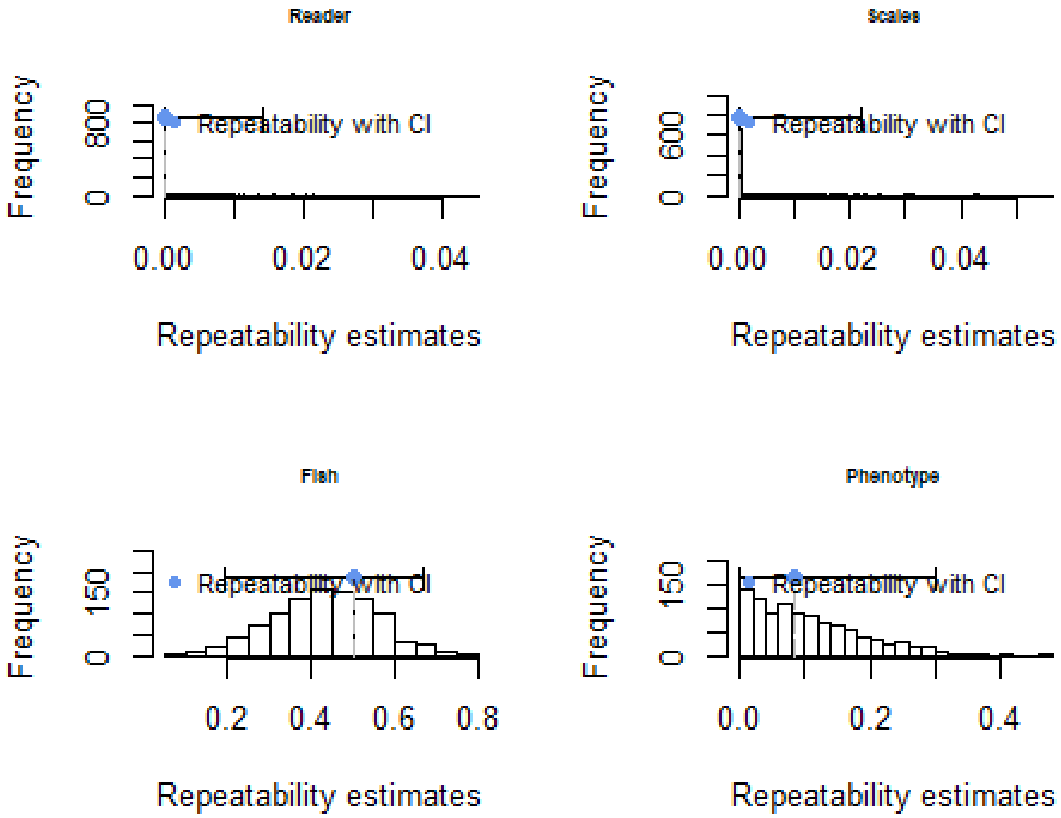
The code below helps plotting the repeatability for TA, either in scale link or scale original. Whatever links are chosen, same results are obtained.

```
par(mfrow=c(2,2))
plot(model3, grname = "Reader", scale="link", cex.main=0.6,main="Reader"
, type = "boot")
plot(model3, grname = "Scales", scale="link",cex.main=0.6, main="Scales"
, type = "boot")
plot(model3, grname = "Fish", scale="link", cex.main=0.6,main="Fish", ty
```

```
pe = "boot")
plot(model3, grname = "Fixed", scale="link", cex.main=0.6,main="Phenotyp
e", type = "boot")
```



```
par(mfrow=c(2,2))
plot(model3, grname = "Reader", scale="original", cex.main=0.6,main="Rea
der", type = "boot")
plot(model3, grname = "Scales",  scale="original",cex.main=0.6, main="Sc
ales", type = "boot")
plot(model3, grname = "Fish",  scale="original", cex.main=0.6,main="Fish
", type = "boot")
plot(model3, grname = "Fixed",  scale="original", cex.main=0.6,main="Phe
notype", type = "boot")
```



Below, you can add the Population effect. Repeatability of Fish decreases and Fixed effect increase. Fish are partly different because they belong to different Population.

```
model4<-rpt(TA ~ Population + Phenotype + (1|Reader) +  (1 | Scales) + (
1 |Fish),
            grname = c("Reader","Scales", "Fish","Fixed"), data = data,
datatype = "Poisson",
            nboot = 1000,  adjusted = F, ratio=T)

## Bootstrap Progress:

print(model4)

##
##
## Repeatability estimation using the glmm method and log link
##
## Repeatability for Reader
## --------------------------------
## Link-scale approximation:
## R  = 0
## SE = 0.005
## CI = [0, 0.015]
## P  = 1 [LRT]
```

```
##      NA [Permutation]
##
## Original-scale approximation:
## R  = 0
## SE = 0.005
## CI = [0, 0.013]
## P  = 1 [LRT]
##      NA [Permutation]
##
## Repeatability for Scales
## --------------------------------
## Link-scale approximation:
## R  = 0
## SE = 0.007
## CI = [0, 0.023]
## P  = 1 [LRT]
##      NA [Permutation]
##
## Original-scale approximation:
## R  = 0
## SE = 0.006
## CI = [0, 0.02]
## P  = 1 [LRT]
##      NA [Permutation]
##
## Repeatability for Fish
## --------------------------------
## Link-scale approximation:
## R  = 0.419
## SE = 0.113
## CI = [0.101, 0.538]
## P  = 1.21e-16 [LRT]
##      NA [Permutation]
##
## Original-scale approximation:
## R  = 0.409
## SE = 0.114
## CI = [0.092, 0.525]
## P  = 1.21e-16 [LRT]
##      NA [Permutation]
##
## Repeatability for Fixed
## --------------------------------
## Link-scale approximation:
## R  = 0.185
## SE = 0.114
## CI = [0.058, 0.495]
```

```
## P  = NA [LRT]
##      NA [Permutation]
##
## Original-scale approximation:
## R  = 0.171
## SE = 0.112
## CI = [0.053, 0.483]
## P  = NA [LRT]
##      NA [Permutation]
```

C Supportive information to Chapter 5. The evolution of growth and body size at age

C.1 Modélisation de la croissance. Résultats préliminaires

Description des jeux de données utilisés

Table C.1: Description du jeu de données S1

Les effectifs en nombres d'écailles et de poissons étudiés sont donnés par rivière et phénotype à la capture.

S1	Acœna		Nord	
	Écailles	Poissons	Écailles	Poissons
Truite résidentes TR	454	115	231	58
Truite de mer TM	204	51	175	44
Total	258	166	406	102

Table C.2: Description du jeu de données S2

Les effectifs sont donnés en nombre de poissons étudiés par rivière, phénotype à la capture et période. P1 = [1960-1970], P2 = [1971-1980], et P3 = [2000-2010].

S2	Château			Total	Norvégienne			Total
	P1	P2	P3		P1	P2	P3	
TS	48	10	67	125	24	21	11	56
TM2	14	11	2	27	9	10	2	21
TM3	7	11	21	39	2	2	11	15
Total	69	32	90	191	35	33	24	92

