Conditionnement des stratégies d'histoire de vie et mécanismes adaptatifs à court terme : approche intégrée par capture-marquage-recapture et application au saumon atlantique (Salmo salar) en condition naturelle

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UNIVERSITÉ MONTPELLIER II
SCIENCES ET TECHNIQUES DU LANGUEDOC

THÈSE

pour obtenir le grade de

DOCTEUR DE L'UNIVERSITÉ MONTPELLIER II

Discipline	Biologie des populations et Ecologie Evolutive
École doctorale	Systèmes Intégrés en Biologie, Agronomie, Géosciences, Hydrosciences, Environnement (SIBAGHE)

présentée et soutenue publiquement
par

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le 5 décembre 2011

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3 Investigating Evolutionary Trade-Offs in Wild Populations of Atlantic Salmon (Salmo Salar) : Incorporating Detection Probabilities and Individual Heterogeneity

4 Explicit modelling of proximate mechanisms for revealing life-history trade-offs in wild conditions.

5 Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross.

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Synthèse

INTRODUCTION

Dans un contexte d'environnement changeant, comprendre comment les populations peuvent y répondre dans des échelles de temps écologique et évolutive, et identifier les processus évolutifs en jeu, constituent des enjeux majeurs. La capacité adaptative d'une population est favorisée par la variabilité des traits phénotypiques (physiologique, comportementaux et traits d'histoire de vie). La diversité des histoires de vie observées dans les populations naturelles résulte de cette variabilité des traits phénotypiques.

La théorie des histoires de vie

La théorie des histoires de vie est au cœur de la biologie évolutive car elle est nécessaire à la compréhension de l'action de la sélection naturelle (Stearns 1992 ; Roff 1992). Elle contribue à expliquer la diversité du vivant et la complexité des cycles biologiques qui les caractérisent. Une histoire de vie est la combinaison de traits démographiques tels que l'âge et la taille à la maturité sexuelle, nombre de juvéniles produits et la durée de vie. L'ensemble de ces traits d'histoire de vie (THV) interagissent et influencent la valeur sélective d'un organisme c'est-à-dire la capacité à transmettre ses gènes à la génération suivante. Ainsi, la variabilité de ces THV implique une diversité des histoires de vie et engendre des différences de valeur sélective. La variabilité des THV peut être d'origine environnementale (i.e. la plasticité phénotypique ; cf.Encadré 2) ou génétique ce qui implique que certains de ces traits sont héritables. La théorie des histoires de vie étudie les causes/mécanismes qui engendrent des différences de valeur sélective entre les variants des histoires de vie.

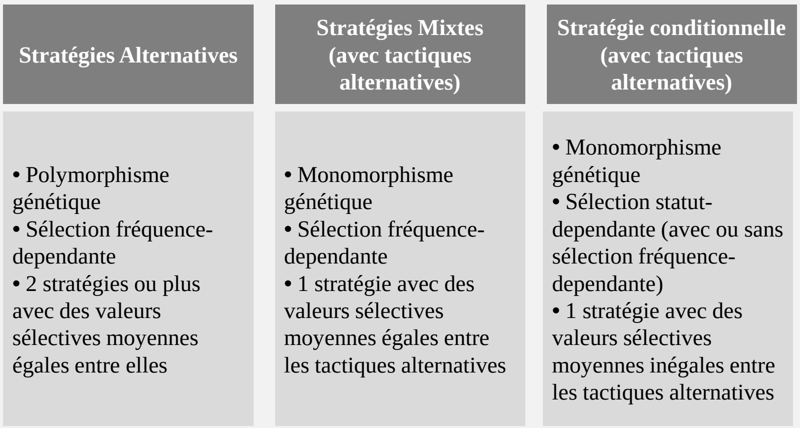
Les stratégies et tactiques d'histoire de vie

Au niveau individuel, une histoire de vie est une combinaison de l'expression particulière des THV. L'ensemble de ces traits d'histoire de vie sont alors reliés entre eux par une structure de conditionnement. Cette structure de conditionnement constitue une stratégie d'histoire de vie dont le but est de maximiser la valeur sélective de l'individu en réponse à un environnement fluctuant (Gross 1996 ; cf.

Encadré 1). Les stratégies d'histoire de vie correspondent donc à l'ensemble des solutions évolutives à la disposition des individus pour assurer leur survie et leur reproduction. La théorie des stratégies d'histoire de vie a pour objectif de prédire les meilleures décisions à prendre lorsque l'organisme fait face à différents problèmes biologiques/écologiques dans différentes situations (Stearns, 1976). Combien de fois un organisme doit-il se reproduire dans sa vie ? Quand ou à quel âge doit-il se reproduire ? Combien de juvéniles doit-il produire ? Ainsi, parmi la multitude de THV, un organisme doit « choisir » ceux qui vont maximiser sa valeur sélective en adoptant la meilleure stratégie.

Encadré 1: LES STRATEGIES CONDITIONNELLES

Gross (1996) propose que la diversité phénotypique (les phénotypes alternatifs observés) peut résulter de 3 types de stratégies : les stratégies alternatives, les stratégies mixtes et les stratégies conditionnelles. Les stratégies alternatives seraient caractérisées par du polymorphisme génétique conduisant à des valeurs sélectives moyennes équivalentes induite par de la sélection fréquence-dépendante. Les stratégies mixtes se caractérisent par une stratégie avec plusieurs tactiques alternatives, du monomorphisme génétique et de la sélection fréquence-dépendante. Les exemples biologiques de ces deux types de stratégies sont relativement rares. En revanche, la stratégie la plus communément observée correspond aux stratégies conditionnelles. Selon Gross (1996), les stratégies conditionnelles se caractérisent par des décisions individuelles entre les tactiques alternatives statut-dépendante et du monomorphisme génétique pour la décision. La tactique choisit par l'individu doit alors maximiser sa valeur sélective. Pour l'auteur, les valeurs sélectives moyennes ne peuvent être équivalentes entre les tactiques alternatives mais les valeurs sélectives attendues sont égales au niveau du seuil de décision. Ce point fait encore l'objet de débats (cf. Tomkins & Hazel, 2007). Les stratégies conditionnelles sont fréquemment observées dans le cas de la reproduction impliquant des tactiques alternatives. Par exemple, lors de la reproduction chez le saumon atlantique, certains individus, les plus gros (les anadromes), vont adopter la tactique dite « combattante » pour maximiser leur succès reproducteur tandis que d'autres, les plus petits (les non migrants) vont adopter la tactique « furtive ». Le choix entre ces tactiques alternatives est donc taille-dépendante.



Stratégies Alternatives	Stratégies Mixtes (avec tactiques alternatives)	Stratégie conditionnelle (avec tactiques alternatives)
• Polymorphisme génétique • Sélection fréquence-dependante • 2 stratégies ou plus avec des valeurs sélectives moyennes égales entre elles	• Monomorphisme génétique • Sélection fréquence-dependante • 1 stratégie avec des valeurs sélectives moyennes égales entre les tactiques alternatives	• Monomorphisme génétique • Sélection statut-dependante (avec ou sans sélection fréquence-dependante) • 1 stratégie avec des valeurs sélectives moyennes inégales entre les tactiques alternatives

Les différents types de stratégies et leurs caractéristiques d'après Gross (1996).

Les expressions de ces THV peuvent être continues (e.g. taille à la migration, taille de ponte,. . .) ou discrètes (souvent dichotomiques) tels que l'âge à la maturation, le dimorphisme des ailes (Roff 1996) ou les tactiques alternatives de reproduction (Gross 1996). Ces traits d'histoire de vie de type discret, aussi appelés tactiques alternatives d'histoire de vie, représentent souvent des transitions majeures au cours de l'histoire de vie des individus. Par exemple, la maturation et la migration impliquent des changements physiologiques, morphologiques ou comportementaux importants et irréversibles.

Les décisions d'histoire de vie

La théorie des stratégies d'histoire de vie implique des « choix » pour tout individu entre les tactiques alternatives d'histoire de vie. Ces décisions doivent conduire à maximiser sa valeur sélective. La sélection individuelle constitue donc la base de toutes tactiques d'histoire de vie (Stearns 1992). Mais ces décisions d'histoire de vie ne peuvent être aléatoires. Elles reposent sur la connaissance de l'organisme des conditions environnementales rencontrées et de sa capacité à assurer les changements biologiques que ces décisions impliquent. Pour cela, l'organisme s'appuie sur des signaux environnementaux ou internes à l'organisme qui le renseigne sur son statut individuel. Dans leur cadre conceptuel sur les décisions d'histoire de vie statut-dépendante, Houston et McNamara (1992) suggèrent que le statut (ils utilisent la terminologie « état ») peut intégrer à la fois les conditions environnementales rencontrées aussi bien que des aspects physiologiques et morphologiques. Comme beaucoup des traits d'histoire de vie dépendent de l'énergie acquise pour leur expression (par exemple, la croissance ou la maturation), le statut énergétique conditionne l'expression des tactiques alternatives d'histoire de vie.

Les compromis entre traits d'histoire de vie

Les THV étant tous interdépendants vis-à-vis de ressources limitées, les histoires de vie sont soumises à des compromis. Le but ultime pour tout individu étant de maximiser sa valeur sélective, chaque individu devrait dans l'idéal optimiser ses THV à cette fin. Les ressources (temps, espace, énergie) disponibles étant limitées pour tout individu, il doit les répartir entre les différentes fonctions essentielles à sa survie et à sa reproduction. L'allocation de ressources à une de ces fonctions se fait nécessairement au détriment des autres. Si des THV sont positivement dépendants de la même ressource, ils sont alors négativement dépendants les uns des autres. Cette structure de dépendance est l'essence même des compromis entre traits. Un individu recherchera de ce fait la combinaison de THV interdépendants qui maximisera sa valeur sélective. Les compromis résultants, dits compromis micro-évolutifs, pourront être optimisés par la sélection naturelle (Stearns, 1992 ; Roff et al., 2006). Stearns (1992) définit 45 types de compromis entre traits d'histoire de vie dont les plus étudiés sont ceux liés aux coûts de la reproduction (compromis entre la reproduction vs la survie, reproduction présente vs future et reproduction vs croissance). Les compromis évolutifs sont considérés comme les facteurs les plus déterminants dans l'évolution des THV (Stearns, 1992 ; Clutton-Brock 1998 ; Reznick et al., 2000 ; Roff et al., 2006). Si l'existence des compromis évolutifs n'est plus à démontrer, leur mise en évidence, leur importance, leur origine proximale et les mécanismes physiologiques impliqués

Encadré 2: LA PLASTICITE PHENOTYPIQUE

Les traits d'histoire de vie (et donc les histoires de vie et les stratégies qui en découlent) varient au sein même des populations du fait de facteurs intrinsèques inhérents aux organismes (génétiques, physiologiques, comportementaux et démographiques) aussi bien qu'extrinsèques (environnementaux) (Stearns 1992 ; Shefferson 2010). L'évolution des stratégies d'histoire de vie est fortement influencée par les patrons de variations environnementales dans l'espace et le temps. Une modification d'un facteur environnemental donné affectera un ou plusieurs THV qui à son (leur) tour redéfinira la stratégie d'histoire de vie optimale. La plasticité phénotypique, i.e. l'expression phénotypique différentielle des THV d'un génotype donné en fonction de l'environnement, joue un rôle majeur dans l'évolution et le maintien des stratégies d'histoire de vie. La plasticité favoriserait l'adaptation et l'évolution en permettant aux individus d'exploiter un environnement nouveau à condition que le génome possède/conserve la capacité d'exprimer un nouveau phénotype adapté à ce nouvel environnement. Elle permet ainsi une réponse immédiate aux changements environnementaux (Ghalambor et al. 2007 ; Gienapp et al. 2008) et peut faciliter la persistance des populations face aux changements de l'environnement (Lande 2009 ; Chevin & Lande 2010). La plasticité phénotypique peut alors être définie comme une réponse évolutive du génome à un environnement fluctuant. La dispersion des juvéniles à travers différents environnements pourrait favoriser la plasticité phénotypique adaptative des histoires de vie (Levins, 1968 ; Hutchings & Myers, 1994). La plasticité peut être maintenue par la sélection (et donc être adaptative) lorsque les organismes font face à des fluctuations environnementales récurrentes et lorsque ceux-ci disposent d'un signal qui leur permet d'ajuster leur réponse phénotypique aux conditions environnementales rencontrées (Ghalambor et al. 2007 ; Reed et al. 2010). La plasticité phénotypique est donc un processus évolutif majeur des stratégies d'histoire de vie. Lorsque cette plasticité est affectée par des pressions anthropiques ou environnementales rapides qui agissent sur sur l'adéquation de la réponse phénotypique aux conditions rencontrées (McNamara et al. 2011), les stratégies d'histoire de vie optimales peuvent être à leur tour affectées.

restent néanmoins d'actualité (Roff et al., 2006).

Les stratégies d'histoire de vie peuvent être donc vues comme un réseau de THV interconnectés et conditionnés par les statuts individuels. Elles impliquent un ensemble de décisions d'histoire de vie qui dépendent du statut individuel. Les stratégies d'histoire de vie font intervenir des processus évolutifs tels que la plasticité phénotypique et les compromis évolutifs qui jouent un rôle majeur dans l'évolution des histoires de vie. Alors que la plasticité phénotypique va favoriser la réponse adaptative des individus aux changements environnementaux, les compromis évolutifs vont contraindre la gamme de réponses possibles. Ainsi, les variations d'histoire de vie observées résultent de variations interindividuelles, d'origine génétique et/ou environnementale, qui conditionnent l'expression des traits d'histoire de vie et donc les stratégies individuelles.

OBJECTIF 1 : Mise en évidence de la structure de conditionnement des stratégies d'histoire de vie.

Pour appréhender le potentiel adaptatif et évolutif des populations, il faut mettre en évidence les variations d'histoire de vie et en comprendre l'origine via les stratégies d'histoire de vie et les processus évolutifs associés. Le premier objectif de ma thèse est donc d'étudier les stratégies d'histoire de vie, en caractérisant leurs structures de conditionnement.

Étudier les stratégies d'histoire de vie et les processus évolutifs en conditions naturelles

L'étude des des histoires de vie et des processus évolutifs en milieu naturel se heurte à des problèmes d'ordre méthodologique. Elle requiert notamment la connaissance de chaque événement composant l'histoire de vie d'un individu. Le point le plus critique réside dans le suivi exhaustif au cours du temps de tous les individus d'une population qui est difficilement réalisable, sinon impossible, en conditions naturelles. La détection d'un individu se fait souvent avec une probabilité inférieure à 1. Les deux composantes de la valeur sélective d'intérêt (survie et reproduction) ne sont que partiellement observables. L'état des individus non détectés est incertain. Sont-ils morts ou vivants ? S'ils sont vivants, sont-ils reproducteurs ? Cette incertitude a longtemps été ignorée en biologie évolutive, un individu non détecté étant généralement considéré comme mort (Clobert, 1995, 2002 ; Cam, 2007). Pourtant son impact sur les inférences déduites d'observations partielles est loin d'être négligeable (Gimenez et al., 2008) en biaisant l'estimation des composantes de la valeur sélective.