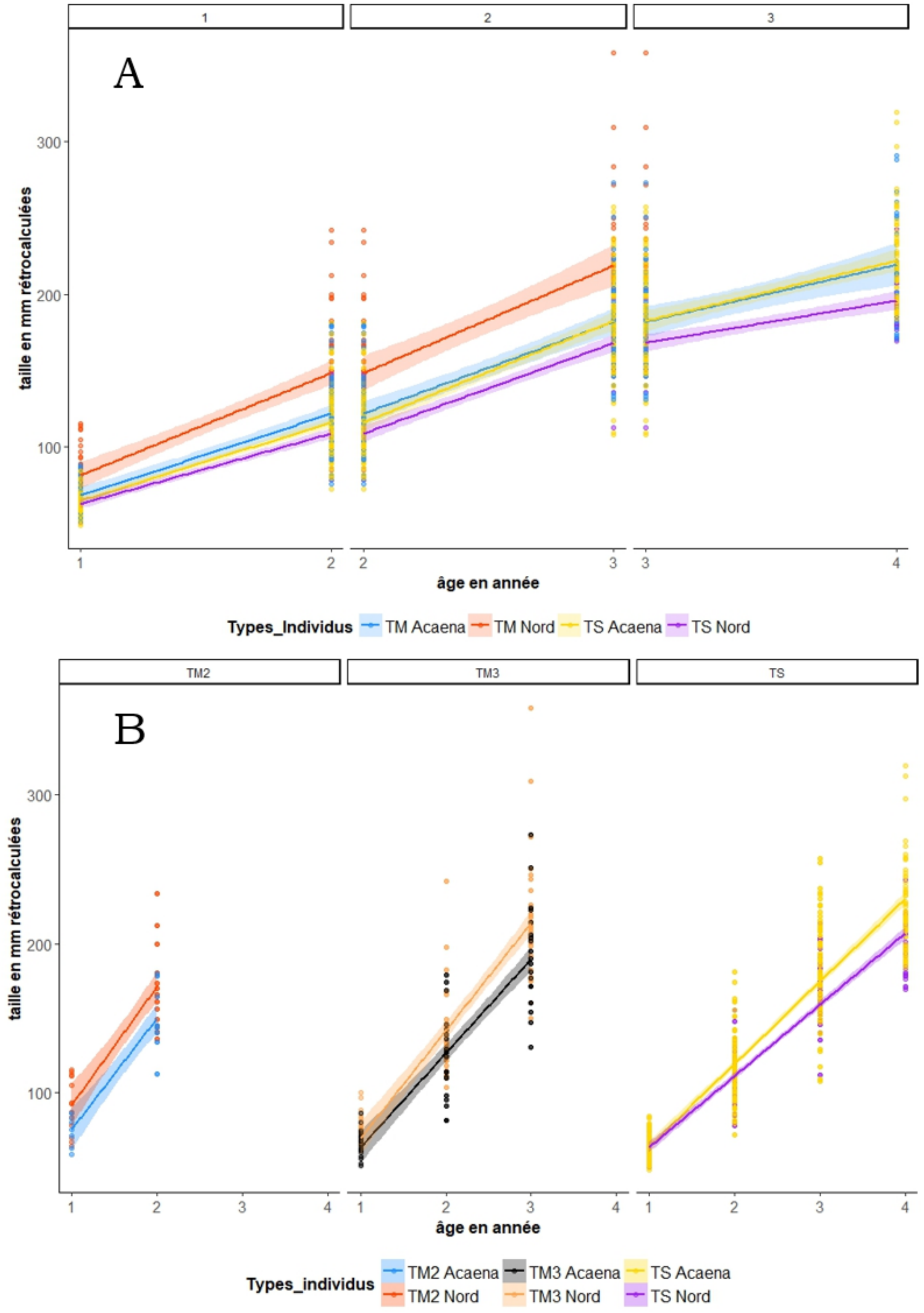
Paramétrages des modèles

Pour chacun des jeux de données S1 et S2, un modèle de Von Bertalanffy a été calibré. Sur S1, seules les variables environnementales (rivières) et le phénotype à la capture ont été supposé influencer les paramètres k et L (Eq.(C.1), pas de prior informatif). Sur S2, les variables environnementales (rivières), temporelles (périodes) et les phénotype à la capture ont été supposé influencés chacun des paramètres du modèle (Eq.(C.2), prior informatif choisi avec les posteriors des arbres de régression).

$$L_t = L_\infty(1 - e^{(-k_{r,p}(t - t_{0_{r,p}}))}) \tag{C.1}$$

$$L_t = L_{\infty_{r,p,pe}}(1 - e^{(-k_{r,p,pe}(t - t_{0_{r,p,pe}}))}) \tag{C.2}$$

Résultats sur le jeu de données S1

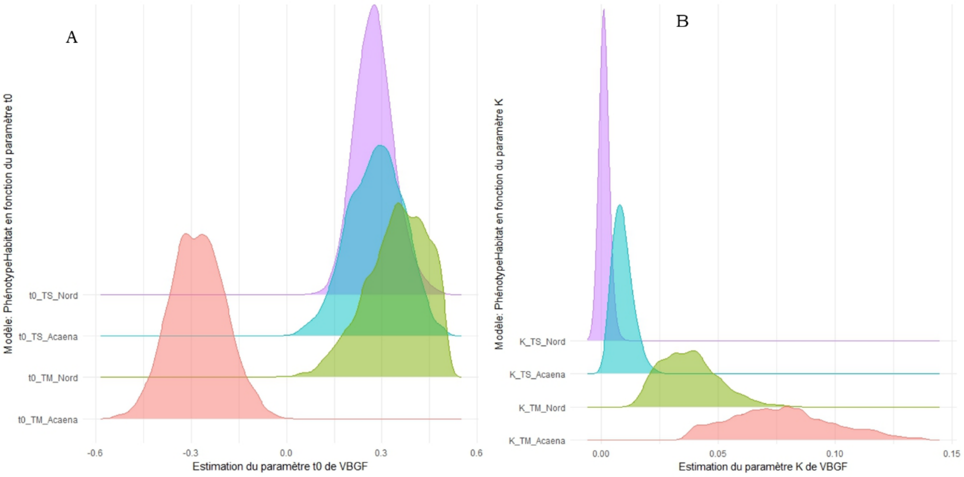


Régressions linéaires ajustées sur les tailles à l'âge rétrocalculées.

*A : Des régressions linéaires sont ajustées en fonction du phénotype et de l'habitat et entre chaque âge (1-2ans, 2-3ans, 3-4ans). B : Des régressions linéaires sont ajustées en fonction du phénotype et du départ en mer pour les truites migrantes. *La croissance des TM4 de 3 à 4 ans n'est pas prise en compte et n'apparait pas dans la figure car il n'y a qu'un seul individu TM4 sur Nord.*

La comparaison de la croissance en phase sédentaire entre phénotypes a permis d'identifier un taux de croissance en phase sédentaire plus élevé des truites de mer par rapport aux truites sédentaires sur la population Nord. Cependant, cette différence de croissance en phase sédentaire n'est pas observée dans la population Acœna.

La comparaison des croissances intra-phénotypes et inter-populations en phase sédentaire indique une différence des trajectoires de croissance des individus migrateurs entre les deux populations. Mais, la croissance des truites sédentaires des deux populations semble peu différente. Un effet population est observé entre les truites migratrices mais n'a pas été montré entre les phénotype sédentaire.

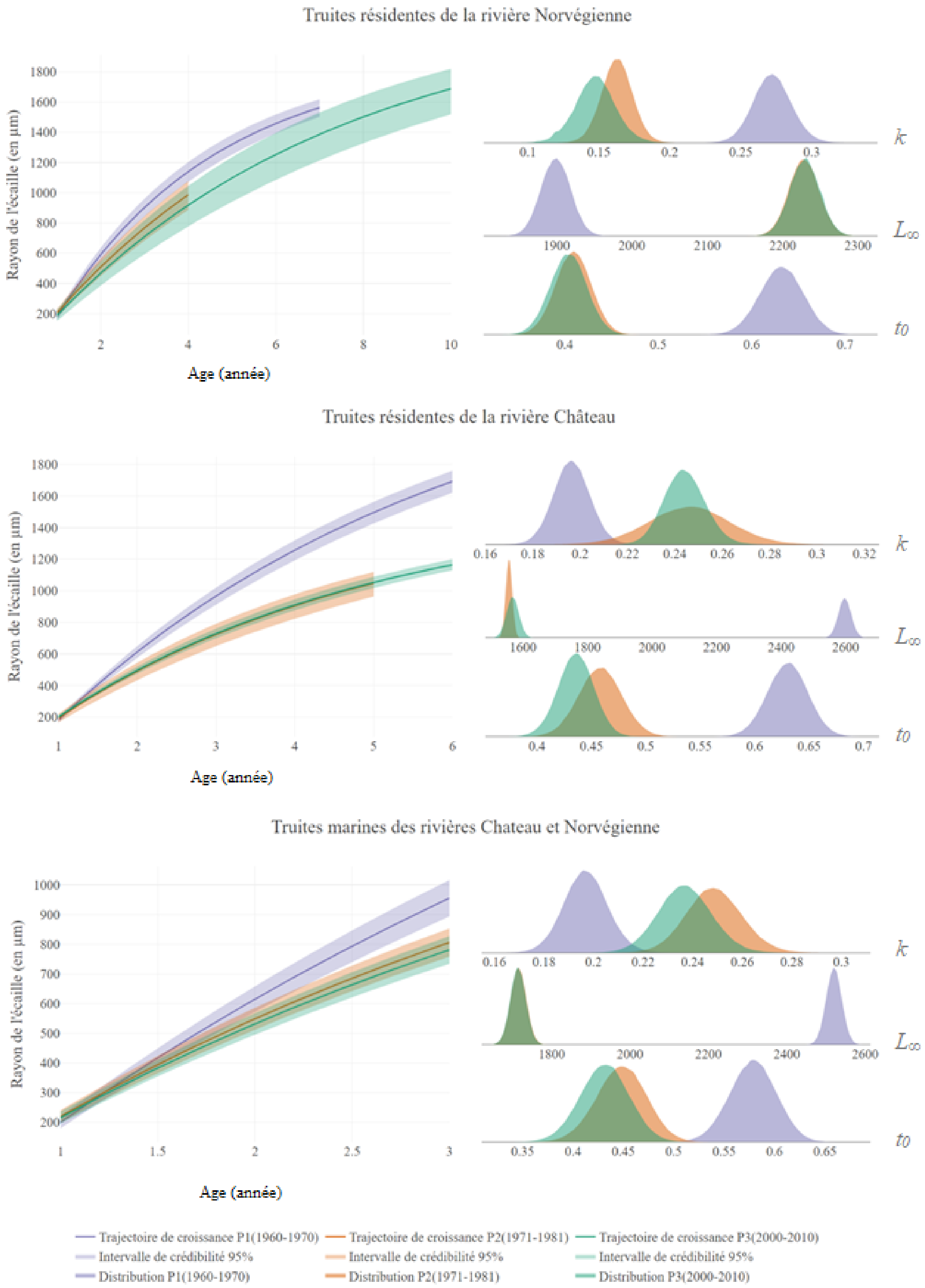


Distributions des estimations des paramètre t0 et K du modèle PH_{Kt_0} : paramètres t_0 (A) et K (B) en fonction du phénotype et de l'habitat.