Confronter modèles théoriques et traitement statistique des données empiriques

Les processus éco-évolutifs mis en jeu dans la théorie des histoires de vie tel que les décisions d'histoire de vie, la plasticité phénotypique et les compromis évolutifs, sont souvent complexes et difficilement observables en conditions naturelles. Les approches théoriques et expérimentales ont permis de décrire et d'apporter des informations importantes sur ces processus. Cependant les patrons mis en évidence dans de telles approches constituent des processus "potentiels" et doivent être confrontés aux données d'observation en condition naturelle. Cela nécessite de comprendre et de représenter les mécanismes qui génèrent les données observées en s'appuyant sur les connaissances théoriques acquises tout en reconnaissant que ces données d'observation ne sont qu'une mesure bruitée ou incomplète de ces mécanismes sous-jacents. De plus, travailler dans un environnement contrôlé et/ou en isolant les processus (par exemple en ne considérant qu'une partie de l'histoire de vie) ne permet pas de capturer leurs interactions (Stearns 1992). Les études des processus évolutifs dans les populations sauvages en conditions naturelles sont donc nécessaires pour révéler les processus à l'œuvre et ne peuvent pas être remplacées par des travaux en conditions expérimentales contrôlées.

Intégrer les mécanismes qui conditionnent les stratégies d'histoires de vie

Une stratégie d'histoire de vie est le moyen pour un individu de maximiser sa valeur sélective conditionnellement à son statut. Pour comprendre comment ces stratégies sont maintenues et évoluent, il est nécessaire de mettre en évidence la structure de conditionnement qui relie les THV entre eux et les facteurs externes qui les conditionnent. La plupart des études s'intéressent seulement aux déterminants ultimes de l'histoire de vie adoptée en comparant la valeur sélective des individus. Elles reposent sur le postulat que la sélection naturelle favorise les stratégies qui maximisent la valeur reproductive. Ces approches ignorent le plus souvent les mécanismes sous-jacents qui gouvernent la décision entre les tactiques alternatives et les contraintes liées aux compromis.

OBJECTIF 2 : Étudier les stratégies d'histoire de vie et les processus évolutifs en conditions naturelles.

Afin d'étudier les stratégies d'histoire de vie et les processus évolutifs associés en conditions naturelles, les approches expérimentales en milieu contrôlé et/ou focalisée sur les déterminants ultimes des histoires de vie ne sont pas suffisantes. Mon deuxième objectif consiste donc à :
1) développer les outils méthodologiques appropriés pour mettre en évidence les histoires de vie et les processus évolutifs en conditions naturelles ;
2) représenter explicitement les mécanismes proximaux qui structurent les stratégies d'histoire de vie (i.e. adopter une approche mécaniste) ;
3) intégrer les théories et concepts de la biologie évolutive dans l'analyse statistique des données d'observations.

Pour répondre à ces objectifs et illustrer notre démarche, nous proposons d'étudier les stratégies d'histoire de vie et les processus évolutifs chez le saumon atlantique (*Salmo salar*).

Les stratégies d'histoire de vie chez le saumon atlantique

Du fait de la complexité et de la diversité des histoires de vie qu'il exprime, le saumon atlantique est un modèle biologique pertinent à plus d'un titre pour aborder les questions de biologie évolutive et notamment pour étudier les stratégies d'histoire de vie et les processus évolutifs associés. Le saumon atlantique est considéré comme une espèce à forte plasticité phénotypique utilisant les stratégies conditionnelles reposant sur des décisions statut-dépendante entre les tactiques alternatives d'histoire de vie (décisions de maturation ou de migration) (Hutchings & Myers 1994 ; Gross 1996 ; Thorpe et al. 1998 ; Garant et al. 2003 ; Hutchings 2004 ; Hutchings 2011).

Espèce emblématique au travers de toute son aire de répartition, elle a été historiquement très étudiée ce qui permet de disposer d'une base solide et riche de connaissances pour développer des approches novatrices. Plus important, elle est susceptible de répondre rapidement et significativement à des évolutions de l'environnement. En effet, elle démontre une forte variabilité en matière de THV. Certains de ces traits d'histoire de vie, en premier lieu l'anadromie et l'âge à la première maturité, ont une importance majeure du point de vue de la pérennité des populations. La diversité des histoires de vie exprimée par le saumon atlantique lui confère un fort potentiel adaptatif. Pour favoriser son adaptation face aux changements de milieu, le saumon atlantique s'appuie sur une forte plasticité phénotypique conduisant à une diversité de tactiques alternatives d'histoire de vie. Cependant, les pressions anthropiques (exploitation par la pêche, dégradation de l'habitat, barrages, . . .) et les changements environnementaux rapides en milieu continental et océanique (température, modifications de la distribution spatiale et de la composition des ressources trophiques. . .) fragilisent ce patrimoine naturel (espèce inscrite à l'annexe II de la directive européenne "Habitats", réseau Natura 2000). L'étude des stratégies d'histoire de vie et des processus évolutifs associés des populations de saumon atlantique contribuera à comprendre leur réponse adaptative face à ces pressions et à déterminer leurs potentiels adaptatifs. *In fine*, cela permettra de prédire les changements évolutifs et leurs conséquences démographiques sur ces populations face au changement environnementaux en cours, dont le changement climatique.

Cycle de vie

Espèce anadrome et philopatrique (Verspoor et al. 2007), le saumon atlantique sépare son cycle de vie entre l'eau douce (phase dulçaquicole), où se déroulent la reproduction et l'élevage de jeunes, et l'océan, où les individus entreprennent des migrations de grande amplitude (plusieurs milliers de kilomètres) vers les aires de croissance maritimes (cf. Figure 1).

En Bretagne, la reproduction a lieu au mois de décembre et les jeunes de l'année (stade alevin) émergent des graviers des sites de reproduction au début du printemps suivant (cf. Figure 2 A). Dès leur première année de vie en eau douce, les juvéniles alors appelés tacons (stade tacons 0+ pour « moins d'un an » ; (cf. Figure 2 B), doivent opter entre migrer vers la mer au printemps suivant (stade smolt 1+ pour « plus d'un an » ; (cf. Figure 2 C) ou résider une année supplémentaire en eau douce (stade tacon 1+). Pour les mâles restant en eau douce, un second choix est à faire entre la maturation sexuelle précoce ou rester immature lors de leur seconde année de vie en eau douce (au stade tacon 1+). Qu'ils aient pu se reproduire préalablement ou non, les individus survivants à l'âge de deux ans migrent tous (à quelque rares exceptions près) vers la mer au printemps (stade smolt 2+).

Le retour des adultes dans leur rivière natale pour se reproduire (ou « homing ») intervient l'année

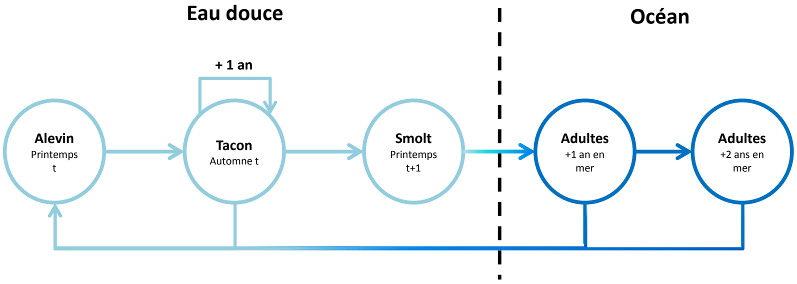


Figure 1: Cycle biologique simplifié du saumon atlantique sur le Scorff (Morbihan, France).

suivant leur migration vers la mer ou l'année d'après (cf. Figure 2 D). La dispersion des adultes dans d'autres rivières est relativement faible, en moyenne de l'ordre de quelques pourcents (Pedersen et al. 2007). La mortalité post-reproduction diffère selon le stade et les populations. Dans les rivières françaises, elle est proche de 100% pour les individus anadromes (faible degré d'itéroparité) alors qu'elle est notablement plus faible pour les mâles atteignant la maturité en tant que tacon.

Le séjour en mer permet un accroissement de taille important, ce qui procure un avantage en termes de succès reproducteur, en particulier pour les femelles dont la production d'œufs est étroitement liée à la taille (Fleming, 1996, 1998). Cependant, l'anadromie engendre un coût de migration pour la survie (forte mortalité en mer) et une mortalité post-reproduction accrue. La résidence et la maturation sexuelle des mâles en eau douce conduirait à un succès reproducteur moyen nettement inférieur à celui des anadromes, mais permet de bénéficier de taux de survie bien supérieurs à celui des anadromes.

Cadre conceptuel des variations d'histoire de vie chez les salmonidés

Thorpe et al. (1998) et Mangel & Satterthwaite (2008) proposent un cadre conceptuel pour représenter et comprendre les variations d'histoire de vie chez les salmonidés. Ce cadre suggère que le cycle biologique du saumon se caractérise par différentes tactiques d'histoire de vie, toutes conditionnées par des caractéristiques / des événements à un temps donné. Il décrit les étapes majeures du cycle biologique des salmonidés et les mécanismes proximaux (physiologiques) que l'individu utilise pour atteindre l'histoire de vie optimale (i.e. qui maximisera sa valeur sélective). Ce modèle propose des périodes critiques (ou fenêtres de décisions) durant lesquelles des changements développementaux majeurs, maturation et smoltification, sont initiés ou inhibés en fonction de la comparaison du

Figure 2: Les différents stades de vie chez le saumon atlantique. (A) Alevins, (B) Tacons, (C) Smolts, (D) Adultes anadromes (Photos Nicolas Jeannot).

statut physiologique de l'individu (signal proximal) et de seuils. Dans ce modèle, les statuts sont principalement déterminés par les conditions environnementales rencontrées tandis que les seuils sont génétiquement déterminés. Ainsi, les stratégies d'histoire de vie sont déterminées à la fois par des facteurs ultimes (à travers la sélection naturelle) qui sélectionnent le niveau des seuils, et à travers des facteurs proximaux qui intègrent les effets environnementaux. Les seuils sont des traits polygéniques dont les valeurs dépendent (1) de la valeur sélective relative des tactiques alternatives (maturation ou non, migration vers la mer vs résidence en eau douce), (2) de la variabilité du statut d'une génération à la suivante. La sélection fréquence-dépendante maintient l'existence de tactiques alternatives dans un état évolutivement stable à travers la sélection sur les seuils (Hutchings & Myers 1994 ; Hutchings 2004, 2011).

La première décision dans l'histoire de vie d'un juvénile de saumon atlantique est la maturation sexuelle précoce (cf. Figure 3). En effet, la maturation est un processus cyclique qui commence dés la fertilisation. Les tissus germinaux se différencient très tôt et l'investissement dans le développement des gonades débute dés le stade embryonnaire. Il est alors possible pour des juvéniles de moins d'un an (tacons 0+) d'initier la maturation si les réserves lipidiques (considérées comme la principale ressource limitante pour la maturation) et les ressources acquises au printemps sont suffisantes pour compléter la maturation (Rowe & Thorpe, 1990a ; Rowe et al., 1991). La décision de maturation serait prise au printemps et dépendrait de la comparaison entre le statut énergétique (lipidique) de l'individu et un seuil pour la maturation. Si un tacon 0+ ne dispose pas des réserves lipidiques suffisantes au printemps il reportera sa décision à l'année suivante (cf. Figure 3).

La deuxième décision concerne la migration en mer. Au cours de l'été de la première année de vie, un individu peut choisir de migrer ou non en mer au printemps suivant (cf. Figure 3). Cette décision résulterait de la comparaison d'un seuil pour la migration et du statut énergétique pour laquelle la taille et/ou la croissance sont considérées comme de bons indicateurs. Si le statut de l'individu en été dépasse le seuil alors il migrera au printemps suivant, sinon il résidera au moins une année supplémentaire en eau douce. Quelque soit l'âge, la migration vers la mer s'accompagne d'une transformation physiologique et comportementale que l'on appelle la smoltification. Le processus de smoltification prépare les individu au milieu marin (en particulier à travers l'osmorégulation) (Thorpe et al., 1992, 1998 ; Duston & Saunders, 1997 ; McCormick et al., 1998). Maturation précoce et migration ne sont pas des tactiques mutuellement exclusives : un individu pourra à la fois maturer une année donnée et migrer l'année suivante. Pour ce qui concerne les adultes anadromes, l'existence de seuils qui déterminent la maturation et le retour en rivière pour la reproduction est également proposée.

Normes de réactions et compromis évolutifs

La croissance, par l'accumulation de réserves énergétiques, joue un rôle majeur pour le choix entre les différentes options d'histoire de vie (Prévost et al., 1992 ; Thorpe et al., 1998 ; Hutchings & Jones, 1998) et la survie (Johnston et al., 2005 ; Saloniemi et al., 2005 ; Jokikokko et al., 2006). La taille et le poids sont révélateurs des conditions de croissance et de l'investissement de l'énergie acquise dans les différents THV, i.e. du statut énergétique de l'individu. Il en résulte des normes de réactions, pour l'âge à la maturité ou à la smoltification, et des survies sélectives taille dépendantes. Étant conditionnés par les mêmes ressources acquises, des compromis peuvent apparaître entre les traits associés à la migration vers la mer, la reproduction et la survie.

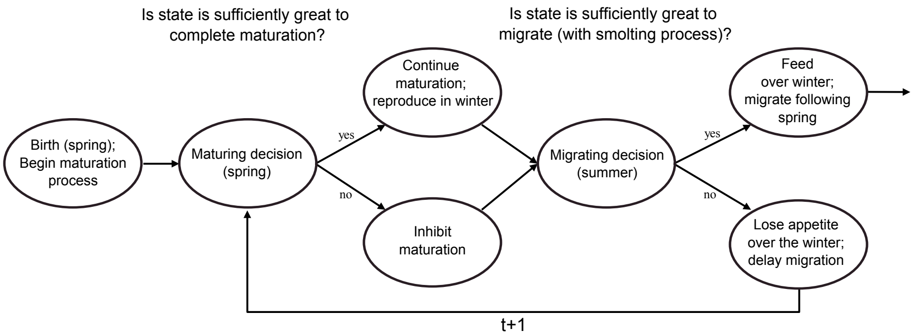


Figure 3: Cadre conceptuel des variations d'histoire de vie chez les juvéniles de saumon atlantique (modifié à partir de Mangel & Satterwaith (2008)).

Je me suis appuyé sur le cadre conceptuel proposé par Thorpe et al. (1998) et Mangel & Satterwaith (2008) (cf. Figure 3) pour étudier les variations d'histoire de vie chez les salmonidés et représenter la structure de conditionnement des stratégies d'histoire de vie chez le saumon atlantique. Le but étant de confronter ce cadre théorique aux données d'observations acquises sur notre site d'étude, j'ai également proposé un cadre statistique permettant de les relier.

Site d'étude

Afin d'étudier le fonctionnement et l'évolution des populations de saumon atlantique dans un contexte de changement global et de fortes pressions anthropiques, un programme de suivi à long-terme d'une population de saumon atlantique a été initié sur le Scorff (petit fleuve côtier du Morbihan, Site de l'Observatoire de Recherche en Environnement « Petits Fleuves Côtiers »,www.inra.fr/ore_pfc/sites_d_etudes/sc

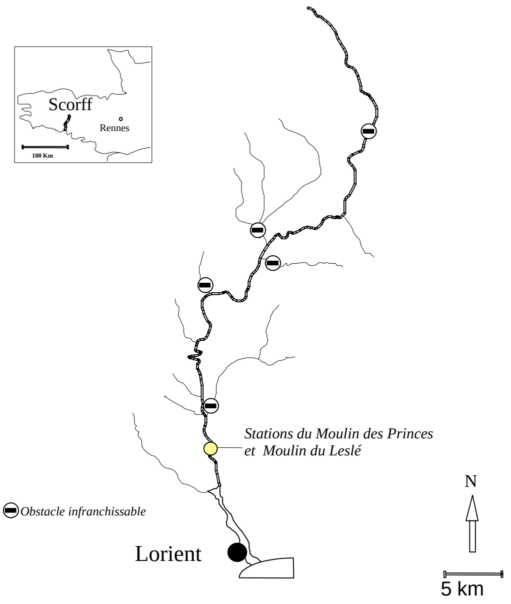


Figure 4: Localisation du Scorff, son réseau hydrographique et emplacement du dispositif de piégeage (Le Moulin des Princes).