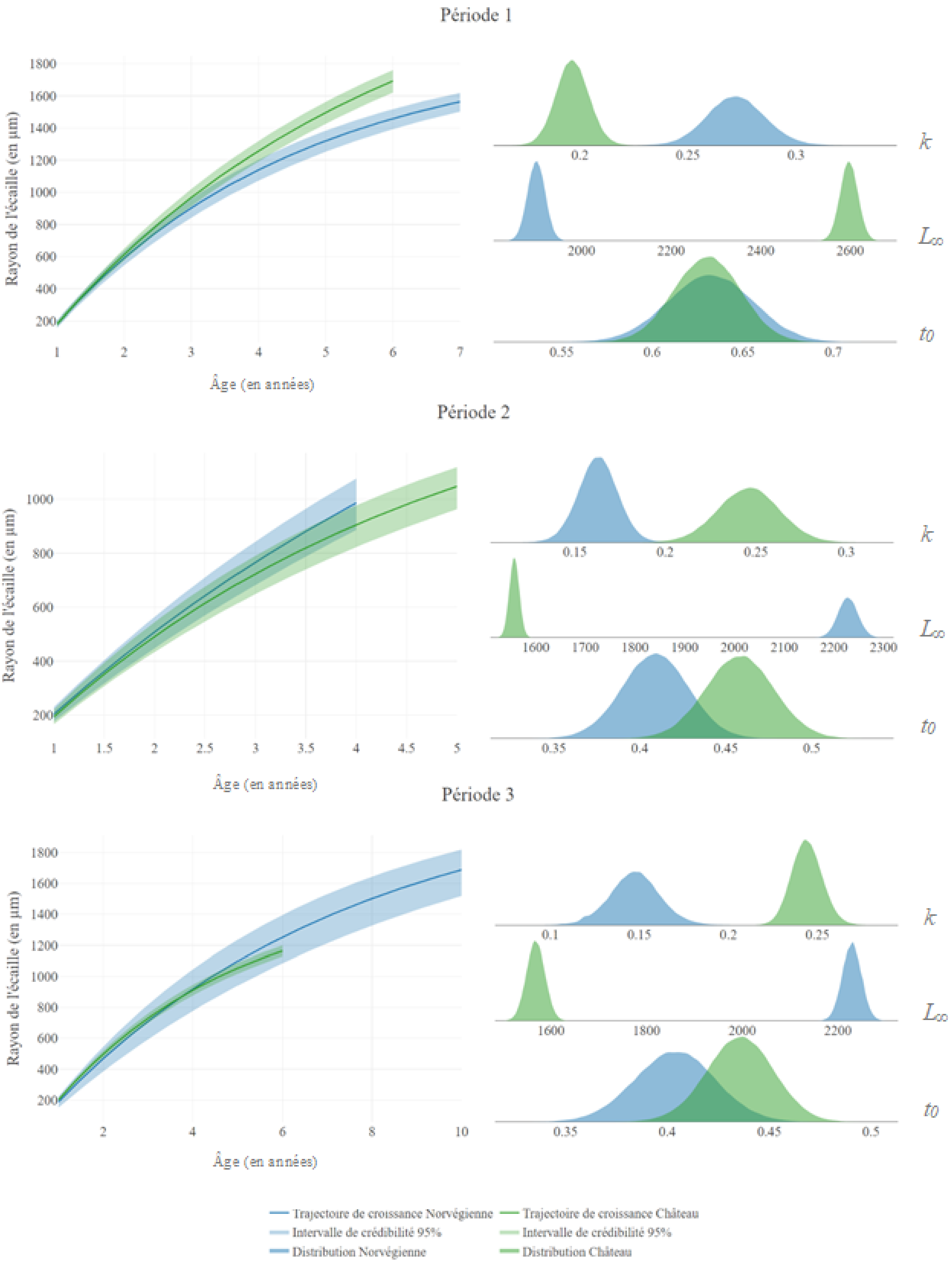
Résultats sur le jeu de données S2

Les trajectoires de croissance sont modifiées au cours du temps suite à la colonisation des rivières. Ce changement a été mis en évidence aussi bien chez les truites résidentes que chez les truites marines dans les deux rivières étudiées. Le fait que le rayon de l'écaille à l'âge soit plus faible pour les truites des périodes éloignées de la colonisation (P2 et P3) comparé à celles des premières périodes post-colonisation (P1) peut s'expliquer par l'augmentation de la densité d'individus. Mais d'autres facteurs qui influences les trajectoires de croissance comme la température. **Les trajectoires de croissance ne sont pas différentes entre les deux rivières** pour les truites marines mais le sont pour les truites résidentes. La similarité des trajectoires de croissance entre les truites marines des deux rivières peut s'expliquer par un flux fréquent d'individus marins entre ces deux populations participant ainsi à leur homogénéisation.

Dans un contexte d'invasion biologie et de la colonisation rapide de milieux vierges, il est possible que la diversité des trajectoires de croissance observée entraine une colonisation plus ou moins rapide de nouveaux cours d'eau par la truite. En effet, la migration marine dépend d'une taille seuil et cette migration est indispensable pour coloniser de nouveaux cours d'eau. Avec des tailles plus grandes, la colonisation de nouvelles rivières s'effectuera plus rapidement durant la première période post-colonisation, que pendant les périodes suivantes. Autrement dit, la taille seuil nécessaire à la migration et donc à la colonisation de nouvelle rivière sera atteinte plus rapidement. Cette dynamique étant aussi modulée suivant les conditions environnementales de la rivière et les prédispositions génétiques (pisciculture, sauvage, phénotype marin, phénotype résident. . .) qui peuvent influencer les trajectoires de croissance.