Le Scorff est un petit fleuve côtier se jetant dans la rade de Lorient (Bretagne sud). Son cours principal s'étend sur environ 75 km dont 15 km d'estuaire (cf. Figure 4). La population de saumon colonise environ 50 km du cours principal allant de Guémené-sur-Scorff à la limite de balancement des marées (Pont-Scorff). Le Scorff bénéficie d'un statut de rivière pilote pour le Saumon atlantique. L'INRA et ses partenaires[1] effectuent un suivi régulier de la population à chaque stade biologique à travers des campagnes d'échantillonnage ce qui nous permet d'observer les histoires de vie et les traits associés (cf. chapitre 1). Dans la partie basse du réseau hydrographique, à la limite de balancement des marées, deux dispositifs de piégeages ont été installés (depuis 1994 ; cf. Figure 5). Celui du moulin du Leslé fonctionne uniquement en période de dévalaison des smolts vers la mer. Plus en aval (environ 600m),la station de piégeage du Moulin des Princes permet la capture à la fois des smolts et des adultes en montaison. Elle est en fonctionnement toute l'année.

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1. INRA (Unité expérimentale U3E, Rennes ; UMR Inra/Uppa Ecobiop, St-Pée s/ Nivelle ; UMR Inra-Agrocampus ESE, Rennes) ; CEFE-CNRS UMR 5175 (Département d'écologie évolutive ; Biostatistique et biologie des populations, Montpellier) ; FDPPMA (Fédération Départemental de pêche et de protection des milieux aquatiques, Morbihan) ; Associations de migrateurs (Bretagne Grand Migrateurs) ; ONEMA ; APPMA Bassin de Plouay et de Guémené.

Figure 5: Les dispositifs de piégeages sur le Scorff : Le Moulin des Princes (photos du haut) et le Moulin du Leslé (photo du bas).

Organisation du manuscrit de thèse

Après cette introduction générale, notre démarche et les résultats sont présentés dans 3 chapitres, correspondant chacun à au moins un article scientifique rédigé en anglais. A chaque chapitre est associé une annexe qui approfondit les éléments apportés dans le chapitre ou dans l'article et/ou présente des résultats complémentaires tels que l'analyse de plusieurs cohortes de saumon atlantique.

Le chapitre 1 répond à notre premier objectif en proposant un cadre de modélisation qui permet de représenter des processus complexes (e.g. les histoires de vie), de s'affranchir des paramètres de nuisances rencontrés en conditions naturelles (problème d'observation partielle) et ainsi de se focaliser sur les processus d'intérêts, i.e. les histoires de vie individuelles et les processus évolutifs à l'œuvre.

Le chapitre 2 constitue une première étape de représentation des stratégies d'histoire de vie en abordant les décisions entre les tactiques alternatives d'histoire de vie et l'étude de la plasticité phénotypique au travers des stratégies conditionnelles. J'y introduis l'idée que l'expression de ces décisions est le résultat de mécanismes proximaux sous-jacents et que, bien que non observables, ils peuvent être inférés à partir de nos observations.

Le chapitre 3 s'intéresse aux difficultés de mise en évidence des compromis entre les THV en milieu naturel et propose de représenter explicitement les mécanismes à l'œuvre pour résoudre ces difficultés.

Ce chapitre synthétise également notre démarche en intégrant la structure de conditionnement qui relie les THV et détermine la stratégie d'histoire de vie.

Enfin, la conclusion est une discussion générale qui synthétise l'ensemble des résultats obtenus, et brosse les perspectives qu'ils ouvrent concernant tout à la fois les questions biologiques abordées, les méthodes développées et le programme de suivi en cours.

1 MODELISATION DES HISTOIRES DE VIE

1.1. Accéder aux histoires de vie et aux caractéristiques individuelles

Le suivi exhaustif de tous les individus d'une population au cours du temps est dans la plupart des cas impossible en milieu naturel. L'échantillonnage successif au cours du temps par les méthodes de capture-marquage-recapture (CMR) permet un suivi temporel et individuel (Lebreton et al., 1992). Les données de CMR donne accès directement, ou via une procédure d'estimation, à des traits d'histoire de vie d'intérêt et à leurs variations individuelles. Le développement des techniques CMR et des méthodes d'analyse des données issues de CMR ont ainsi largement contribué à la mise en évidence des processus évolutifs en milieu naturel (Nichols et al., 1994 ; Clobert 1995 ; Cam et al., 1998 ; Yoccoz et al., 2002 ; Townsend & Anderson, 2007 ; Cam 2009).

1.1.1. Programme de Capture-Marquage-Recapture

Capture et marquage des tacons à l'automne

Une campagne d'échantillonnage automnale est menée chaque année sur le Scorff depuis 1994. Elle vise le dénombrement des tacons capturés par pêche électrique en un temps donné (5 mn de pêche effective), sur des secteurs d'habitats favorables aux juvéniles de saumons (Prévost & Baglinière 1995 ; Prévost & Nihouarn 1999). Durant cette campagne, 43 stations sont échantillonnées, dont 39 régulièrement espacées sur le cours principal du Scorff et 4 sur des affluents. Depuis 2005, un vaste programme de marquage individuel a été initié sur le Scorff. Sept cohortes successives ont été marquées (de 2005 à 2011 ; seuls les tacons 1+ ont été marqués en 2008). Mais seules les trois premières cohortes ont été suivies à tous les stades à l'heure actuelle. Les juvéniles de l'année (tacons 0+) capturés sont anesthésiés (Benzocaïne, 0.3 ml/l d'eau), mesurés (mm), pesés (0.1 g) et marqués par insertion d'une puce électronique de type « PIT tag » (« Passive Integrated Transponder ») porteuse d'un code unique (Prentice et al., 1990 ; Achord et al., 1996 ; Gibbons & Andrews, 2004). Ces marques mesurent 11 mm de long pour 2.2 mm de diamètre et un poids de 0.1 grammes. Elles sont insérées dans la cavité péritonéale, postérieurement à la nageoire pectorale par incision chirurgicale (cf. Figure 6). Cette technique de marquage est réputée pour avoir peu d'effet sur les jeunes salmonidés avec un très faible taux de perte de marque (cf. Annexe 1).

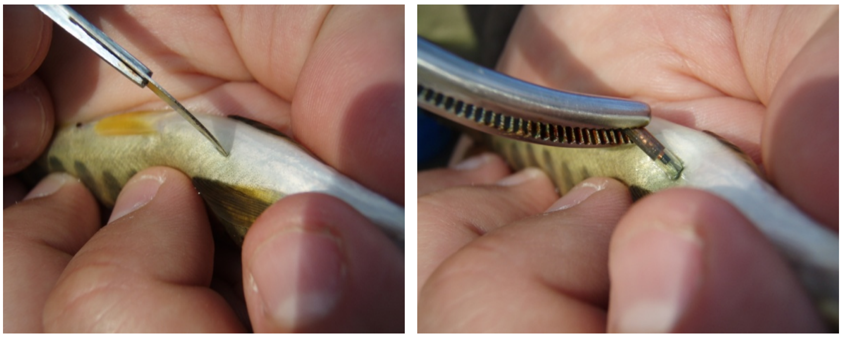


Figure 6: Marquage d'un juvénile de saumon atlantique avec une puce de type « PIT-tag ».

Recapture des smolts 1+ et 2+ aux printemps et des tacons 1+ à l'automne suivant

Au printemps suivant, les smolts âgés d'un an (smolts 1+) peuvent être capturés une première fois au Moulin du Leslé où ils sont mesurés et pesés. Les individus marqués par PIT tag sont identifiés grâce à un lecteur/enregistreur à distance (type IER Planète Long range et Galaxy). Les individus non-porteurs d'un PIT tag sont à leur tour marqués individuellement par Implant Visible en Elastomère (IV) (marque colorée porteuse d'un code alphanumérique insérée dans le tissu post-operculaire) et par ablation d'un fragment de nageoire pelvienne. Cette technique n'a pas d'effet significatif sur la croissance et la mortalité (taux de mortalité <1%) chez les salmonidés (Close, 2000 ; Olsen & Vøllestad, 2001 ; Summers et al., 2006). Elle présente un fort taux de rétention de la marque (>95% à l'horizon de quelques semaines ; Prévost, données non publiées). La deuxième occasion de capture se situe environ 600m en aval du Moulin du Leslé, au moulin des Princes où les individus marqués par PIT tag et/ou IV sont identifiés.

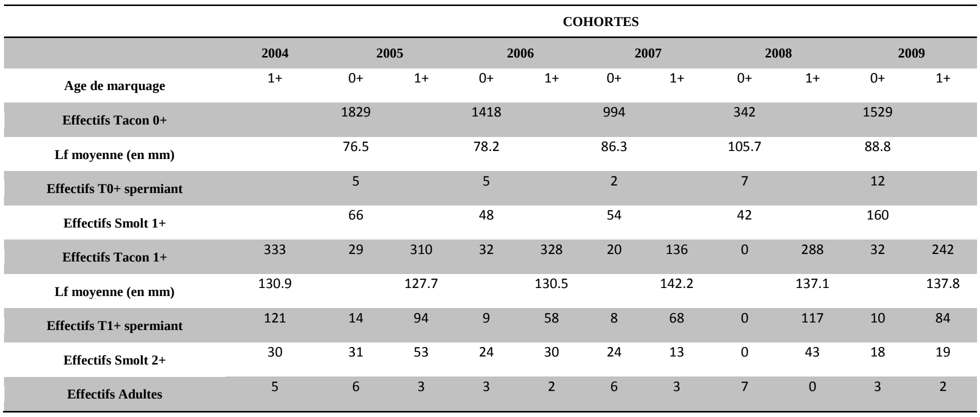
A l'automne suivant (deuxième année de vie), l'identification des tacons 1+ marqués a été réalisée en parallèle à la campagne d'échantillonnage des tacons 0+ grâce au même lecteur/enregistreur que pour les smolts. Les tacons 1+ capturés mais non marqués au stade tacon 0+ sont marqués suivant un protocole similaire à celui des tacons 0+ décrit précédemment.

Au printemps suivant (deuxième année de vie), les smolts 2+ marqués par PIT tags (au stade tacons 0+ à l'automne de la première année de vie et au stade tacons 1+ à l'automne de la deuxième année de vie) ont été identifiés suivant un protocole similaire à celui des smolts 1+ décrit précédemment.

Enfin, les adultes anadromes peuvent être recapturés lors de leur retour en rivière (après un à deux ans passé en mer) lors de leur passage à la station du Moulin des Princes, lors des captures hivernales sur les sites de reproduction ou lors de captures par la pêche à la ligne.

A chaque occasion de capture, la longueur fourche et le poids de chaque individu sont relevés. Pour les tacons 1+, la détection des mâles matures sexuellement (spermiants) se fait par simple pression sur les flancs. Les effectifs capturés et marqués pour chaque cohorte suivie sont donnés en Tableau 1.

Tableau 1: Effectifs de saumon atlantique capturés (et marqués aux stades 0+ et 1+, colonne "Age de marquage") à chaque occasions et pour chaque cohorte sur le Scorff.



	COHORTES										
	2004	2005		2006		2007		2008		2009	
Age de marquage	1+	0+	1+	0+	1+	0+	1+	0+	1+	0+	1+
Effectifs Tacon 0+		1829		1418		994		342		1529	
Lf moyenne (en mm)		76.5		78.2		86.3		105.7		88.8	
Effectifs T0+ spermiant		5		5		2		7		12	
Effectifs Smolt 1+		66		48		54		42		160	
Effectifs Tacon 1+	333	29	310	32	328	20	136	0	288	32	242
Lf moyenne (en mm)	130.9		127.7		130.5		142.2		137.1		137.8
Effectifs T1+ spermiant	121	14	94	9	58	8	68	0	117	10	84
Effectifs Smolt 2+	30	31	53	24	30	24	13	0	43	18	19
Effectifs Adultes	5	6	3	3	2	6	3	7	0	3	2

1.1.2. Hétérogénéité individuelle

Les variations individuelles constituant le matériel de base pour la sélection naturelle, leurs prises en compte dans l'étude des processus évolutifs est nécessaire. Par exemple, du fait de l'inégalité des individus dans l'acquisition des ressources (Stearns 1992 ; Cam, 2009), la qualité individuelle peut interférer dans la mise évidence des compromis (Nichols et al., 1994 ; Cam et al., 2002). L'hétérogénéité individuelle peut être d'origine connue, telle la taille des juvéniles de saumon atlantique dans notre étude, ou bien d'origine inconnue. Dans le premier cas, elle peut être introduite dans un modèle via une covariable observée sous la forme d'un effet fixe ; dans le second cas, on utilisera un effet aléatoire individuel qui permet de quantifier la part de variabilité non expliquée par les effets fixes. Cam et al. (2002) et Wintrebert et al. (2005) montrent que cette prise en compte explicite de l'hétérogénéité individuelle via des effets aléatoires est essentielle pour mettre en évidence un coût de la reproduction et des phénomènes de sénescence chez la mouette tridactyle (*Rissa tridactyla*). Cependant, ces études reposent sur l'hypothèse d'une probabilité de détection égale à 1 et les auteurs soulignent la nécessité de disposer d'une approche cohérente tenant compte explicitement de la probabilité de détection.

Pour lever les limites des méthodes actuelles d'étude des histoires de vie et des processus évolutifs en conditions naturelles à partir de données de CMR, nous proposons une approche intégrée qui permet de :
i) modéliser les histoires de vie et les transitions d'histoire de vie au cours du cycle biologique (vivant ou mort, reproducteur ou non reproducteur, migrant ou résident) ;
ii) intégrer l'hétérogénéité individuelle d'origine connue (effet fixe) ou inconnue (effet aléatoire) comme facteur influençant les traits d'histoire de vie et les compromis ;
iii) tenir compte explicitement des problèmes de détection.

1.2. Modélisation à structure cachée

L'idée maîtresse de ce travail a été de considérer que le biologiste n'a qu'une vision partielle, et bien souvent bruitée, des processus biologiques à l'œuvre dans la population naturelle (processus écologiques) ou au sein même des individus (processus physiologiques ou génétiques). Tout ce qu'il observe n'est que la conséquence de ces processus sous la forme de données d'observation. L'étude des processus écologiques et évolutifs en conditions naturelles nécessite donc le développement d'approches statistiques cohérentes avec les mécanismes qui génèrent les données d'observation et leurs incertitudes. La modélisation hiérarchique (HM) constitue une approche naturelle pour représenter ce type de données hiérarchiquement structurées. L'approche hiérarchique distingue 3 niveaux : les données d'observation, les processus sous-jacent d'intérêt et les paramètres qui gouvernent ces processus (Cressie et al. 2009). Formellement, nous supposons que les données d'observation notées Y sont issus d'une certaine distribution dépendante d'un processus caché X (qui génère les données) et d'un ensemble de paramètres θ_Y gouvernant l'incertitude dans la relation entre Y et X tel que : $[Y \mid \theta_Y]$ (cf. Figure 7). La notation $[A \mid B]$ indique que la variable A est distribuée conditionnellement à la variable B. Le processus sous-jacent X est lui-même issue d'une certaine distribution, gouverné par ces propres paramètres θ_X : $[X \mid \theta_X]$. En combinant ces deux hypothèses, le modèle hiérarchique permet de modéliser à la fois l'incertitude dans les données d'observation (le processus d'observation) et le processus sous-jacent (cf. Figure 7) via la distribution conditionnelle jointe de Y et X étant donné l'ensemble des paramètres associés θ_Y et θ_X :

$$[Y, X \mid \theta_Y, \theta_X] = [Y \mid X, \theta_Y] \times [X \mid \theta_X] \tag{1.1}$$

Cette formulation est assez générique de telle sorte que le processus d'intérêt X peut représenter les histoires de vie ou les processus physiologiques au niveau individuel.