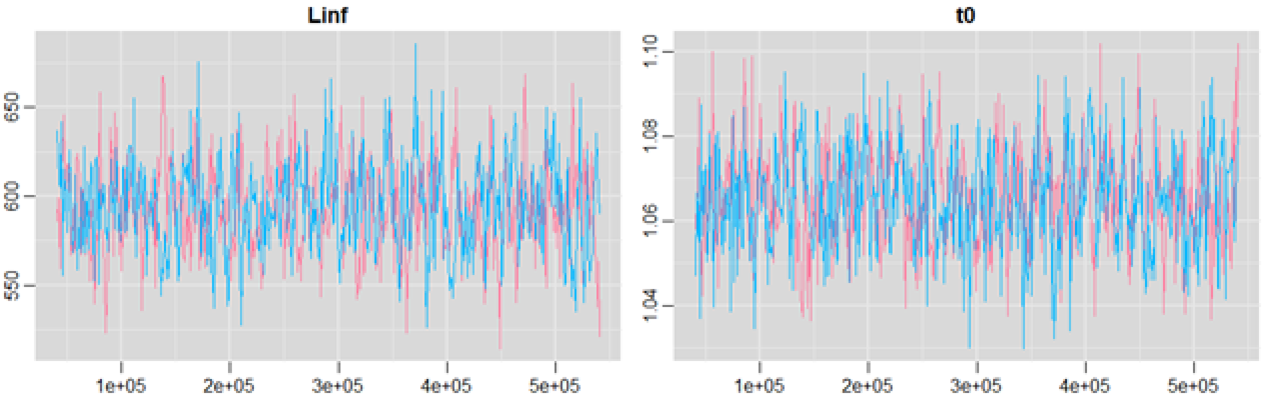


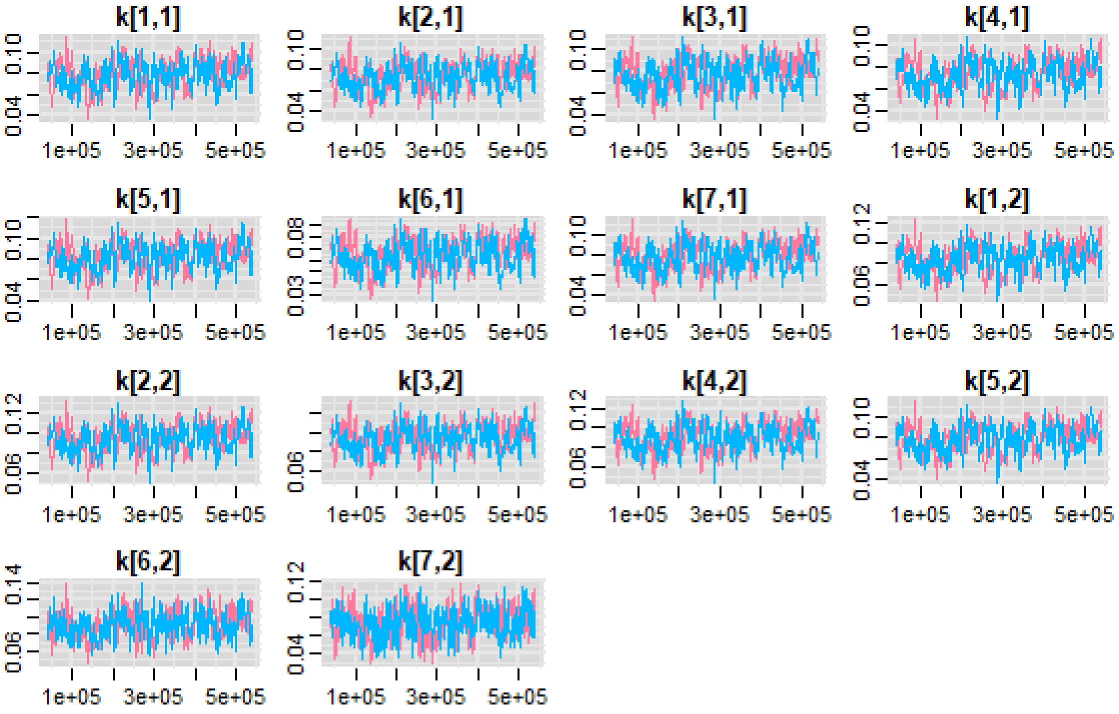
À gauche, les trajectoires de croissance et leurs intervalles de crédibilité à 95% associés pour les truites résidentes de Norvégienne (A) et de Château (C) ainsi que les truites marines des 2 rivières (E). À droite, la distribution à posteriori des 3 paramètres de la fonction de Von Bertalanffy pour les truites résidentes de Norvégienne (B) et Château (D) ainsi que les truites marines des 2 rivières (F). Le code couleurs correspond aux différentes modalités de la variable Période.

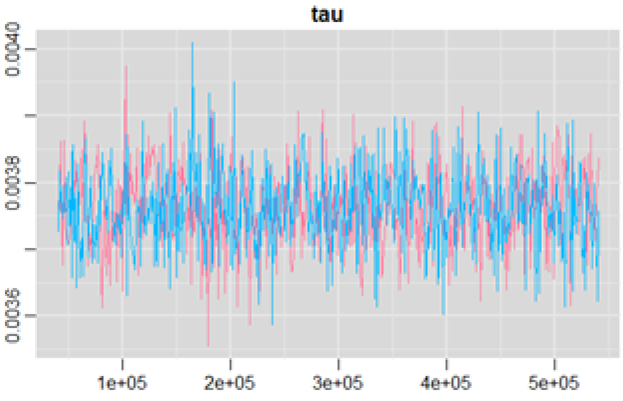


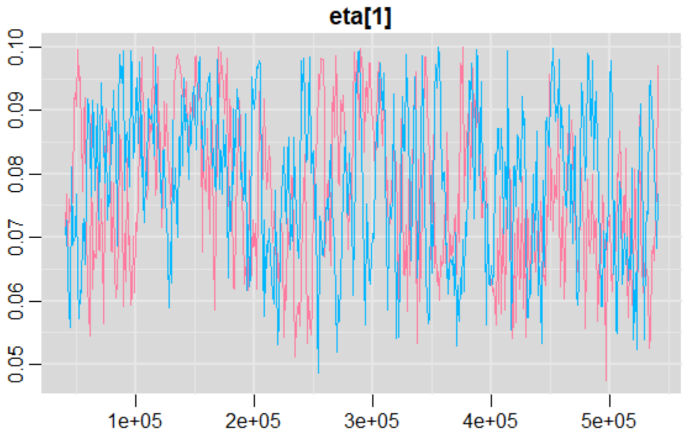
À gauche, les trajectoires de croissance des truites résidentes et leurs intervalles de crédibilité à 95% associés pour la période 1 (A), période 2 (C) et période 3 (E). À droite, la distribution à posteriori des 3 paramètres de la fonction de Von Bertalanffy pour les truites résidentes de la période 1 (A), 2 (C) et 3 (E). Le code couleurs correspond aux différentes modalités de la variable Rivière : Château et Norvégienne.