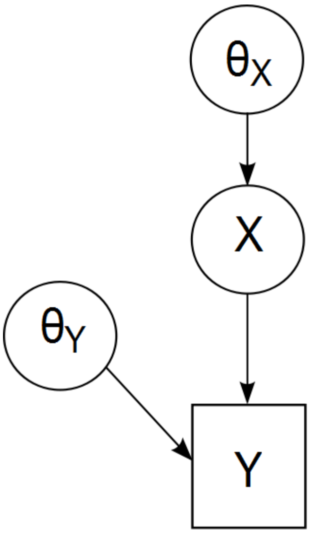


Figure 7: Graphe Acyclique Orienté du modèle hiérarchique. Les carrés représentent les données d'observation Y et les cercles les quantités inconnues à estimer. Les flèches pleines représentent les dépendances stochastiques. La variable X correspond au processus sous-jacent d'intérêt qui génère les données mais n'est pas observé directement, c'est une structure cachée.

1.2.1. Modélisation des données longitudinales au niveau individuel

Les données issues des programmes de CMR dont on dispose via le processus d'observation, constituent la partie visible des évènements qui constituent le cycle de vie de l'espèce considérée, i.e. le processus dynamique. La nécessité de disposer d'une approche flexible et cohérente prenant explicitement en compte ces deux composantes pour modéliser les histoires de vie partiellement observées a conduit au développement des modèles hiérarchiques dits modèles à structure cachée (« state-space models ») (Rivot & Prévost 2004 ; Gimenez et al. 2007 ; Schofield 2007a ; Schofield et al. 2007b). La séparation de ces deux processus nous donne accès au processus biologique d'intérêt en formalisant explicitement les histoires de vie des individus tout en intégrant l'hétérogénéité individuelle (Royle, 2008). Ces modèles formalisent la structure de conditionnement liée au processus dynamique qui régit l'évolution temporelle des états cachés non observables et font la distinction entre ces derniers et les données.

Pour illustrer notre démarche de modélisation à structure cachée, prenons le cas d'un individu qui subit un événement de survie entre deux occasions. Conditionnellement à son état à l'occasion $t-1$ (vivant ou mort), l'individu i peut être vivant ou mort à l'occasion suivante t. Cette survie est un aléa. La variable aléatoire $X_{i,t}$ est une variable binaire, correspondant à l'état de l'individu i à l'occasion t, et prend la valeur 1 si l'individu est en vie à l'occasion t, 0 sinon. Alors, $X_{i,t}$ étant donné$X_{i,t-1}$ est régie par une loi de Bernoulli dépendante de la probabilité de survie $\phi_{i,t-1}$ (Gimenez, 2007 ; Royle, 2008).

La probabilité de survie $\phi_{i,t-1}$ correspond à la probabilité de transition d'un individu i entre deux états ($X_{i,t-1}$ et $X_{i,t}$). La probabilité de survie correspond aux paramètres associés θ_X de l'équation 1. La formulation de l'équation du processus dynamique devient :

$$[X_{i,t} \mid X_{i,t-1}, \phi_{i,t-1}] \sim Bernoulli(X_{i,t-1} \times \phi_{i,t-1}) \tag{1.2}$$

Même si l'individu i est en vie à l'occasion t ($X_{i,t} = 1$), il peut être observé ou non à cette occasion tandis que si il est mort ($X_{i,t} = 0$), il sera nécessairement non observé. Cet aléa d'observation est modélisé par la variable binaire aléatoire$Y_{i,t}$ qui prend la valeur 1 si l'individu est observé à l'occasion t, 0 sinon. Alors, $Y_{i,t}$ est régie par une loi de Bernoulli dépendante de la probabilité de détection p à l'occasion t (p_t) conditionnellement à l'état du processus dynamique sous-jacent à l'occasion t ($X_{i,t}$). La probabilité de détection p_t correspond aux paramètres associés θ_Y de l'équation 1. La formulation du processus d'observation devient :

$$[Y_{i,t} \mid X_{i,t}, p_t] \sim Bernoulli(X_{i,t} \times p_t) \tag{1.3}$$

En appliquant cette approche de modélisation à l'ensemble du cycle de vie, nous pouvons représenter les états successifs qui composent l'histoire de vie d'un individu, qu'il soit connu ou non. Ainsi, en plus de l'estimation des probabilités de transitions, la modélisation hiérarchique à structure cachée permet d'inférer les états (e.g. survivant, migrant ou reproducteur) de tous les individus à un temps donné et accéder ainsi aux histoires de vie complètes. Cette approche correspond à la démarche générique de modélisation appliquée à des données de CMR proposée par Gimenez et al. (2007) et Royle (2008). Elle est sous tendue par deux hypothèses fondamentales d'indépendance (conditionnelle) des individus :
i) vis à vis du processus dynamique (conditionnellement aux covariables qui peuvent influer sur son déroulement, par exemple la taille) ;
ii) vis à vis du processus d'observation (conditionnellement à leur état d'histoire de vie ; cf. Annexe 1).

1.2.2. Combinaison entre l'approche bayésienne et le modèle à structure cachée

L'approche bayésienne par MCMC (cf. Encadré 3 et Annexe 2) est bien adaptée pour l'analyse de données issues de CMR via un modèle à structure cachée (Clark, 2003 ; Gimenez et al., 2007 ; Royle, 2008). Ces principaux atouts sont :
1) la structure de conditionnement du modèle à structure cachée, puis du processus d'observation

conditionnellement aux états cachés est cohérente avec le raisonnement conditionnel de l'approche bayésienne. Elle permet le transfert d'information des données vers les états cachés puis des états vers toutes les autres inconnues du modèle. Les états latents intermédiaires sont ainsi estimés comme toutes les autres grandeurs inconnues du modèle. Par exemple, nous pouvons estimer l'état latent de maturation pour l'ensemble des tacons 1+ alors que nous avons une vision partielle de cet état uniquement pour les tacons 1+ recapturés à l'automne ;
2) elle facilite l'intégration de sources multiples d'informations via :
i) diverses sources de données correspondant aux différents processus d'observation, ou bien des données annexes nous renseignant de façons complémentaires sur ces mêmes processus (cas des données de marquage des smolts par IV) ;
ii) l'intégration de connaissances disponibles (par exemple issues d'études antérieures ou similaires) via la spécification des distributions *a priori* (cf. Annexe 2).

L'approche bayésienne offre ainsi un cadre unique et cohérent permettant d'estimer les grandeurs d'intérêt de notre modèle conditionnellement aux données de CMR observées. Ceci est réalisé en intégrant à la fois incertitudes (liées au caractère aléatoire des processus d'histoire de vie et de capture) et connaissances (hypothèses structurant le modèle et information disponible *a priori*).

Encadré 3: STATISTIQUE BAYÉSIENNE

L'approche bayésienne permet d'ajuster notre modèle en assimilant l'information issue des données et ainsi estimer les grandeurs d'intérêts (Gelman et al., 2003 ; Brooks, 2003 ; Link & Barker 2010). Cette estimation est résumée par la distribution de probabilité jointe, dite *a posteriori*, de toutes les grandeurs inconnues du modèle (état d'histoire de vie, probabilité de transitions entre stade d'histoire de vie, probabilités de captures). Elle s'interprète comme des degrés de crédibilité comparée des inconnues conditionnellement aux données. L'analyse Bayésienne fait la synthèse de l'information issue des données (à travers la fonction de vraisemblance $[Y \mid \theta]$) et de l'expérimentateur (à travers la distribution de probabilité *a priori* ou Prior $[\theta]$) pour obtenir la distribution *a posteriori* ($[\theta \mid Y]$) des grandeurs d'intérêts via la formule de Bayes (cf. Annexe 2).

En pratique, on a donc recours à des méthodes numériques d'approximation pour résoudre le problème de la résolution analytique d'intégrales multidimensionnelles. La méthode d'échantillonnage de Monte Carlo par chaînes de Markov (MCMC) est la plus largement utilisée actuellement (Gelman et al. 2004 ; Brooks et al. 2011). Une description méthodologique de l'inférence bayésienne et du traitement du modèle par MCMC est donnée en annexe 2. L'échantillonnage MCMC est réalisé à l'aide des logiciels OpenBUGS (Lunn et al., 2009) ou JAGS (Plummer et al., 2003). Les logiciels nécessitent de spécifier la structure (vraisemblance) du modèle, les lois de probabilités *a priori* et les données. Ils réalisent alors le tirage d'un échantillon dans la loi *a posteriori* jointe de toutes les grandeurs inconnues. La distribution empirique de cet échantillon permet d'approximer la distribution *a posteriori* de n'importe quelle grandeur d'intérêt, sous réserve que l'échantillonnage MCMC ait convergé, c'est-à-dire que la distribution empirique soit représentative de la distribution *a posteriori*. Cette convergence est assurée quand la taille de l'échantillon simulant la distribution *a posteriori* est suffisamment grande. Dans la pratique elle peut être testée par diverses techniques (cf. Annexe 2).

Nous nous sommes placés dans ce cadre de modélisation pour représenter le processus dynamique caché et le processus d'observation conformément aux étapes successives structurant les histoires de vie des juvéniles de saumon atlantique et les différentes occasions de capture. Cette approche a plus particulièrement été appliquée à la phase juvénile en eau douce du cycle biologique du saumon atlantique à partir d'un jeu de données de CMR collecté sur le Scorff (Bretagne sud). En effet, le saumon atlantique présente un cycle de vie complexe incluant une grande variété d'histoire de vie qui doivent être étudier dans un cadre unique si on veut comprendre les variations d'histoire de vie et les mécanismes qui les génèrent.

Ce travail a fait l'objet d'une publication scientifique (cf. **Article 1**). L'objectif premier a été de démontrer que l'étude des processus évolutifs requiert la modélisation des histoires de vie complètes des individus tout en tenant compte des paramètres de nuisances (problème de détection) qui peuvent altérer nos inférences. Nous montrons ainsi que l'approche hiérarchique est tout à fait adaptée pour aborder les questions de biologie évolutives en milieu naturelle car elle permet dans un cadre unique :
1) de modéliser des phénomènes complexes tel que les histoires de vie et les transitions entre états associées ;
2) d'intégrer les processus évolutifs d'intérêt ;
3) de prendre en compte l'incertitude dans les données d'observation.

En dépit de l'augmentation de la complexité de notre modèle, nous montrons que l'intégration pas-à-pas des différents composantes du cycle de vie et du processus d'observation permet de mettre en évidence des processus évolutifs qui peuvent être mal estimés ou ignorés si on n'intègre pas l'ensemble des événements des histoires de vie et toute l'information disponible. Nos résultats mettent ainsi en évidence une norme de réaction pour la smoltification taille-dépendante, des survies sélectives (avantage de la smoltification en terme de survie) et des compromis évolutifs (coût de la reproduction) chez les juvéniles de saumon atlantique (cf. **Article 1** et **Article 3**).

Enfin, nous discutons les avantages et inconvénients inhérent à ce type de modélisation, reconnaissant que ce type d'approche nécessite une connaissance pointue des méthodes misent en œuvre mais présente un grand potentiel pour aborder des questions de biologie évolutive en milieu naturel qui ne peuvent pas être mis en évidence en laboratoire ou avec des études à court-termes.

➤ Article 1

2 DÉCISIONS D'HISTOIRE DE VIE STATUT-DÉPENDANTES

Les décisions entre les tactiques alternatives d'histoire de vie constituent un cas de plasticité phénotypique. La réponse phénotypique est discontinue et statut-dépendante. Les décisions d'histoire de vie statut-dépendante peuvent être représentées par des normes de réactions sous la forme de modèles à seuil(s). Les normes de réaction continues montrent des changements graduels du phénotype en fonction d'un gradient continu du statut tandis que les normes de réaction discontinues impliquent un changement brutal dans la réponse phénotypique quand la valeur du statut dépasse une valeur seuil. Les THV qui suivent ce type de configuration sont aussi communément appelés « caractères à seuils » (Roff 1996), « stratégie conditionnelle » (Hazel et al. 1990 ; Gross 1996) ou « polyphénisme » (Stearns 1989). Cette configuration résulterait d'un mécanisme physiologique sous-jacent et de contraintes évolutives (Schlichting & Pigliucci 1995). Elle serait favorisée par la sélection disruptive et par l'existence de signaux qui renseignent l'individu sur la meilleure tactique à adopter.

2.1. Modélisation des décisions d'histoire de vie

Le cadre conceptuel des normes de réaction probabiliste (Heino et al. 2002) a été proposé comme un cadre statistique pour représenter les normes de réaction discontinues (phénotypes alternatifs) en fonction du statut représentatif de l'environnement. Elles sont largement utilisées pour étudier la décision de maturation statut-dépendante (Dieckman & Heino 2007). Il décrit la relation entre la probabilité de maturation et le statut (e.g. la taille), les variations de statut étant prioritairement attribuées aux variations des conditions environnementales. Dans l'**article 2**, nous nous sommes intéressés à la décision de migration statut-dépendante des juvéniles de saumon atlantique. En effet, l'âge à la smoltification dépend positivement de le croissance au cours de la première année de vie en eau douce (Nicieza et al., 1991 ; Baglinière et al., 1993 ; Thorpe et al. 1998). En reprenant le cadre conceptuel des normes de réaction probabilistes, nous représentons la liaison entre la probabilité de smoltifier et la taille au stade tacon 0+ (cf. **Article 3**). Nos résultats révèlent l'existence d'une norme de réaction taille-dépendante très nette pour la smoltification. Des normes de réaction poids-dépendante pour la maturation sexuelle précoce ont également été mise en évidence (Piché et al. 2008).

Ce résultat, corroboré par des analyses complémentaires (cf. Annexe 3), soutient l'existence d'une taille seuil pour déclencher la décision. Hutchings (1994) suggère ainsi que la tactique de maturation sexuelle précoce chez les juvéniles de saumon atlantique est dépendante d'un seuil de croissance. Les choix entre les tactiques alternatives d'histoires de vie seraient alors dépendantes à la fois du statut des individus et d'un seuil à dépasser pour enclencher le processus de maturation ou de smoltification tel que proposé dans le cadre conceptuel proposé par Thorpe et al. (1998) et Mangel & Satterwaith (2008). Gross (1996) propose le cadre des stratégies conditionnelles, dans lequel la capacité d'un individu à choisir la tactique adéquate dépend également de son statut. Il propose alors de représenter les stratégies conditionnelles à travers le modèle de sélection statut-dépendante (SDS). Dans le modèle SDS, les valeurs sélectives des tactiques alternatives sont dépendantes du statut. Les individus avec un statut élevé auront un avantage sélectif s'ils adoptent la tactique Y alors que s'ils ont un statut faible ils auront une plus grande valeur sélective s'ils adoptent la tactique X (cf. Figure 8 a). Il existe alors un seuil pour lequel les valeurs sélectives des deux tactiques alternatives sont égales (intersection des droites de valeur sélective pour chaque tactique X et Y, cf. Figure 8 a). Un individu serait alors capable d'opter pour la tactique (i.e. d'exprimer le phénotype) qui maximisera sa valeur sélective via la comparaison de son statut avec un seuil. Dans le cadre des stratégies conditionnelles, les conditions environnementales sont le principal déterminant de leur statut des individus et le seuil serait invariant entre les individus.

Le modèle à seuil environnemental (Environmental Threshold model (ETM) ; Hazel et al. 1990 ; Tomkins & Hazel 2007 ; cf. Encadré 4) a ainsi été développé pour comprendre l'évolution et le maintient des tactiques alternatives dans les populations. Il postule que les individus diffèrent dans leur réponse phénotypique aux signaux environnementaux du fait de la variation génétique dans le seuil qui détermine le phénotype alternatif à exprimer conditionnellement au statut. Il repose sur les approches de génétique quantitative, lequel est considéré comme un trait quantitatif distribué normalement et qui peut être soumis à la sélection. La variation génétique dans la distribution du seuil permet ainsi d'expliquer la variabilité dans l'expression des phénotypes alternatifs pour une valeur de statut donné. Plus la variation génétique dans la distribution du seuil est grande, plus la variation dans la réponse phénotypique sera grande et donc la courbe de fréquence cumulée d'une tactique donnée en fonction du statut sera « plate » (cf. Figure 8 b et c).

Ce modèle d'écologie théorique permet ainsi d'étudier dans un cadre unique la plasticité phénotypique (à travers la distribution des statuts) et l'évolution des stratégies conditionnelles (à travers la distribution du seuil). Cependant, ce modèle mathématique a rarement été appliqué à des études de cas car il n'offrait pas un cadre statistique pour analyser des données d'observations.

2.2. Étude des stratégies conditionnelles à partir de données d'observations

Les cadres conceptuels proposés pour aborder les stratégies conditionnelles semblent peu appropriés car ils ne représentent pas le mécanisme sous-jacent qui génère les données (notamment dans le cas des normes de réactions probabilistes) et/ou n'offrent pas un cadre statistique pour analyser des

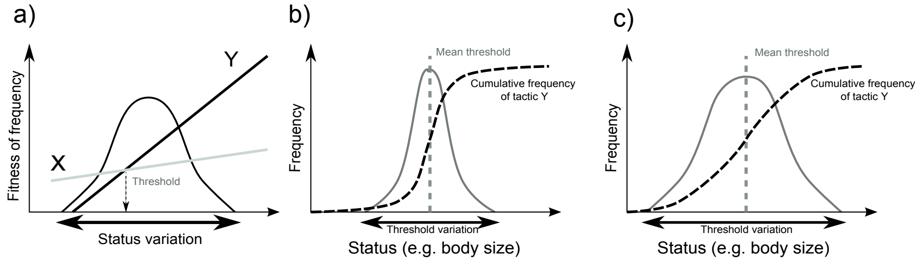


Figure 8: (a) Le modèle de sélection statut-dépendante (SDS ; Gross(1996)) ; (b) et (c) Le modèle environnemental à seuil (ETM). Le seuil est variable au niveau individuel et sa variation détermine la pente de la norme de réaction (i.e., la fréquence cumulée de la tactique Y).

données empiriques. Ainsi, nous suggérons que les traits phénotypiques observables (tel que la taille et les phénotypes alternatifs) sont les manifestations visibles d'un processus sous-jacent dans lequel le statut énergétique serait le signal proximal (Dieckmann & Heino 2007) pour le déclenchement de processus physiologiques ou morphologiques coûteux énergétiquement (e.g. la maturation et la smoltification).

Dans l'**article 2**, nous proposons un modèle statistique plus cohérent biologiquement pour étudier la plasticité phénotypique au travers des stratégies conditionnelles et leur évolution. Ce modèle (LETM « Latent Environmental Threshold Model ») représente les mécanismes sous-jacents et permet d'analyser des données d'observations. Il donne accès aux statuts individuels (i.e. signal proximal) et aux seuils individuels ouvrant la voie à l'étude de leur évolution. L'idée maîtresse de cet article est que les phénotypes alternatifs sont issus d'un mécanisme sous-jacent impliquant un signal proximal et un seuil au niveau individuel qui ne sont pas mesurables directement mais peuvent être inférés à travers leurs relations avec des traits phénotypiques observés. Par exemple, bien que ne connaissant pas le statut énergétique d'un individu, nous savons qu'il est corrélé avec un trait observé tel que la taille ou le poids. Nous utilisons alors la modélisation hiérarchique à couche latente (cf. **chapitre 1**) pour séparer la couche latente (le mécanisme sous-jacent, i.e. le modèle ETM ; Encadré 4) de son observation au travers de mesures phénotypiques. En séparant la variabilité environnementale (variabilité du signal proximal) de la variabilité génétique (variabilité du seuil) nous montrons qu'il est possible d'obtenir une estimation fiable de l'héritabilité des stratégies conditionnelles dans un cadre méthodologique de génétique quantitative.

Encadré 4: LE MODELE A SEUIL ENVIRONNEMENTAL

Le modèle à seuil environnemental (Environmental Threshold Model, ETM) a été proposé pour représenter les stratégies conditionnelles (Tomkins & Hazel 2007). Ce modèle est fondé sur l'idée que la réponse phénotypique alternative d'un individu résulte de la comparaison d'un signal environnemental assimilé à son statut et d'un seuil déterminé génétiquement. Le seuil est considéré comme un trait quantitatif et polygénique et pour chaque génotype, il existe une valeur seuil à comparer au signal environnemental. Dans le cas de deux phénotypes alternatifs X et Y, si le signal environnemental est au-dessus du seuil, le phénotype Y est exprimé, sinon le phénotype X est exprimé. La stratégie conditionnelle peut alors être vue comme une norme de réaction propre à chaque génotype (cf. Figure E4 a) dépendante du signal environnemental. La distribution du seuil dans la population est continue et normale (cf. Figure E4 b). Le seuil moyen peut alors être estimé comme la valeur du signal pour laquelle les fréquences des deux tactiques sont égales. Au niveau populationnel, la fréquence cumulée des tactiques évolue en fonction du signal environnemental (cf. Figure E4 c). Dans ce modèle, la sélection agit sur la distribution des seuils à travers la valeur sélective des tactiques alternatives. Ainsi, le modèle ET permet de prendre en compte dans un cadre unique à la fois la plasticité phénotypique, à travers des changements de la distribution du signal environnemental, et son évolution, à travers des changements de la distribution des seuils.

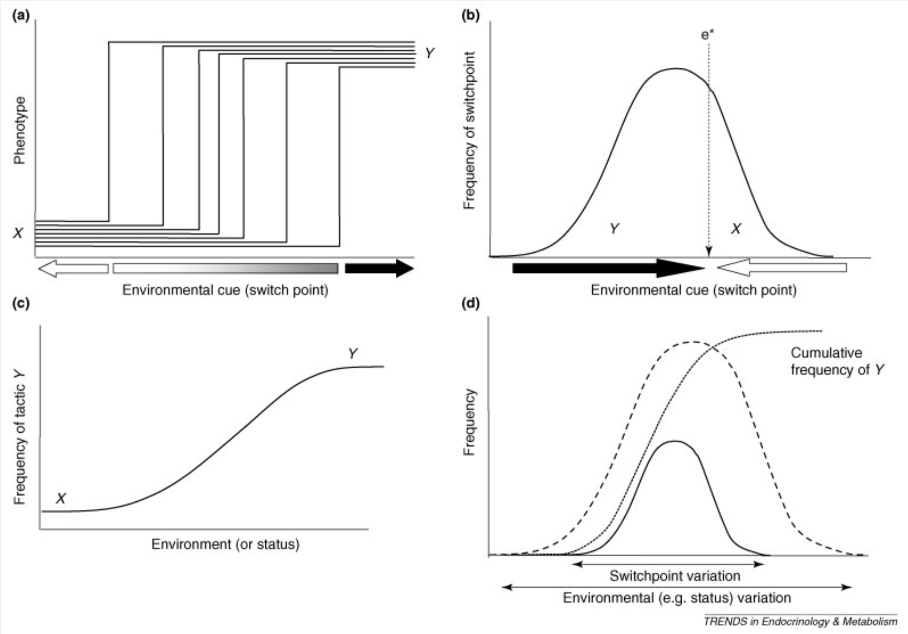


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Figure E4 : Le modèle Environnemental à seuil (ETM ; Hazel et al. 1990, Tomkins & Hazel, 2007). (a) Normes de réaction pour 7 génotypes (seuils) en fonction du signal environnemental (i.e. statut). Les flèches indiquent les changements d'expression des tactiques (X ou Y) en fonction du signal environnemental. (b) Distribution normale des seuils et domaine d'expression des phénotypes alternatifs pour une valeur de signal environnemental donnée*. (c) Fréquence cumulée des tactiques alternatives X et Y en fonction de la variation du signal. (d) La variance du seuil ('switchpoint', trait plein) est généralement plus petite que la variance du signal (en pointillés). La fréquence cumulée de l'expression de la tactique alternative Y est le révélateur de la moyenne et de la variance des seuils sous-jacents.

2.3. Décisions d'histoire de vie chez le saumon atlantique

Nous illustrons cette approche par l'étude de la décision d'histoire de vie entre migration et résidence chez les juvéniles de saumon atlantique. Le saumon atlantique peut être considéré comme une espèce adoptant une stratégie conditionnelle avec différentes tactiques alternatives (par exemple, migration ou non, maturation ou non). Le choix entre ces dernières dépendrait du statut énergétique des individus et de seuils énergétiques à dépasser à des périodes clés (« fenêtres de décision » ; Thorpe et al. 1998 ; Mangel & Satterwhaite 2008 ; Hutchings & Myers 1994 ; Hutchings 2011). Le choix de migration dès la première année de vie dépendrait ainsi du statut énergétique de l'individu, reflété par sa croissance /taille, et d'un seuil énergétique à dépasser lors de la période estivale pour enclencher le processus de smoltification. Nous montrons que la forte plasticité phénotypique mise en évidence pour la migration a vraisemblablement une composante génétique (bien que la variance des phénotypes observés reste élevée par rapport à la variance du seuil ; cf. Annexe 3).

➤ Article 2

3 COMPROMIS ÉVOLUTIFS ENTRE TRAITS D'HISTOIRE DE VIE

L'étude des compromis dans l'évolution des THV a longtemps été limitée par des méthodes inappropriées et affectée par de nombreux facteurs confondants (Townsend & Anderson, 2007). En particulier, la mise en évidence de compromis nécessite d'évaluer la valeur sélective, ou au moins certaines de ses composantes, par un suivi individuel durant toute ou partie de l'histoire de vie de l'individu. Les expérimentations en milieu contrôlé permettent un suivi précis des individus tout au long de leur vie donnant ainsi accès à leur valeur sélective. Cependant, les patrons mis en évidence sont des compromis « potentiels » (Viallefont et al., 1995 ; Townsend & Anderson, 2007), l'étude en milieu contrôlé ne permettant pas de tenir compte des interactions environnementales (Stearns, 1992).

Dans l'**article 3**, nous avons utilisé la modélisation hiérarchique bayésienne telle que proposée au **chapitre 1** (« Modélisation des histoires de vie ») pour représenter les histoires de vie complètes des juvéniles de saumon atlantique et ainsi mettre en évidence des compromis évolutifs en milieu naturel. Le point central de cet article est que notre approche permet la détection des compromis y compris pour des traits qui n'ont été que partiellement observés. Par exemple, dans le cas de l'étude des compromis chez les juvéniles de saumon atlantique en conditions naturelles, la principale difficulté réside dans l'accès au choix de smoltification (i.e. un individu non observé a-t-il migré ou non ?) de chaque individu avant l'événement de survie. Notre approche de modélisation qui incorpore explicitement ce choix au moyen d'une variable d'état cachée, couplée avec des observations par CMR, permet de résoudre cette difficulté. Elle met en évidence une survie sélective dépendante du choix de smoltification qui peut être vue comme un coût lié au choix de résidence en eau douce une année supplémentaire : les futurs smolts 1+ ont une plus grande probabilité de survie hivernale que les futurs tacons 1+. Ce résultat n'est pas la conséquence d'une confusion avec une survie hivernale des tacons 0+ taille dépendante. Il est par ailleurs plutôt paradoxal compte tenu des connaissances disponibles qui plaident en faveur d'un coût opposé (plus faible survie pour les futurs smolts 1+). En effet, la smoltification est un processus coûteux en énergie qui exige un rendement métabolique élevé et une acquisition importante en ressources (Metcalfe & Thorpe 1992 ; Metcalfe et al. 1995) qui se ferait au détriment de la survie via un risque de prédation accrue et la difficulté d'obtention des ressources. Il ne semble pas non plus reproductible chaque année, peut-être en lien avec les variations annuelles des conditions environnementales et de leurs effets sur les caractéristiques individuelles des juvéniles. Tous ces points sont présentés et discutés plus en détail dans l'Annexe 4.

Cette étude met également en évidence un coût de la reproduction pour la survie : les tacons 1+ matures ont une plus faible probabilité de survie hivernale post-reproduction que les tacons 1+ non matures. Ce résultat est conforme aux études antérieures (Baglinière et al., 1993 ; Whalen & Parrish, 1999 ; Whalen et al., 2000 ; Jonsson & Jonsson, 2005). La maturation est un processus énergétiquement coûteux (Thorpe, 1994). La mobilisation des réserves énergétiques de l'animal en faveur des gonades peut se faire au détriment de celles nécessaires à la survie hivernale (Arndt, 2000). Le coût de la reproduction peut également être imputé aux interactions agonistiques et aux blessures infligées par les mâles anadromes de plus grande taille durant la reproduction (Hutchings & Myers, 1987).

L'**article 3** constitue un premier essai de représentation des stratégies d'histoire de vie comme un réseau de traits d'histoire de vie liés par une structure de conditionnement à l'échelle de l'individu. En revanche cet article ne représente pas les mécanismes proximaux sous-jacents qui génèrent les décisions d'histoire de vie et les compromis qui les relient ; c'est l'objet de la section suivante.

➤ Article 3

3.1. Vers une approche mécaniste des compromis

L'**article 3** montre que la mise en évidence des compromis peut-être délicate quand elle se fonde sur des comparaisons interindividuelles. Il met en évidence un avantage en termes de survie hivernale pour les futurs migrants par rapport aux résidents alors qu'un effet négatif de la smoltification sur la survie était attendu. Ce résultat inattendu a motivé le besoin de comprendre et d'expliciter les mécanismes sous-jacents. De nombreuses études empiriques voulant mettre en évidence des compromis évolutifs en milieu naturel ont montré des corrélations positives (ou nulles) entre THV alors que des corrélations négatives (compromis) étaient attendues (Glazier 1999 ; Brown et al. 2003 ; King et al. 2010). Pour expliquer de tels résultats, Van Noordwijk & De Jong (1986) proposent un modèle (le modèle 'Y' ; cf. Encadré 5) qui montre que de fortes variations entre les individus dans l'acquisition de leurs ressources peuvent masquer les compromis sous-jacent. Ce type de configuration est particulièrement susceptible de se produire en conditions naturelles où la variabilité de l'environnement est forte et ne peut être contrôlée par l'analyste.