C.2 Convergence des chaînes du modèle de Von Bertalanffy





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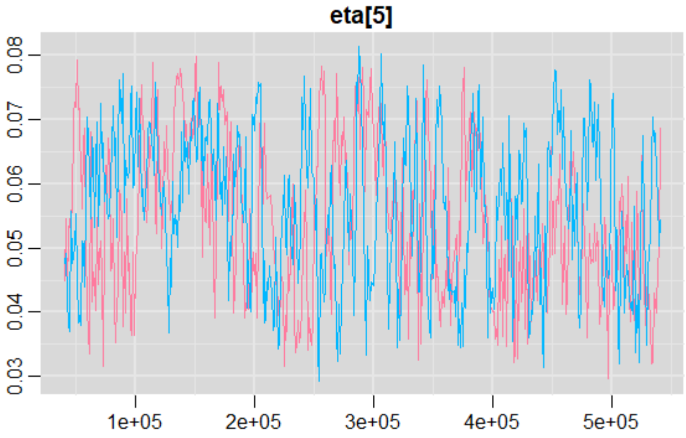
5e+05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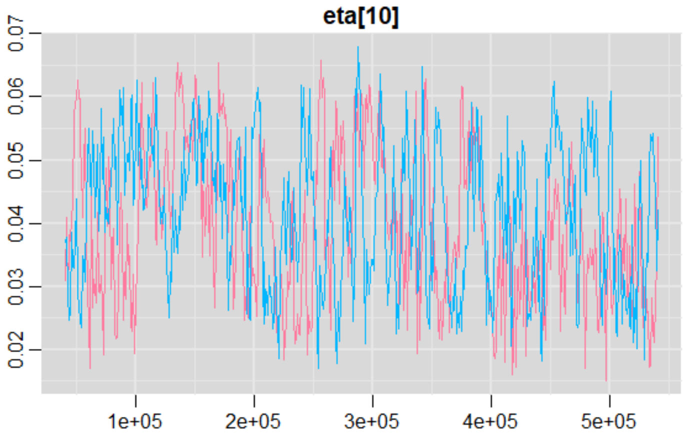
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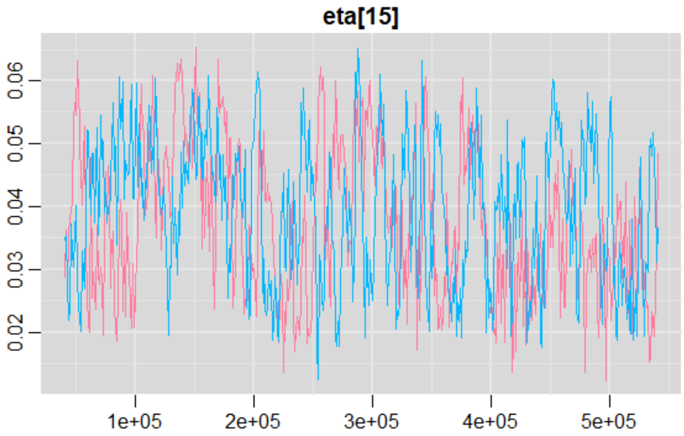
5e+05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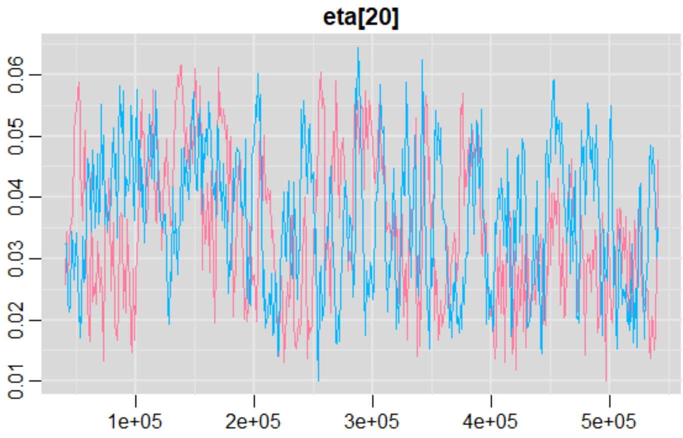
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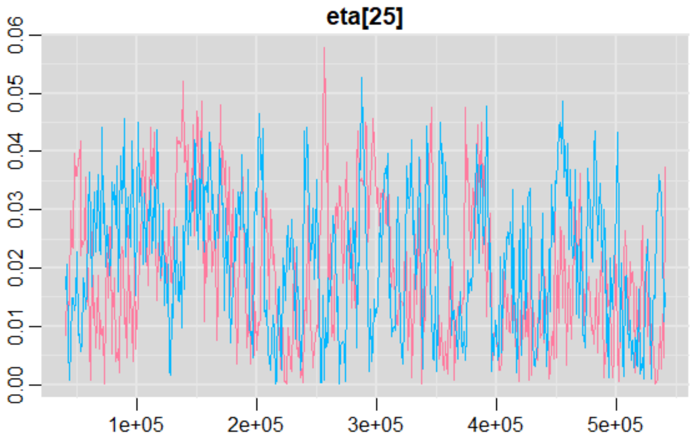
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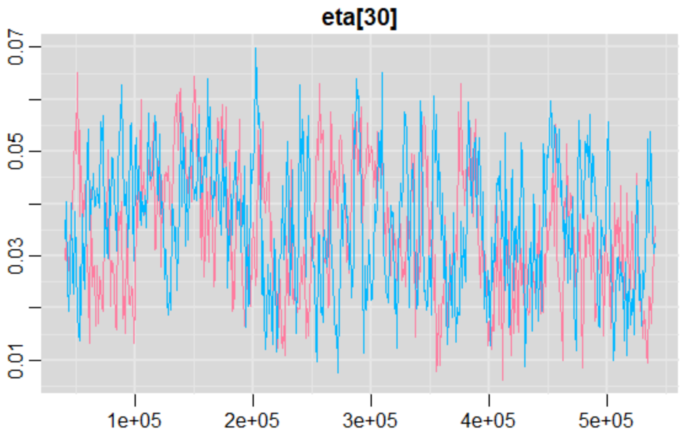
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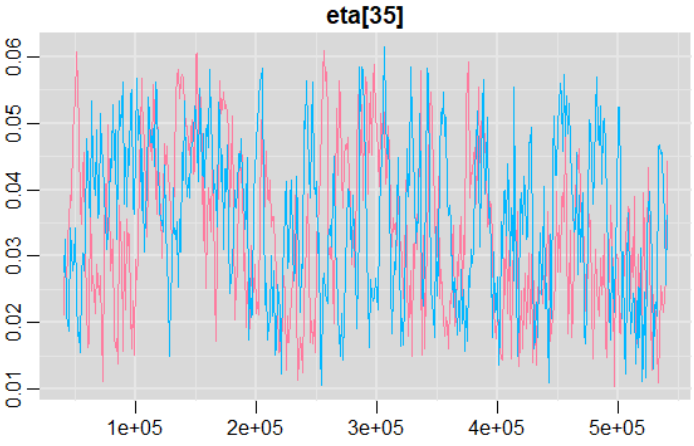
2e+05
3e+05
4e+05
5e+05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0.05
0.04
0.03
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0.01
1e+05
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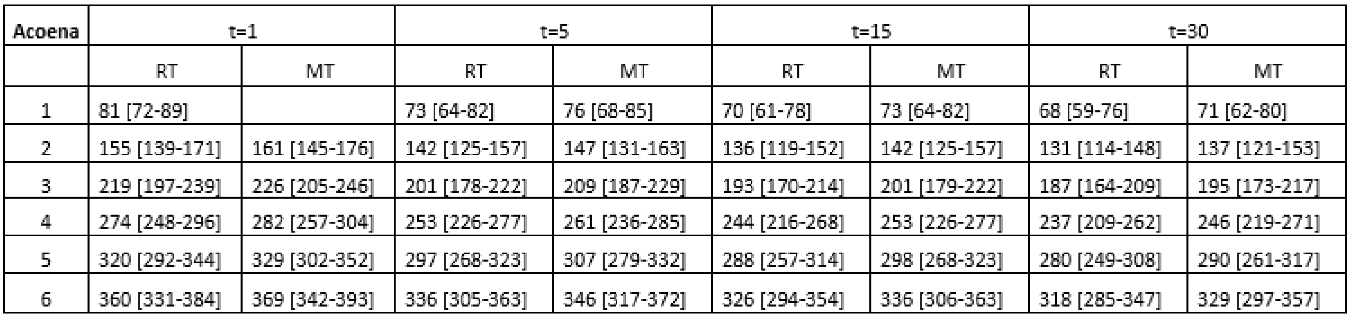
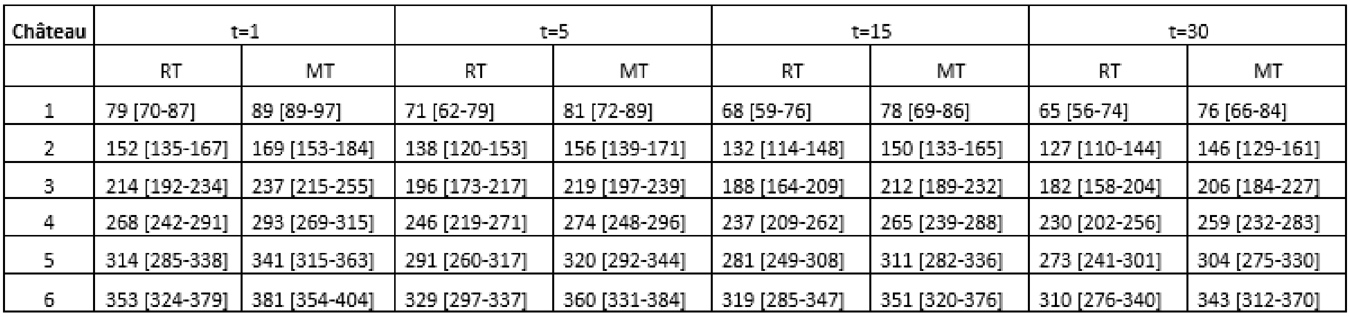
3e+05
4e+05
5e+05

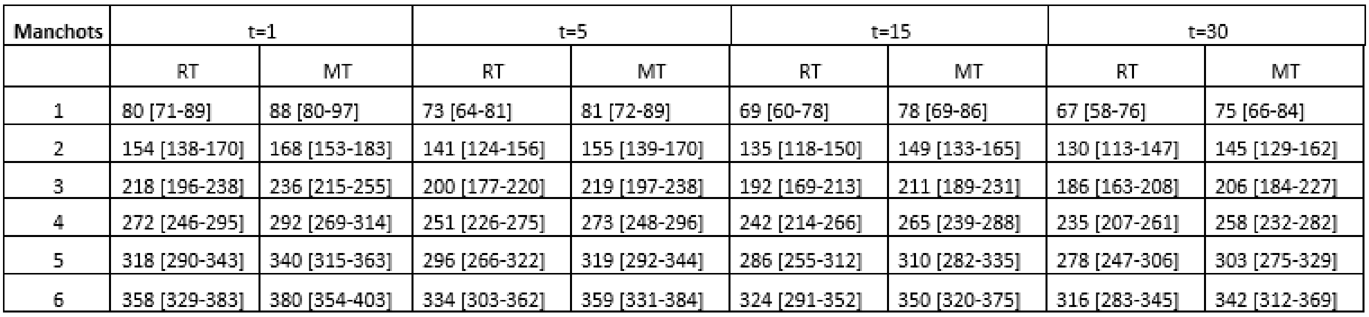
C.3 Estimates of body size at age by rivers



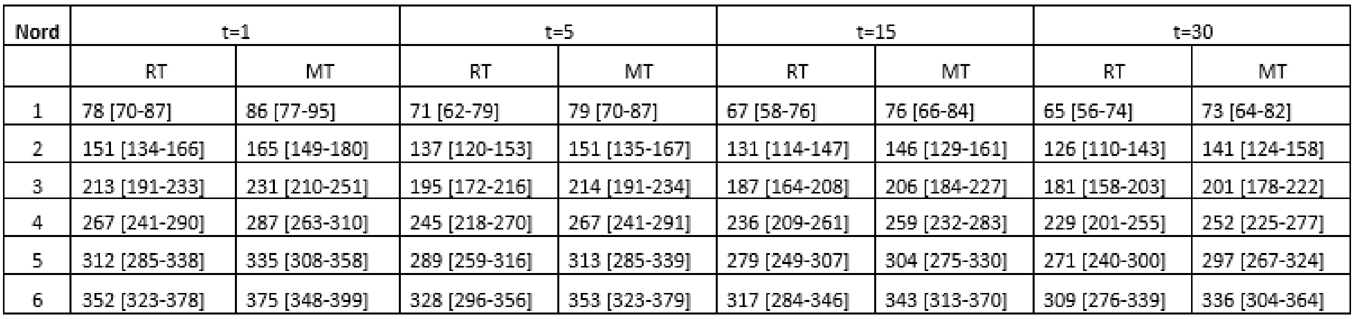
Acoena	t=1		t=5		t=15		t=30	
	RT	MT	RT	MT	RT	MT	RT	MT
1	81 [72-89]		73 [64-82]	76 [68-85]	70 [61-78]	73 [64-82]	68 [59-76]	71 [62-80]
2	155 [139-171]	161 [145-176]	142 [125-157]	147 [131-163]	136 [119-152]	142 [125-157]	131 [114-148]	137 [121-153]
3	219 [197-239]	226 [205-246]	201 [178-222]	209 [187-229]	193 [170-214]	201 [179-222]	187 [164-209]	195 [173-217]
4	274 [248-296]	282 [257-304]	253 [226-277]	261 [236-285]	244 [216-268]	253 [226-277]	237 [209-262]	246 [219-271]
5	320 [292-344]	329 [302-352]	297 [268-323]	307 [279-332]	288 [257-314]	298 [268-323]	280 [249-308]	290 [261-317]
6	360 [331-384]	369 [342-393]	336 [305-363]	346 [317-372]	326 [294-354]	336 [306-363]	318 [285-347]	329 [297-357]