La mise en évidence des compromis à partir de données d'observation requiert donc de représenter explicitement les mécanismes proximaux reliant statut individuel et expression des THV. Dans l'**article 4**, nous proposons un modèle à la fois mécaniste et statistique permettant (1) de représenter la structure de conditionnement qui lie les THV et (2) d'accéder aux compromis sous-jacents. L'idée principale de cette démarche est que la mise en évidence des compromis requiert la prise en compte des variations interindividuelles dans l'acquisition et l'allocation des ressources conformément au modèle théorique proposé par Van Noordwijk & De Jong (1986). Comme les variations dans l'acquisition et l'allocation de ressources sont difficilement accessibles en conditions naturelles, nous proposons

Encadré 5: LE MODELE « Y »

Van Noordwijk & De Jong (1986) proposent un modèle pour comprendre les observations de corrélations positives entre traits d'histoire de vie alors que des compromis, i.e. des corrélations négatives, sont attendues. Ils présentent un modèle "Y" dans lequel deux traits S et R (e.g. survie et reproduction) sont en compétition pour la même ressource A (e.g. l'énergie). Ainsi, pour chaque individu :

$$A = R + S$$

Ils considèrent alors que les individus diffèrent aussi bien dans leur capacité à acquérir des ressources (A) que dans l'allocation de celles-ci aux différents traits interdépendants (B, cf. figure E5 a). Ainsi, la quantité de ressource disponible pour le trait S dépend positivement de la quantité de ressources acquises (A) et négativement de la proportion allouée aux autres traits (R). Lorsque, la variation dans l'acquisition des ressources (A) est faible par rapport à la variation dans l'allocation de ces dernières (B) entre les traits (S et R), alors des comparaison interindividuelles doivent faire apparaître des compromis (cf. figure E5 c). En revanche, lorsque la variation dans l'acquisition des ressources est élevée par rapport à la variation dans l'allocation entre les traits (cf. figure E5 b), les compromis qui opèrent au niveau individuel peuvent être masqués lorsque leur identification est basée sur des comparaisons interindividuelles (Van Noordwijk & De Jong 1986 ; Brown 2003). En effet, les individus qui ont une forte capacité d'acquisition des ressources (A élevé) peuvent investir plus dans les deux traits. Les compromis sous-jacents au niveau individuel (découlant de l'allocation différentielle de ressources limitées) ne sont alors détectables que par une approche se basant sur une comparaison interindividuelle conditionnellement à la quantité de ressources acquises.

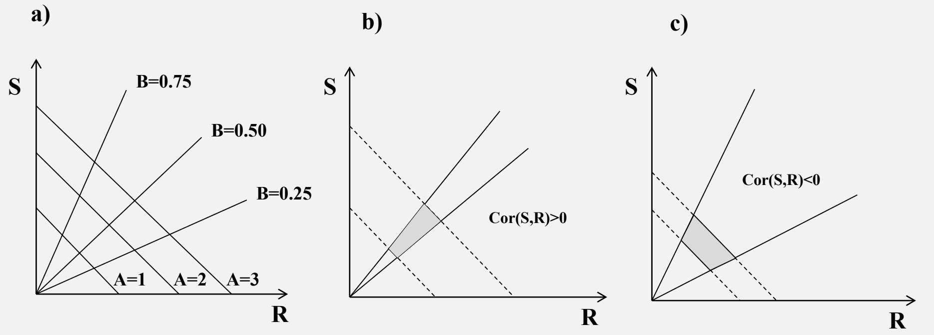

Figure E5 : Illustration du modèle Y de Van Noordwijk & De Jong (1986).
a) les composantes du modèle sont les ressources acquises (A), leur allocation (B) entre les différents traits (R et S) ; b) la variation de A est large et celle de B est petite de telle sorte que l'on observe une corrélation positive entre R et S au niveau populationnel masquant le compromis sous-jacent ; c) la variation de A est petite (ressources limitantes) et celle de B est grande de telle sorte que l'on observe une corrélation négative entre R et S au niveau populationnel révélant le compromis sous-jacent.

d'utiliser le statut individuel comme révélateur de la composition corporelle d'un individu et son investissement dans un trait d'histoire de vie donné (e.g. la maturation ou la smoltification). Ainsi, les compromis peuvent être mis en évidence conditionnellement au statut des individus.

3.2. Transposition au cas des compromis évolutifs chez le saumon atlantique

Cette approche a été appliquée au cas des juvéniles de saumon atlantique pour mettre en évidence des compromis évolutifs (cf. **Article 4**). Nous avons considéré les trois traits qui structurent l'histoire de vie des juvéniles : deux tactiques démographiques successives (maturation puis smoltification) et la survie hivernale. Ces traits discrets sont associés à des décisions d'histoire de vie statut dépendantes et sont donc modélisés en utilisant le cadre du LETM (cf. **chapitre 2**, **Article 2**). On considère qu'il existe deux signaux proximaux qui renseignent les organismes sur le niveau de leur réserve et de leur structure. Les ressources acquises sont réparties au sein des organismes entre ces deux compartiments selon la théorie du « Dynamic Energetic Budget » (DEB ; Sousa et al. 2010). Chaque signal proximal est alors corrélé à un signal observable : les réserves sont corrélées au poids des individus, tandis que la structure est corrélée à la taille des individus (longueur). La maturation dépend du signal proximal indicateur des réserves et la migration dépend de celui indicateur de la structure. La survie hivernale dépend positivement des réserves et négativement de la structure : en conditions hivernales où l'approvisionnement en énergie peut être limitant, les réserves favorisent la survie alors que les besoins énergétiques (pour assurer la maintenance de l'organisme) augmentent avec la structure et influent donc négativement sur la survie. La maturation et la reproduction qui suivent consomment des réserves et donc peuvent avoir un impact négatif sur la survie. Le choix de migration (fait à l'automne précédent) pousse les individus à augmenter leur structure et donc influence négativement la survie. En adoptant une approche mécaniste et en modélisant explicitement ces compromis, nos résultats mettent clairement en évidence un effet négatif de la smoltification sur la survie (compromis sous-jacent attendu) alors qu'une approche « classique » de corrélation entre traits d'histoire de vie mettait en évidence une corrélation positive (cf. **Article 3** et Annexe 4).

Cet article constitue également une étape plus aboutie de représentation des stratégies d'histoire de vie en intégrant les mécanismes évolutifs à l'œuvre : la plasticité phénotypique à travers les décisions d'histoire de vie et les stratégies conditionnelles, et les compromis évolutifs qui relient les THV et contraignent le champ d'action possible des organismes (i.e. les stratégies d'histoire de vie possibles). Il synthétise les idées conceptuelles proposées par Thorpe et al. (1998) et Mangel & Satterthwaite (2008) pour représenter les variations d'histoire de vie chez les salmonidés tout en intégrant des modèles mécaniste théorique cachés (Modèles « LETM » et « Y ») et en les confrontant aux données d'observation.

➤ Article 4

CONCLUSION ET PERSPECTIVES

> « Biologists cannot simply peek behind the screen and directly observe the actual causal processes. All that can be directly observed are the consequences of these processes in the form of complicated patterns of association and independence in the data. »
>
> *Shipley (2000)*

Conclusion

Appréhender le potentiel adaptatif et évolutif des populations et comprendre l'origine des variations d'histoire de vie passe par l'étude et la mise en en évidence des stratégies d'histoire de vie et des processus évolutifs qui les gouvernent. Le premier objectif de ma thèse était donc d'étudier les stratégies d'histoire de vie à travers la mise en évidence des décisions d'histoire de vie et des compromis évolutifs ainsi que leurs conditionnements par les caractéristiques individuelles. La mise évidence de ces mécanismes en conditions naturelles se heurte à des problèmes d'ordre méthodologiques. En effet, il est nécessaire d'accéder aux histoires de vie complètes des individus et à leurs THV. Or le suivi exhaustif des individus d'une population au cours de leur vie est difficilement réalisable en conditions naturelles. Les méthodes de capture-marquage-recapture utilisées ici permettent une observation partielle des histoires de vie et des THV. Mon travail a ainsi été accompli avec l'idée que nos observations sont bruitées et qu'elles ne sont que la partie visible de processus sous-jacents. L'ignorer conduit à ne pas reconnaître le processus qui génère nos observations et à biaiser nos inférences en confondant la variabilité inhérente aux processus éco-évolutifs et l'incertitude liée aux méthodes d'observation.

La première partie de mon travail a consisté à proposer des outils méthodologiques appropriés pour mettre en évidence les histoires de vie et les processus évolutifs en conditions naturelles (Objectif 2, point 1). Les outils statistiques les plus récents décrits dans ma thèse (la modélisation bayésienne hiérarchique en particulier) permettent désormais de représenter explicitement les processus sous-jacents d'intérêt tout en tenant compte l'incertitude liée à l'acquisition des données. Mon travail a alors consisté à porter ce cadre de modélisation dans le domaine de la biologie évolutive en conditions naturelles. En particulier, j'ai représenté les histoires de vie complètes des juvéniles de saumon atlantique à partir de données CMR en séparant le processus d'observation et le processus dynamique d'intérêt et en intégrant la variabilité interindividuelle. Ce faisant, des normes de réaction pour la smoltification et des compromis évolutifs ont pu être mis en évidence (cf. **chapitre 1**).

J'ai souhaité approfondir ce raisonnement en considérant que les THV et les phénotypes observés étaient eux-mêmes issus de mécanismes individuels sous-jacent (physiologiques, génétiques,. . .). En d'autres termes, les phénotypes observés ne sont que la manifestation de mécanismes non-observables directement. Ainsi, pour comprendre le fonctionnement et le déterminisme de ses stratégies d'histoire de vie, il est nécessaire de représenter explicitement ces mécanismes. J'ai adopté une approche mécaniste au niveau individuel intégrant plus explicitement les mécanismes proximaux qui conditionnent les stratégies d'histoire de vie (Objectif 2, point 2). J'ai ainsi pu représenter le mécanisme qui conduit aux décisions d'histoire de vie (Cf. **chapitre 2**) et mettre en évidence des compromis évolutifs qui n'auraient pu être mis évidence par des approches classiques (cf. **chapitre 3**).

Un autre enjeu de ma thèse a été d'intégrer les théories et concepts de la biologie évolutive dans l'analyse statistique des données d'observations (Objectif 2, point 3). Pour comprendre et représenter les mécanismes mis en jeu dans les décisions d'histoire de vie et les compromis, je me suis alors basé sur des modèles théoriques proposés et/ou sur des observations expérimentales (par exemple, le modèle ET pour les stratégies conditionnelles et modèle d'acquisition/d'allocation des ressources pour les compromis). En effet, l'étude des processus évolutifs a longtemps été confinée aux expérimentations en laboratoire ou abordé du seul point de vue théorique. Ces approches fournissent un base de connaissance et un cadre de réflexion importants pour l'étude des processus éco-évolutifs. Cependant, leur pertinence doit être évaluée de façon critique car elles reposent souvent sur des techniques et méthodes peu fiables ou inadaptées et/ou ne permettant pas une analyse statistique adéquate des données empiriques.

Ce travail pose des bases méthodologiques et conceptuelles pour la représentation des histoires de vie et les mécanismes de conditionnement qui sous-tendent les stratégies d'histoire de vie. Ces dernières sont vues comme un agencement de normes de réactions et de compromis évolutifs qui peuvent être représentés au moyen de modèles probabilistes fondés sur le raisonnement conditionnel. Les approches de modélisation statistique développées dans ma thèse offrent des perspectives intéressantes car elles permettent de représenter ces phénomènes complexes dans un cadre unique et cohérent tout en intégrant aisément toutes les sources d'informations disponibles. Modéliser cette complexité biologique nécessite un apprentissage certain des outils statistiques modernes pour les maîtriser. Pour autant, dans un tel contexte, l'écologiste ne peut pas se reposer entièrement sur les statisticiens. Il se doit de maîtriser ces outils afin d'assurer une pertinence des hypothèses biologiques elles mêmes complexes introduites dans les modèles.

Les suivis à long-terme offrent une opportunité unique d'aborder des questions de biologie évolutive en conditions naturelles et d'illustrer les processus qui ne pouvaient pas être mis en évidence par des études à court terme ou en laboratoire (Clutton-Brock & Sheldon 2010). Cela nécessite le développement de modèles de plus en plus complexes et l'intégration de sources multiples d'information. Le cadre de modélisation proposé dans ma thèse constitue une approche flexible et cohérente pour conduire des inférences statistiques dans de tels contextes.

Perspectives

Mon travail appliqué au saumon atlantique constitue une première tentative de représentation des stratégies d'histoire de vie comme un réseau de THV interconnectés. Il devrait être poursuivi en se focalisant sur différents points d'intérêts majeurs pour comprendre le fonctionnement des populations de saumon atlantique et mieux appréhender leur réponse adaptative et évolutive face aux changements environnementaux. Ces différents points sont détaillés par la suite.

Décisions entre tactiques d'histoire de vie sexe-dépendantes

« The selective forces operating on males can be quite different from those operating on females » (Darwin, 1859).

Il apparaît nécessaire de tenir compte explicitement du sexe dans le processus dynamique d'histoire de vie chez le saumon atlantique, et ce dès la phase juvénile (stade tacons 0+). En effet, la maturation sexuelle de tacons femelles est très rarement observée (Baglinière & Maisse, 1985). On peut donc considérer que pour elles, l'accès à la reproduction est peu probable en restant en eau douce, leur valeur sélective (dépendant principalement du nombre et de la taille des œufs) étant étroitement liée à leur taille (Fleming & Gross, 1990). Considérant que les femelles doivent obligatoirement migrer en mer pour atteindre la maturité sexuelle et en tenant compte des coûts en terme de survie de la phase eau douce, nous prédisons un fort gradient de sélection pour une croissance en eau douce rapide dés la première année de vie pour les femelles (les contraintes et les coûts liés à cette croissance restent cependant à identifier). Une sélection dans la même direction doit opérer chez les mâles mais ces derniers ont la possibilité de se reproduire en eau douce sans migration en mer (maturation sexuelle précoce). Le gradient de sélection pour la migration dés la première année de vie devrait donc être moins fort pour les mâles que pour les femelles.

Pour vérifier ces hypothèses et étudier les décisions de tactiques d'histoire de vie sexe-dépendantes, il est donc nécessaire de déterminer le sexe des individus. Par exemple, la décision de maturation poids-dépendante chez les tacons 1+ mâles n'a pu être vérifiée du fait de la non distinction du sexe. Or, pour le moment la détermination du sexe sur des individus vivants reste problématique. Les mâles immatures et les femelles ne peuvent être distingués lors de la phase juvénile en eau douce. En outre, parmi les adultes anadromes, l'identification du sexe sur des critères visuels n'est possible qu'à partir de l'automne, à l'approche de la période de reproduction. Les données de sexage ainsi disponibles n'ont pas été suffisantes pour mener une analyse séparée des sexes. Les méthodes de sexage moléculaire (par l'identification des gènes contrôlant le sexe) semblent prometteuses pour mener à bien cet objectif. Cependant, le contrôle moléculaire du déterminisme du sexe et de la différenciation sexuel chez les poissons est encore peu connu (pour revue, Volff et al. 2007). La mise en évidence d'un tel déterminisme permettrait vraisemblablement à terme l'identification précoce du sexe des individus par analyse des échantillons génétique prélevés (cf. programme de suivi génétique ; Annexe 5). Des travaux sont actuellement en cours sur le saumon atlantique.

Croissance compensatoire

Les données collectées sur le Scorff indiquent l'existence de croissance compensatoire chez les juvéniles de saumon atlantique. Nous avons mis en évidence une norme de réaction probabiliste taille-dépendante pour la smoltification et certains individus ayant une faible probabilité de migrer au printemps suivant du fait de leur petite taille, s'engage tout de même dans cette voie. Ils se caractérisent par une forte croissance au cours de la transition entre la capture automnale et la recapture au stade smolt au printemps suivant. Il serait alors intéressant d'évaluer la fréquence, la dépendance vis-à-vis des conditions environnementales et les coûts associés de la croissance compensatoire sur les stratégies histoire de vie (Mangel & Munch 2005).

Spatialisation des stratégies d'histoire de vie

Les variations spatiales sont importantes pour comprendre l'évolution de la dispersion et l'adaptation locale. Au Canada (rivière Sainte-Marguerite), Aubin-Horth et al. (2006) ont observé un gradient longitudinal dans la fréquence de maturation sexuelle précoce. Les auteurs montrent que la fréquence de maturation des tacons mâles est plus basse dans les parties en aval de la rivière et plus élevée en amont. Ces résultats pourraient être notamment liés aux coûts engendrés par la migration eux mêmes associés à un gradient amont-aval. Une analyse préliminaire sur la première cohorte sur le Scorff ne semble pas indiquer l'existence d'un tel effet. Cependant, les analyses devraient être approfondies et étendues à l'ensemble des cohortes suivies, en portant à la fois pour la smoltification et la maturation.

Étude du déterminisme génétique des traits d'histoire de vie chez le saumon atlantique

L'étude du conditionnement des traits d'histoire de vie par les caractéristiques individuelles révèle la réponse adaptative de la population à une échelle de temps écologique, en particulier via la plasticité phénotypique. Mais la mise à jour du potentiel évolutif des caractères nécessite d'évaluer le déterminisme génétique de ces derniers. Ainsi, pour comprendre et prédire les changements évolutifs et leurs conséquences démographiques sur la population, il est nécessaire de quantifier (1) l'intensité de la sélection qui agit sur la distribution des phénotypes et (2) l'héritabilité génétique afin que les changements de distribution phénotypique induits soient transmis aux générations suivantes. Cette héritabilité doit être estimée par des approches de génétique quantitative qui évaluent la part génétique de la variabilité phénotypique et renseignent ainsi sur le potentiel évolutif d'un trait face à la sélection. En conditions naturelles, cela peut être mené par couplage des données de CMR avec les relations d'apparentement entre les individus marqués (le pedigree) obtenues grâce aux méthodes génétiques moléculaires récentes (reconstitution de pedigree à partir de marqueurs microsatellites de l'ADN). Dans le cas de la population de saumon du Scorff, cela nécessite la mise en place d'un programme de suivi génétique à long terme en parallèle au programme CMR. Un tel programme à long-terme a été initié en 2010 (cf. Annexe 5). J'ai également eu l'occasion de me familiariser avec les méthodes de génétique quantitative au cours de ma thèse (Papaïx et al. 2010 ; Charmantier et al. 2011 ; Lane et al. 2011 ; cf. Articles 5-7) en prévision de l'analyse future des données collectées sur le Scorff.

Estimation des paramètres démographiques lors de la phase marine et mise en évidence des relations entre la phase eau douce et la phase marine.

Lors de ma thèse, je me suis plus particulièrement focalisé sur la phase juvénile. En effet, moins d'une trentaine d'adultes anadromes appartenant aux 5 premières cohortes marquées ont été recapturés à ce jour (cf. chapitre 1, Tableau 1). L'accumulation de données via la pérennisation du programme CMR[1] sur le Scorff permettra de répondre à différentes questions d'intérêts : les THV de la phase eau douce ont-ils une influence sur les choix d'histoire de vie en mer (temps de séjour avant la reproduction en particulier) ? Quels sont les coûts et les bénéfices associés à la migration en mer ? Comment le compromis entre le succès reproducteur et la mortalité en mer influe sur le temps de séjour en mer ? Quel avantage sélectif lors de la phase marine est associé à la décision de rester une année supplémentaire ? La croissance en eau douce et/ou en mer a-t-elle un effet sur le temps de séjour en mer par une action sur le succès reproducteur et/ou la survie en mer ?

Vers la démographie évolutive

Dans un contexte d'environnement changeant, comprendre comment les populations peuvent répondre à ces changements dans une échelle de temps écologique et évolutive et identifier les mécanismes évolutifs en jeu constituent des enjeux majeurs. En adoptant une approche phénotypique et génétique (par un suivi individuel), le suivi à long terme d'une population permet d'étudier son évolution sous l'effet des variations temporelle de son environnement. Les processus évolutifs et les variations interindividuelles, le matériel de base pour la sélection naturelle, ont des conséquences écologiques sur les populations et vice-versa (Pressey et al. 2003). L'étude de ces interactions est au cœur de la démographie évolutive (« eco-evolutionary dynamics » ; Pelletier et al. 2009 ; Ezard et al. 2009 ; Carlson et al. 2011). Elle est d'un intérêt majeur si l'on veut comprendre le fonctionnement des populations et appréhender leur potentiel adaptatif et évolutif. Par exemple, introduire les approches de génétique quantitative dans des modèles démographique pourrait aider à comprendre l'évolution des THV chez le saumon atlantique et leurs conséquences écologiques (Pelletier et al. 2009 ; Coulson et al. 2010).

In fine, je suis convaincu que le programme actuellement développé sur le Scorff constitue un outil formidable pour aborder ces questions de démographie évolutive. Par la mise à jour de l'évolution

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[1] Le programme a été reconduit en 2009 et s'inscrit comme un programme à long terme dans un ORE piloté par l'INRA (U3E et UMR ESE, Rennes et UMR Ecobiop, St-Pée s/ Nivelle) en collaboration avec le CEFE (CNRS).

temporelle et spatiale de la diversité génétique et des traits phénotypiques en lien avec la valeur sélective, il permettra de mieux comprendre les relations entre génotype, phénotype et démographie chez le saumon atlantique en conditions naturelles. Dans le contexte de changement climatique en cours, la pérennisation de ce programme et la poursuite des travaux initiés dans ma thèse contribueront à comprendre et prédire les changements évolutifs et leurs conséquences démographiques sur les populations de saumon atlantique de la marge sud de l'aire de répartition de l'espèce.

Annexes

ANNEXE 1

Effet du marquage et taux de perte de marque.

Aucun effet significatif du marquage interne sur la croissance, le comportement alimentaire, la nage et la survie des juvéniles de salmonidés de plus de 55mm n'a été à ce jour détecté (Ombredane et al., 1998 ; Roussel et al., 2000 ; Dare, 2003 ; Newby et al., 2007). Cependant, Sigourney et al. (2005) détecte une mortalité post-marquage taille-dépendante pour des juvéniles de saumon de taille comparable à la partie basse de la distribution de taille observée dans notre étude. Cette mortalité n'est significative que pour les individus les plus petits (25% pour 60 mm) et elle est nulle dès 65-70 mm. De même, Acolas et al. (2007) ont observé un taux de survie proche de 95% pour des juvéniles de truites fario (*Salmo trutta*) de taille supérieur à 52 mm et 99% pour des poissons de plus de 57 mm en condition expérimentale. En ce qui concerne la capture par pêche électrique, Sigourney et al. (2005) n'ont pas observé d'effet significatif sur la croissance et la survie. Cependant, des effets à plus long terme peuvent apparaître et devraient être étudiés.

Le taux de rétention de la marque est supérieur à 97% (Ombredane et al., 1998 ; Roussel et al., 2000 ; Dare, 2003). Néanmoins, Acolas et al. (2007) rapporte un taux de perte de marque dépendant de la taille sur des juvéniles de truite commune (*Salmo trutta*), ce taux étant de l'ordre de 20% pour des juvéniles de truites de taille comprise entre 57 et 63 mm. Outre que la technique d'insertion (au moyen d'une seringue) est légèrement différente de celle utilisée dans notre cas (les incisions chirurgicales seraient plus précises et éviteraient d'endommager les organes internes), la taille de juvéniles de saumon marqués sur le Scorff est notablement plus élevée que celle des poissons utilisés par Acolas et al. (2007) (cf. **tableau 1** ; 76,5 mm pour la cohorte 2005, la plus petite enregistrée, contre 49 mm). Dans notre cas, l'absence de taille-dépendance dans la survie hivernale des tacons 0+ (cf.Appendice B, Figure A1.1) conforte l'hypothèse d'un effet négligeable du marquage sur la survie et d'un faible taux de perte de marque. Pour autant, les taux de survie estimés par notre étude sont certainement légèrement biaisés. En revanche, la mortalité et le taux de rétention peuvent également être dépendants des conditions (en laboratoire ou en milieu naturel) et de la zone de marquage (cavité péritonéale, intra-musculaire) (Dieterman & Hoxmeier 2009). C'est pourquoi une étude sur les effets du marquage *in situ* pourrait être conduite.

Le processus de capture ne dépendant pas des traits d'histoire de vie.

Nous n'avons pas réalisé de test formel pour vérifier l'hypothèse d'une probabilité de capture dépendante des traits d'histoire de vie (en premier lieu de la taille) mais rien dans notre protocole ne va dans le sens d'un tel effet. En effet, à l'automne, les tacons (0+ et 1+) évoluent dans une gamme de taille assez réduite ce qui limite les possibilités de probabilité de capture taille dépendante (cf. **tableau 1**). Les pièges utilisés pour la recapture des smolts sont des engins passifs à faible maillage donc a priori non sélectifs vis à vis de la taille. De plus, la gamme de taille des smolts est également assez réduite. Un exercice de validation a posteriori de notre modèle (technique de réplication de données ; Gelman et al., 2004) ne montre pas d'incohérence majeure entre les moyennes et écart-type prédites par le modèle et celles observées. Ceci conforte l'hypothèse d'indépendance du processus de capture vis à vis de la taille, tout comme l'hypothèse d'un effet négligeable du marquage sur la survie.

ANNEXE 2

Au cours des dernières années, les méthodes d'analyse de données issues de programme de marquage individuel ont fait l'objet de nombreuses études (Lebreton et al., 1992 ; Besbeas et al., 2002 ; Catchpole et al., 2004 ; Brooks et al., 2004). Les méthodes d'estimation utilisées incluent l'approche classique (fréquentiste) (Lebreton et al., 1992 ; Brooks et al., 2004a) et le paradigme bayésien (Dupuis, 1995 ; Brooks et al., 2000, 2002 ; Rivot & Prévost, 2004 ; Brooks et al., 2004a, 2004b ; Clark et al., 2005 ; Gimenez et al. 2007). L'approche Bayésienne permet de s'affranchir de certaines difficultés des méthodes fréquentistes. Elle facilite par exemple la combinaison de l'information issue de différentes sources de données dans un modèle unique et d'estimer les grandeurs d'intérêts et leurs incertitudes (Brooks et al., 2004). Une des différences vient également du fait que l'expérimentateur peut formaliser le degré de connaissance *a priori* vis-à-vis des inconnues à estimer en leur assignant une distribution de probabilité. L'analyse Bayésienne fait donc la synthèse de l'information issue des données (à travers la fonction de vraisemblance) et de l'expérimentateur (à travers la distribution *a priori* ou Prior). Ce Prior, suivant la distribution de probabilité affectée et les valeurs des paramètres, peut être alors informatif ou non informatif. Dans ce dernier cas, les données constitueront la principale source d'information (Brooks, 2003 ; Figure 9).

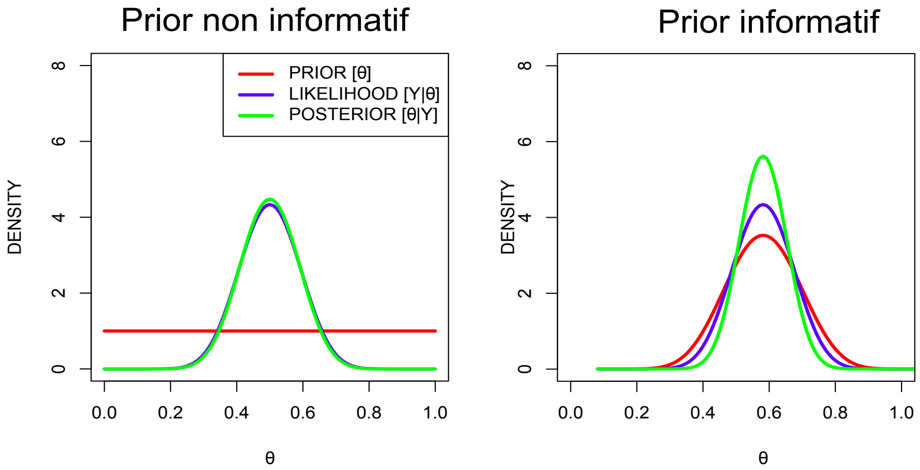

Figure 9: Distributions *a posteriori* (en vert) d'un paramètre θ (e.g. une probabilité de survie) obtenues à partir de la mise à jour du prior (en rouge ; non informatif à gauche ou informatif à droite) par la vraisemblance (en bleu). Les distributions sont issues de loi beta (succès vs. échec) définies entre 0 et 1 (cf. Figure 10).

Principe de l'inférence Bayésienne

Le cadre Bayésien assigne une distribution de probabilité à toute grandeur inconnue d'un modèle, telle que ses paramètres. La distribution de probabilité reflète le degré de crédibilité comparé des différentes valeurs. Les inférences bayésiennes sont réalisées sur la base de la distribution *a posteriori* conditionnellement aux données observées (notée $[\theta \mid Y]$) qui combine l'information apportée par les données et la connaissance *a priori* représentée sous la forme d'une distribution de probabilité*a priori* (notée $[\theta]$). L'information contenue dans les données est traduite par la vraisemblance (notée $[Y \mid \theta]$). Elle exprime le degré de crédibilité des données conditionnellement aux paramètres. La combinaison de la loi *a priori* et de la vraisemblance permet d'obtenir la distribution *a posteriori* (cf. equation 1.1) via le théorème de Bayes.

$$[\theta \mid Y] = \frac{[\theta] \times [Y \mid \theta]}{\int_{\theta} [\theta] \times [Y \mid \theta] d\theta} \tag{1}$$

Le théorème de Bayes permet donc de passer de la probabilité *a priori* d'un paramètre, le Prior, à sa nouvelle probabilité dite *a posteriori* compte-tenu des résultats d'observation (Brooks, 2003).

Choix des priors

L'approche bayésienne impose de spécifier les distributions *a priori* de toutes les grandeurs inconnues libres de notre modèle, c'est-à-dire toutes celles qui ne sont conditionnées par aucune autre grandeur. Le choix de la distribution *a priori* se fonde sur les connaissances disponibles préalablement à l'expérience. Les grandeurs libres du modèle sont principalement des probabilités auxquelles sont affectées des priors plus ou moins informatifs. Pour ce type de paramètres, un prior non informatif correspond à une loi uniforme entre 0 et 1 ou de façon équivalente une loi beta régie par deux paramètres égaux à 1 (loi Beta(1,1)). Des priors plus informatifs peuvent aussi être intégrés. Différents degrés d'information peuvent être introduits sous la forme de priors faiblement informatifs à très informatifs. Par exemple, des priors faiblement informatifs peuvent correspondre à une loi Beta(2,2) (centrée sur la valeur 0.5, cette loi donne une probabilité nulle au voisinage de 0 et de 1) ou des lois Beta(1,2) et Beta(2,1) dites « triangulaires » (ces lois donnent une probabilité maximale respectivement nulle au voisinage de 0 et au voisinage de 1) (cf. Figure 10).