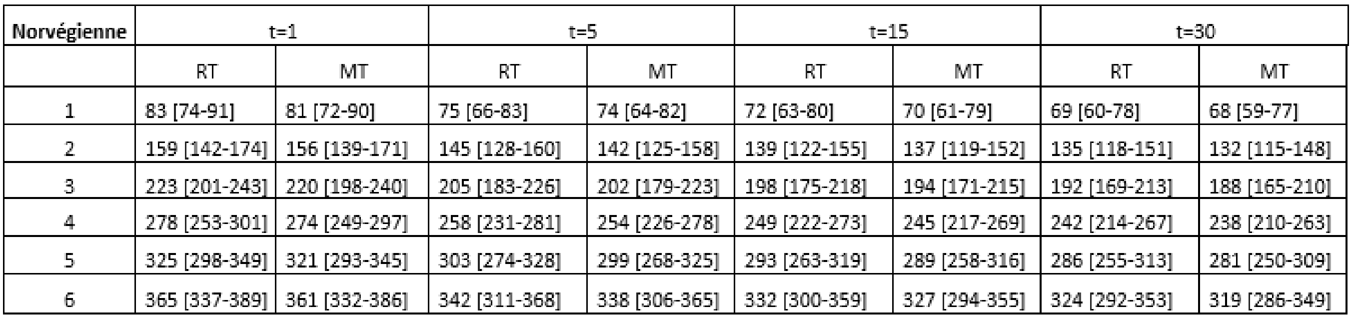
Château	t=1		t=5		t=15		t=30	
	RT	MT	RT	MT	RT	MT	RT	MT
1	79 [70-87]	89 [89-97]	71 [62-79]	81 [72-89]	68 [59-76]	78 [69-86]	65 [56-74]	76 [66-84]
2	152 [135-167]	169 [153-184]	138 [120-153]	156 [139-171]	132 [114-148]	150 [133-165]	127 [110-144]	146 [129-161]
3	214 [192-234]	237 [215-255]	196 [173-217]	219 [197-239]	188 [164-209]	212 [189-232]	182 [158-204]	206 [184-227]
4	268 [242-291]	293 [269-315]	246 [219-271]	274 [248-296]	237 [209-262]	265 [239-288]	230 [202-256]	259 [232-283]
5	314 [285-338]	341 [315-363]	291 [260-317]	320 [292-344]	281 [249-308]	311 [282-336]	273 [241-301]	304 [275-330]
6	353 [324-379]	381 [354-404]	329 [297-337]	360 [331-384]	319 [285-347]	351 [320-376]	310 [276-340]	343 [312-370]



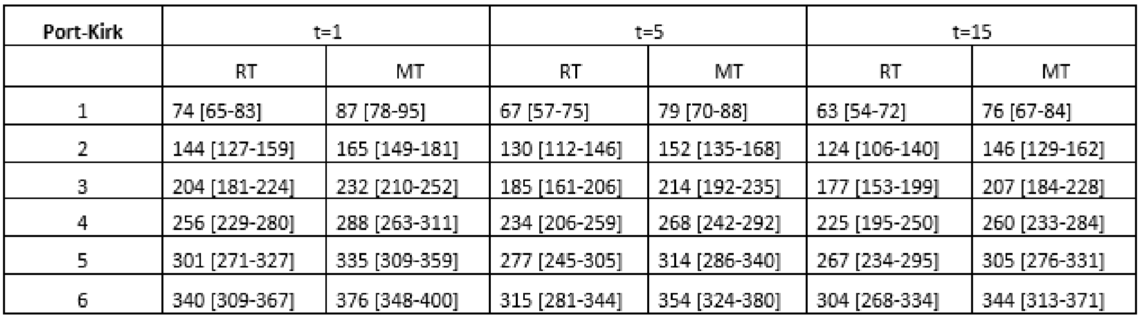
Manchots	t=1		t=5		t=15		t=30	
	RT	MT	RT	MT	RT	MT	RT	MT
1	80 [71-89]	88 [80-97]	73 [64-81]	81 [72-89]	69 [60-78]	78 [69-86]	67 [58-76]	75 [66-84]
2	154 [138-170]	168 [153-183]	141 [124-156]	155 [139-170]	135 [118-150]	149 [133-165]	130 [113-147]	145 [129-162]
3	218 [196-238]	236 [215-255]	200 [177-220]	219 [197-238]	192 [169-213]	211 [189-231]	186 [163-208]	206 [184-227]
4	272 [246-295]	292 [269-314]	251 [226-275]	273 [248-296]	242 [214-266]	265 [239-288]	235 [207-261]	258 [232-282]
5	318 [290-343]	340 [315-363]	296 [266-322]	319 [292-344]	286 [255-312]	310 [282-335]	278 [247-306]	303 [275-329]
6	358 [329-383]	380 [354-403]	334 [303-362]	359 [331-384]	324 [291-352]	350 [320-375]	316 [283-345]	342 [312-369]



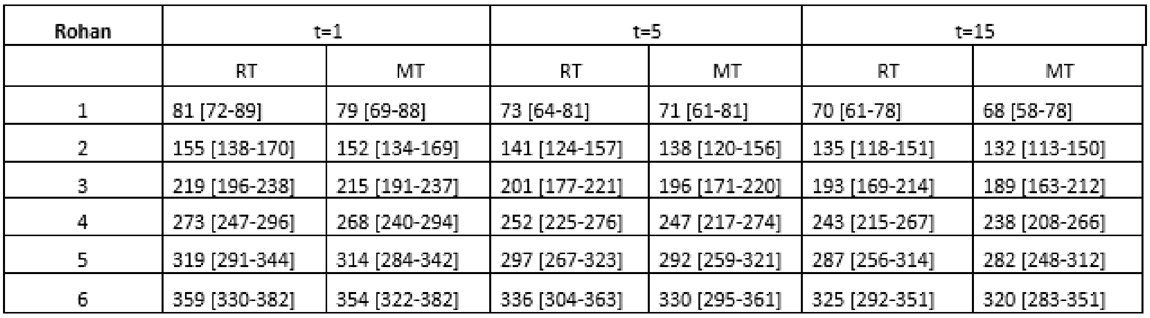
Nord	t=1		t=5		t=15		t=30	
	RT	MT	RT	MT	RT	MT	RT	MT
1	78 [70-87]	86 [77-95]	71 [62-79]	79 [70-87]	67 [58-76]	76 [66-84]	65 [56-74]	73 [64-82]
2	151 [134-166]	165 [149-180]	137 [120-153]	151 [135-167]	131 [114-147]	146 [129-161]	126 [110-143]	141 [124-158]
3	213 [191-233]	231 [210-251]	195 [172-216]	214 [191-234]	187 [164-208]	206 [184-227]	181 [158-203]	201 [178-222]
4	267 [241-290]	287 [263-310]	245 [218-270]	267 [241-291]	236 [209-261]	259 [232-283]	229 [201-255]	252 [225-277]
5	312 [285-338]	335 [308-358]	289 [259-316]	313 [285-339]	279 [249-307]	304 [275-330]	271 [240-300]	297 [267-324]
6	352 [323-378]	375 [348-399]	328 [296-356]	353 [323-379]	317 [284-346]	343 [313-370]	309 [276-339]	336 [304-364]



Norvégienne	t=1		t=5		t=15		t=30	
	RT	MT	RT	MT	RT	MT	RT	MT
1	83 [74-91]	81 [72-90]	75 [66-83]	74 [64-82]	72 [63-80]	70 [61-79]	69 [60-78]	68 [59-77]
2	159 [142-174]	156 [139-171]	145 [128-160]	142 [125-158]	139 [122-155]	137 [119-152]	135 [118-151]	132 [115-148]
3	223 [201-243]	220 [198-240]	205 [183-226]	202 [179-223]	198 [175-218]	194 [171-215]	192 [169-213]	188 [165-210]
4	278 [253-301]	274 [249-297]	258 [231-281]	254 [226-278]	249 [222-273]	245 [217-269]	242 [214-267]	238 [210-263]
5	325 [298-349]	321 [293-345]	303 [274-328]	299 [268-325]	293 [263-319]	289 [258-316]	286 [255-313]	281 [250-309]
6	365 [337-389]	361 [332-386]	342 [311-368]	338 [306-365]	332 [300-359]	327 [294-355]	324 [292-353]	319 [286-349]



Port-Kirk	t=1		t=5		t=15	
	RT	MT	RT	MT	RT	MT
1	74 [65-83]	87 [78-95]	67 [57-75]	79 [70-88]	63 [54-72]	76 [67-84]
2	144 [127-159]	165 [149-181]	130 [112-146]	152 [135-168]	124 [106-140]	146 [129-162]
3	204 [181-224]	232 [210-252]	185 [161-206]	214 [192-235]	177 [153-199]	207 [184-228]
4	256 [229-280]	288 [263-311]	234 [206-259]	268 [242-292]	225 [195-250]	260 [233-284]
5	301 [271-327]	335 [309-359]	277 [245-305]	314 [286-340]	267 [234-295]	305 [276-331]
6	340 [309-367]	376 [348-400]	315 [281-344]	354 [324-380]	304 [268-334]	344 [313-371]



Rohan	t=1		t=5		t=15	
	RT	MT	RT	MT	RT	MT
1	81 [72-89]	79 [69-88]	73 [64-81]	71 [61-81]	70 [61-78]	68 [58-78]
2	155 [138-170]	152 [134-169]	141 [124-157]	138 [120-156]	135 [118-151]	132 [113-150]
3	219 [196-238]	215 [191-237]	201 [177-221]	196 [171-220]	193 [169-214]	189 [163-212]
4	273 [247-296]	268 [240-294]	252 [225-276]	247 [217-274]	243 [215-267]	238 [208-266]
5	319 [291-344]	314 [284-342]	297 [267-323]	292 [259-321]	287 [256-314]	282 [248-312]
6	359 [330-382]	354 [322-382]	336 [304-363]	330 [295-361]	325 [292-351]	320 [283-351]

C.4 Selection of age-1 fish with Neural Network Learning

Objective: Make use of at least some parts of our incomplete database for captures, focusing on the brown trout (*Salmo trutta* L.) growth for individuals between 1 and 2 year old (therefore, 1^+ individuals).

Based on the work developed by Jacques Labonne, I extracted all the brown trout caught between 50 and 249mm, aged or not. I collected also their sampling dates (when the precision was daily), their river sampling location, the date at which the river was colonized and therefore the timing between this colonization date and their capture date. In this dataset, 6191 fish were aged and 40050 were not aged. The day information was transformed into a number between 1 and 365 (so there is a one day error every 4 years), 1 being the 1st of July. 6191 fish had their age calculated in days, and were grouped in 3 categories: age-0, age-1 and ages superior or equal to 2.

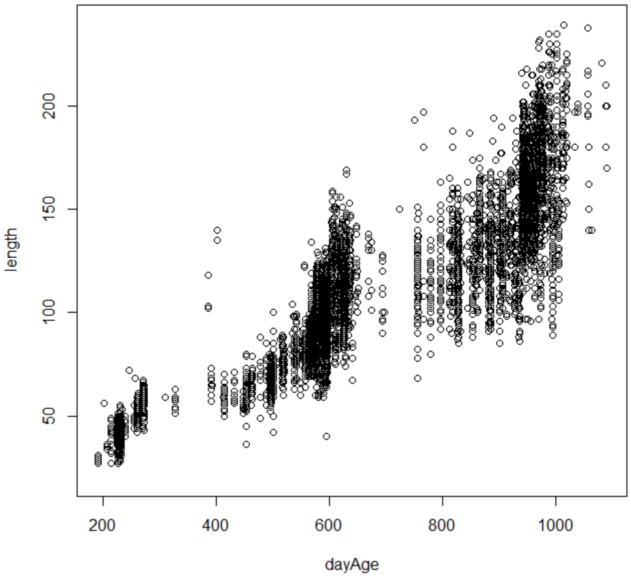


Figure **C.1**: Size distribution by dayAge of the 6191 aged fish in the database.

As we were only interested into obtaining the age class of the 40050 non-aged fish, we did not attend to develop a parametric model, relying on parameters inference, which are the very things on which we later want to test some hypotheses. Neural networks, at least, do not make any assumptions, they just tear things apart based on Euclidian distances. If we do one assumption here, it is maybe that the process that we want to study 'growth evolution' is not strong enough to completely alter the age structure in the age/body size relationship, so the neural network will be efficient enough.

We used the K-Nearest Neighbour Classification (knn function of class R package, *ver.* 7.3-14) on the known age fishes, using 4000 of them to train, and the remaining 2000 (about) to predict. On average, the percentage of accurate assignation to age class is 97%, using only body size at capture, and the day of capture in the year. On the 46241 fish available, were redistributed to the age-1 category. We extracted 22871 that were redistributed to the age-1 category and caught during the period were growth was thought to be monotonous (between 45 and 275 days), to simplify the following analysis on body size at age.

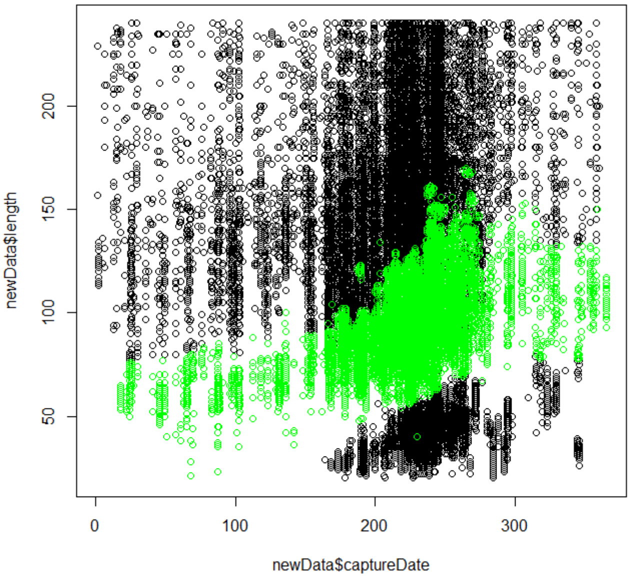


Figure **C.2**: Age-1 redistribution according to the body size of fish and date at capture.

As we want the exact size at the age of 1 year old (not the size at capture), we need to recalculate size at 365 days. The fish are estimated to measure on average 28 mm at 180 days. We therefore applied a log-linear relation between size and age fro each fish, such that :

$$\begin{aligned} log(size) &\sim age \\ size &= size - at - capture - 28 \\ age &= dayAge - 180 \end{aligned} \tag{C.3}$$

We used the estimated coefficient to rebuilt the size at age-1 for each fish.

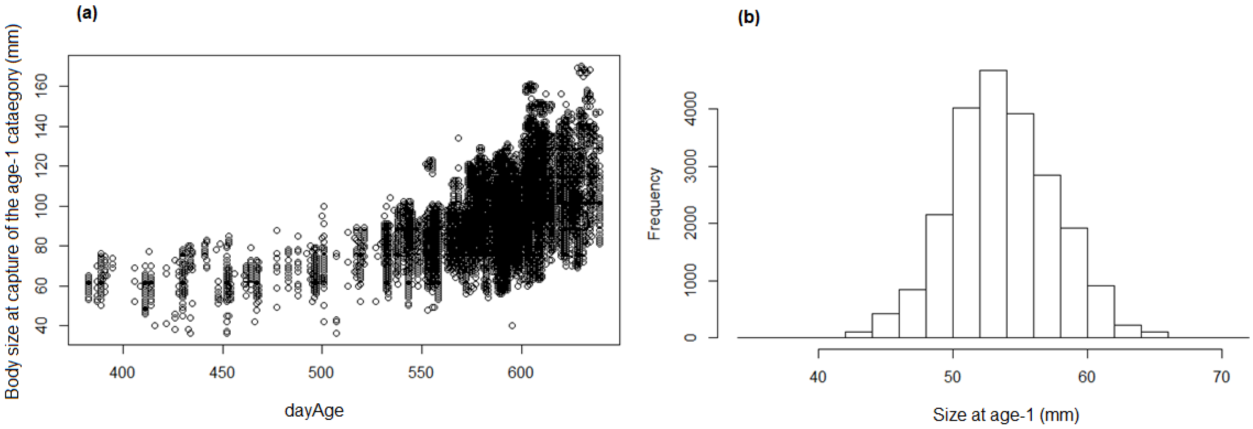


Figure **C.3**: Age-1 body size according to dayAge (a) and the distribution of size at the exact age of one year old (b).

D Activités scientifiques

Liste des établissements et des unités de recherche d'exercice

2015	4 mois	Natural Resources Institute Finland (Luke)	Stage de Master 1 (1 publication acceptée)
2016	6 mois	Centre d'Ecologie Fonctionnelle et Evolutive (CEFE) CNRS UMR 5175	Stage de césure - Equipe HAIR
2016-2017	1 an	Université de Montpellier UMR 1224 INRAE/UPPA ECOBIOP	Apprentissage Master 2
2017-2020	3 ans	UMR 1224 INRAE/UPPA ECOBIOP	Doctorat (1publication acceptée, 2 en préparation)

Publications scientifiques

Aulus Giacosa L., Aymes J-C., Gaudin P., Vignon M. *Hierarchical variance decomposition of fish scale growth and age to investigate the relative contributions of readers and scales.* **Marine and Freshwater Research**, CSIRO Publishing, 2019, 70 (12), pp.1828-1837. 10.1071/MF19059.

Valkonen, S., Aulus Giacosa, L., Heikkinen, J. *Tree mortality in the dynamics and management of uneven-aged Norway spruce stands in southern Finland.* **Eur J Forest Res** 139, 989–998 (2020). https://doi.org/10.1007/s10342-020-01301-8

Aulus Giacosa L., Vignon M., Labonne J. *The evolution of body size of partial migratory population on shifting expanding range.* **In preparation for publication**

Aulus Giacosa L., Vignon M., Labonne J, Buoro M. *Towards the evolution of threshold size at migration.* **In preparation for publication**

Communications orales

Conférences nationales et internationales

Aulus Giacosa L., Vignon M.,Gaudin P., *Spatio-temporal evolution of life history traits: Brown tout colonization of the sub-Antarctic Kerguelen Islands*, **Colloque de la Société Française de l'Ecologie**, Rennes, FRANCE (23-25 Octobre 2018).

Exposés à l'occasion de séminaires ou de groupes de travail

Aulus Giacosa L., Vignon M.,Gaudin P., *Shifting threshold: Is there an evolution of migratory life histories in Brown trout (Salmo trutta)?*, **Young Modellers in Ecology (YOMOS)**, online Workshop 2020 (25-28 May 2020)

Aulus-Giacosa L., Gaudin P., Vignon M. (2018). *Spatio-temporal evolution of life history traits: Brown tout colonization of the sub-Antarctic Kerguelen Islands.* **Groupement de Recherche "Invasions Biologiques"**, le 22 Octobre 2018, Rennes.

Aulus-Giacosa L. (2018). *Evolution of anadromy and its impact on invasion dynamics: the case of long term monitored introduced brown trout (Salmo trutta L.) in the Kerguelen Islands.* **Séminaire Zone Atelier Antactique (ZATA)**, le 2 Octobre 2018, St-Pée sur Nivelle.

Aulus-Giacosa L., **Gouzou P.**, **Magne G.** (2018). *Exploring invasiveness through growth and migratory tactics in the sub-antarctic Kerguelen Islands. Variation in growth and its implication for life-history.* **Séminaire scientifique annuel d'unité, UMR 1224 ECOBIOP**, le 2 Mai 2018, St-Pée sur Nivelle.

Aulus-Giacosa L. (2017). *Growth estimation methods to characterize Salmo trutta probabilistic reaction norm for age and size at migration in Kerguelen Islands.* [Online]. **Réseau 'Salmonidés et Poissons Amphihalins Migrateurs' (SPAM)**, du 9 au 11 Mai, 2017, Aquapôle INRA – St-Pée sur Nivelle.

Posters

Lauréate première place des présentations de poster lors des journées de l'ED 211 - 21/06/2019

Aulus-Giacosa L., **Vignon M.**, Gaudin P., Gueraud F., Aymes J.C. (2018). *The effect of ageing errors on Von Bertalanffy parameters estimation using a Bayesian sensitivity analysis approach.* Poster session, **6th International Otolith Symposium 2018 (IOS2018)**, 15-20 April 2018 Keelung, Taiwan.

Aulus-Giacosa L., Vignon M., Buoro M., Gaudin P., Gueraud F., Aymes J.C. (2017). *Growth models and estimation of migratory reaction norm for invasive brown trout (Salmo trutta L.) in Kerguelen Islands.* General poster session, **"International Long Term Ecological Research Network and LTER-France (Zones Ateliers Network and Critical Zone Observatories) joint conference"** followed by the ILTER Coordinating Committee Meeting, October, 2 - 4, 2017 – Nantes.

Activités et responsabilités en matière d'enseignement

Enseignements. UFR des Sciences et Techniques de la côte basque (UPPA), Anglet (69h).

2017-2018	L1	TP	Biologie Animale	28h
2018-2019	L2	TD	Biologie évolutive	6h
	L1 Biologie L1 Informatique	TD	Ecologie, Evolution, Environnement	30h
	M2	Projet tuteurée		5h

Co-encadrement de stagiaires

Lucille Baron (2017), Caractérisation de traits de vie chez la truite commune (*Salmo trutta*) dans un contexte d'invasion biologique aux îles Kerguelen. Stage de L3

Gautier Magne (2018) Comparaison de croissance entre deux populations de truites communes aux îles Kerguelen. Stage de M1

Paul Gouzou (2018) Croissance compensatoire chez la truite commune (*Salmo trutta*) aux îles Kerguelen dans un contexte d'invasion biologique. Stage de L3

Jon Levy (2018), Caractérisation de traits de vie chez la truite commune (*Salmo trutta*) dans un contexte d'invasion biologique aux îles Kerguelen. Stage de L2

Valentin Santanbien (2019), Comparaison de croissance entre deux populations de truites communes aux îles Kerguelen dans un contexte d'invasion biologique. Stage de M2.

Hervé Rogissart (2019), Caractérisation de traits de vie chez la truite commune (*Salmo trutta*) dans un contexte d'invasion biologique aux îles Kerguelen. Stage de M1

Autres interactions avec des stagiaires

Hervé Rogissart (2020) Effets transgénérationnels (microchimie et croissance) chez la truite brune Salmo trutta, Stage de M2.

Campagne de terrain

Participation à la campagne de terrain du programme SALMEVOL dans les îles sub-antarctiques de Kerguelen (Dec. 2018 – Fev. 2019)

Formation

Stage journée d'expérimentation animale (Juin 2017)

Formation à la recherche documentaire et à la publication scientifique (12h)

Formation à l'éthique de la recherche et à l'intégrité scientifique (4h)

Enseigner Mode d'emploi (12h)

Stage Voix et Gestes (18h)

Séminaire d'Insertion Professionnelle (12h)

Anglais certification Cambridge – Niveau C1 (Juin 2019)

Autres activités

2018 - Co-organisatrice du séminaire scientifique de l'UMR 1224 - ECOBIOP

2018 à 2020 - Représentante des doctorants au sein du Bureau et du Conseil de l'ED SEA - Université de Pau et des Pays de l'Adour (UPPA)

24-25 Mai 2018. Odyssées des Juniors, Du Flocon à la Vague, Animation du stand scalimétrie/ otolithométrie, Jardin Botanique de St Jean de Luz

Résumé

Grâce à ses capacités dispersives et adaptatives, la truite commune (*Salmo trutta* L.), poisson anadrome facultatif, est un bon candidat à la colonisation de nouveaux milieux. L'introduction de l'espèce dans les années 1950 dans les îles subantarctiques de Kerguelen fournit un modèle d'étude unique pour comprendre les causes et les mécanismes de la dispersion, grâce à l'étude des traits d'histoire de vie en lien avec la migration (*e.g.* croissance, âge à la migration). L'étude de leur évolution temporelle le long d'un front de colonisation est le cœur de ce travail de thèse. A travers l'étude des écailles recueillies dans le cadre de ce programme à long terme, les histoires de vie de près de 5000 poissons ont été reconstruites. Ce travail démontre l'importance de la méthodologie utilisée afin de reconstruire les traits de vie individuel. La modélisation de l'évolution de la croissance en eau douce, de la taille à l'âge et de l'âge à la première migration démontre que des processus évolutifs sont en œuvre dans les populations en expansion. Notamment, le ralentissement de la croissance avec le temps ainsi que la diminution de la taille à l'âge le long du front de colonisation laissent à penser que la capacité de dispersion diminue à mesure que les populations sont en marges de la zone d'expansion. L'évolution de la valeur seuil à la première migration confirme ce résultat, et illustre l'importance de la plasticité phénotypique et de l'adaptation locale dans le choix de la tactique migratoire. Toutefois, l'approche menée dans ce manuscrit se concentre sur l'évolution de la migration, et bénéficierait de l'étude de l'évolution conjointe des traits impliqués dans la valeur sélective (balance coûts-bénéfices), tels que la reproduction, ou la croissance en mer.

Mots clés: colonisation, croissance, migration partielle, norme de réaction, *Salmo trutta*, traits d'histoire de vie.

Abstract

It is an ongoing issue to better understand colonization process, adaptation potential to new environments, and invasiveness of a species. The sub Antarctic Kerguelen Islands are a perfect model to model population dynamics in an invasion context, because it represents a simplified case of invasion by brown trout (*Salmo trutta* L.), a facultative anadromous fish. Introduced in the 1950s, and thanks to its dispersive and adaptive capacities, the brown trout provides a unique study model for understanding the causes and mechanisms underlying biological invasions. Understanding dispersal mechanisms, through the study of life history traits related to migration (*e.g.* growth, age at migration) and their temporal evolution in shifting expansion range population, is the core of this thesis work. Through the study of scales collected in this unique framework, the life histories of nearly 5000 fish have been rebuilt. This work demonstrates the importance of the methodology to determine accurate estimates of individual life history traits. Modelling the evolution of freshwater growth, body size at age and age at first migration demonstrates that evolutionary processes are at work according to the time since colonization. In particular, the decrease in growth rate over time and the decrease in body size at age over time and space suggest that the dispersal capacity is decreasing in populations located at the margins. The evolution of the threshold size at first migration confirms this results, and illustrates the importance of phenotypic plasticity and local adaptation in the choice of migratory tactics. However, the approach taken in this manuscript focuses on the evolution of migration, and would benefit from the study of the joint evolution of traits involved in fitness (costs-benefits balance), such as reproduction, or growth at sea.

Keywords: colonization, growth, life-history traits, partial migration, reaction norm, *Salmo trutta.*