Simulation de Monte Carlo par chaînes de Markov

La distribution *a posteriori* jointe des paramètres est approximée par la distribution empirique d'un échantillon obtenue par simulation de Monte Carlo par chaînes de Markov (MCMC) en utilisant l'algorithme de Gibbs. Ce dernier consiste à échantillonner successivement dans les lois condition-

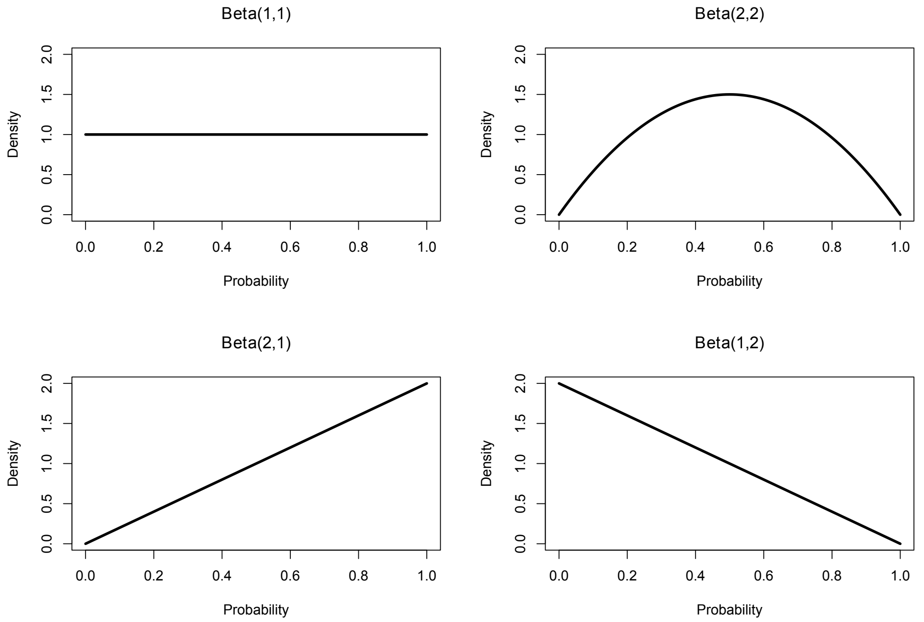

Figure 10: Distributions *a priori* de la loi beta pour différentes valeurs de paramètres : lois Beta(1,1), Beta(2,2), Beta(2,1) et Beta(1,2). Les deux paramètres de la loi beta (a,b) s'interprètent comme le poids que l'on donne aux succès (a) et aux échecs (b).

nelles pleines (unidimensionnelles) de chacune des variables étudiées. La distribution marginale d'un des paramètres peut se déduire par une intégration multidimensionnelle. Par exemple l'expression de l'intégrale du paramètre α (où $\theta = \{\alpha, \beta, \gamma, \delta\}$) est :

$$[\alpha \mid Y] = \int \int \int_{\alpha} [\alpha, \beta, \gamma, \delta \mid Y] d\beta d\gamma d\delta \tag{2}$$

Un des avantages des méthodes d'échantillonnages, tel que les algorithmes MCMC, sont qu'elles permettent de contourner le problème de la résolution analytique de ces intégrales multidimensionnelles. Sur la base d'un échantillon tiré dans la distribution jointe, le problème des intégrations multidimensionnelles n'est plus un problème. La distribution marginale d'un paramètre peut être déduite directement à partir de la distribution empirique de l'échantillon en isolant les valeurs échantillonnées par les simulations MCMC pour la grandeur d'intérêt considérée. Les simulations de MCMC génèrent un échantillon suivant un tirage aléatoire dans une distribution dépendant du point précédent (processus Markovien). Sous certaine conditions, vérifiées dans le cas de l'algorithme de Gibbs, la simulation par MCMC assure la convergence des chaînes simulées vers la distribution « cible » c'est-à-dire la distribution *a posteriori* quand le nombre de pas de simulation tend vers l'infini. Dans la pratique nous devons donc vérifier la convergence des chaînes simulées pour s'assurer que notre échantillon MCMC est bien représentatif de la loi *a posteriori*. Il n'est cependant pas possible de montrer en pratique l'existence d'une convergence mais il est possible de montrer que rien ne s'y oppose. La stationnarité intra-chaînes et le mélange inter-chaînes constituent des conditions nécessaires à la convergence (Gelman & Meng, 1995 ; Spiegelhalter et al., 2005). Les trajectoires des chaînes ne doivent pas présenter une tendance d'évolution en moyenne, la variabilité intra-chaînes doit se stabiliser au cours du temps et différentes chaînes ayant des points initiaux distincts doivent donner les mêmes résultats (atteindre la distribution cible). Le test de convergence de Brooks, Gelman et Rubin (Brooks & Gelman, 1998) nécessite 3 chaînes (au moins) de Markov. Le mélange inter-chaînes est analysé par la statistique de Gelman-Rubin basé sur le ratio R (« estimated potential scale reduction ») de la variabilité (normalisée) inter-chaînes sur la variabilité (normalisée) moyenne intra-chaînes. Le calcul de la variabilité est réalisé sur la base d'une largeur d'intervalle de variation de 80%. Le mélange est considéré satisfaisant lorsque R tend vers 1.

Validation a posteriori

Une analyse bayésienne complète doit rechercher les aspects de la réalité qui ne seraient pas restitué par notre modèle et pouvant conduire à des interprétations erronés. Elle doit comporter un test d'adéquation du modèle avec les données ("posterior predictive check") et une investigation de l'influence du choix des priors sur les distributions *a posteriori* (analyse de sensibilité) (Gelman et al., 2004). Le principe du test d'adéquation réside dans la simulation de données répliquées sur la base du modèle et les distributions *a posteriori* jointe des grandeurs estimées (Gelman et al., 1995, 2004 ; équation 2). Le test consiste alors à déterminer les distributions *a posteriori* prédictives des données répliquées et de comparer l'échantillon résultant avec nos données observées. Si le réplica ne correspond pas aux données observées, cela indique que le modèle, sous les hypothèses introduites, ne restitue pas certains aspects de la réalité.

$$[Y^{rep} \mid Y] = \int_{\theta} [Y^{rep} \mid \theta] \times [\theta \mid Y] d\theta \tag{3}$$

La question primordiale dans une analyse de sensibilité est de savoir comment (et de combien) fluctue les distributions *a posteriori* si l'on spécifie des priors différents au modèle de référence. Le principe est de tester un (ou plusieurs) modèle alternatif, différant uniquement dans la spécification des priors, et de comparer les distributions *a posteriori* des grandeurs d'intérêts résultantes avec le modèle de référence. Dans notre cas, nous avons comparé les distributions *a posteriori* du modèle incluant des priors faiblement informatifs tel que discuté précédemment, et avec des priors non informatifs plus standards.

ANNEXE 3

Normes de réaction pour la smoltification et la maturation

Cette annexe présente des résultats complémentaires portant sur l'analyse des cohortes successives suivies de saumon atlantique sur le Scorff et leurs interprétations. Elle constitue un prolongement du **chapitre 2**.

Dans ce travail, nous avons mis clairement en évidence une norme de réaction probabiliste taille-dépendante pour la smoltification : les plus grands individus ont une plus grande probabilité de smoltifier (cf. Figure 11). Cette mise en évidence est à notre connaissance le premier cas d'application du cadre théorique des normes de réaction probabilistes (Heino et al., 2002) à la smoltification chez le saumon atlantique, qui plus est en conditions naturelles. Pour autant, la nature taille-dépendante de cette norme de réaction a déjà été révélée par de nombreuses études (Fängstam et al., 1993 ; Baglinière et al., 1993 ; Jonsson et Jonsson, 1998). Elle serait le reflet de deux trajectoires d'histoire de vie engagées dès le printemps/été de la première année de vie en eau douce. Le choix de smoltification serait alors conditionné par les conditions de croissance entre le printemps et l'automne de l'année précédant la migration ainsi que par les réserves énergétiques disponibles (Duston et Saunders, 1997 ; Thorpe et al., 1998 ; Metcalfe, 1998 ; Jonsson & Jonsson, 2005). La taille à l'automne précédent la migration pourrait alors être vue comme un élément révélateur du choix de smoltification plutôt que véritablement comme l'élément déclencheur (Jonsson & Jonsson, 2005 ; Zabel et al. 2005). Le conditionnement de la smoltification par la croissance est généralement expliqué par un coût taille-dépendant. Le taux de mortalité au cours de la transition entre la rivière et le milieu marin, en liaison avec l'osmorégulation et la prédation, est plus élevé pour les plus petits individus (Økland et al., 1993 ; Duston & Saunders, 1997 ; Thorpe & Metcalfe, 1998).

Le cadre conceptuel des normes de réactions probabilistes utilisé dans l'article 3 n'a pu être appliqué à la décision de maturation car, sur le Scorff, trop peu de tacons 0+ maturent la première année (cf. **chapitre 1**, **tableau 1**). La proportion de maturants la deuxième année est beaucoup plus importante mais nous ne disposons que d'une information partielle concernant le statut individuel pour les tacons 1+ capturés et marqués au stade 0+. Nous avons les statuts individuels (taille et poids) pour les tacons 1+ capturés à l'automne mais non marqués au stade 0+. En revanche, nous ne pouvons distinguer les mâles et femelles alors que seuls les mâles peuvent maturer en eau douce. Nos inférences sur la probabilité de maturation poids-dépendante peuvent donc être biaisées puisque les femelles, quelque soit leur poids, ne matureront pas en rivière.

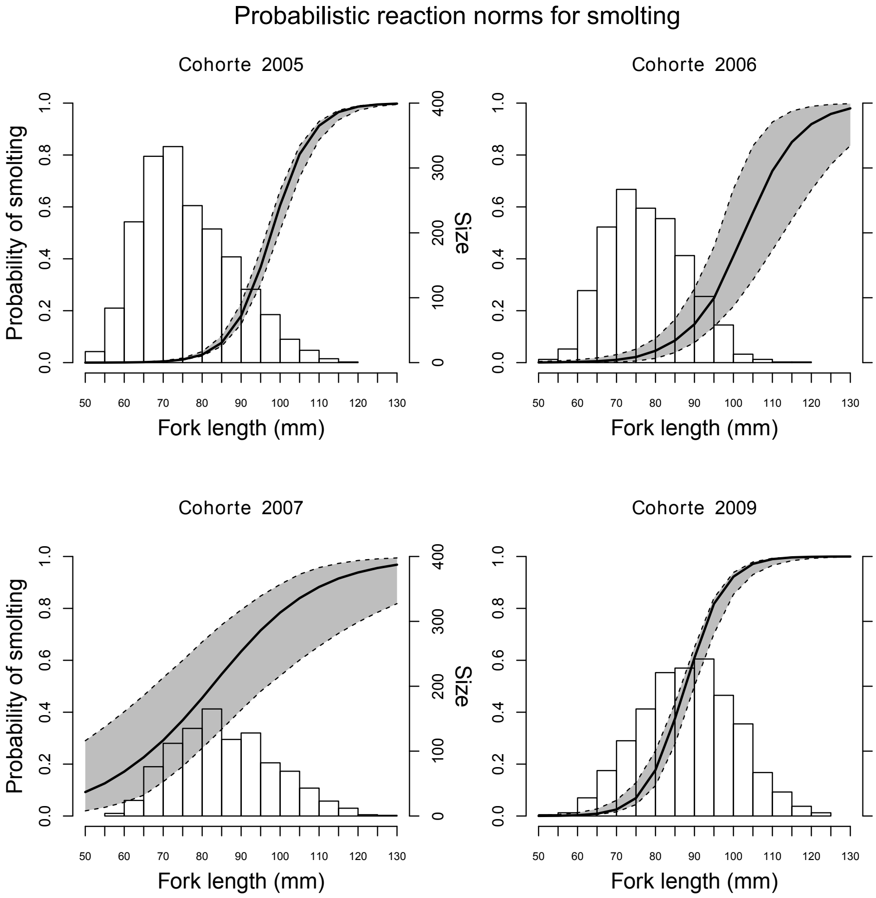

Figure 11: Normes de réaction probabiliste taille-dépendante pour la smoltification à l'âge de 1 an pour les 4 cohortes suivies. Les distributions en taille des tacons 0+ sont représentées en noire (histogramme). La courbe pleine indique la médiane de la distribution a posteriori de la probabilité de smoltifier pour une taille donnée. Les courbes pointillées indiquent l'intervalle de crédibilité à 95%.

Modélisation des décisions de migration comme une stratégie conditionnelle.

En développant un cadre statistique plus approprié pour analyser les données d'observation, nous avons voulu représenter explicitement le mécanisme qui engendre les décisions d'histoires de vie. Ainsi, le modèle LETM permet d'accéder aux paramètres d'intérêt que sont les seuils, les statuts proximaux et l'héritabilité des stratégies conditionnelles. L'application du LETM au cas du saumon atlantique est conforme aux idées développées par Thorpe et al. (1998), Hutchings (2004) et Mangel & Satterwaithe (2008) qui suggèrent que maturation et migration sont contrôlées par un mécanisme à seuil. Nous avons appliqué ce modèle aux décisions de migration dés la première année de vie pour les juvéniles de saumon atlantique pour 4 cohortes suivies. Nous avons fait l'hypothèse que tous les individus localisés sur une station appartenaient à la même fratrie (différentes structure génétique ou d'apparentement ont été évaluées dans l'Appendice 2). Les moyennes et écart-types des seuils sont relativement proches (cf. Figure 12). En revanche, on observe une forte incertitude dans le cas de la distribution a posteriori de l'héritabilité malgré une bonne mise à jour du prior (distribution uniforme entre 0 et 1, cf. Appendice 2) dans le cas des cohortes 2006 et 2009 (cohortes pour lesquelles les données sont les plus importantes).

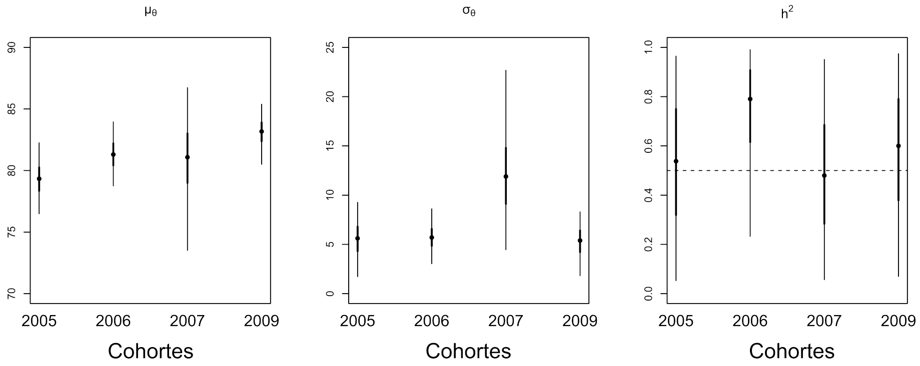

Figure 12: Distributions *a posteriori* pour les paramètres d'intérêt du LETM (moyennes μ_θ et écart-types σ_θ des seuils et héritabilités h^2) pour la décision de migration à l'âge de 1 an pour les 4 cohortes suivies. Les points noirs indiquent la médiane et les traits pleins indiquent l'intervalle de crédibilité à 95% (traits fins) et à 50% (trait plein gras).

ANNEXE 4

Une mortalité sélective taille-dépendante ?

De nombreux travaux ont montré une mortalité sélective taille-dépendante chez les juvéniles de salmonidés en eau douce (Meekan et al., 1998 ; Hutchings et al., 1999 ; Letcher et al., 2002 ; Johnston et al., 2005). Les futurs smolts 1+ appartiennent à la gamme supérieure de distribution en taille au stade tacons 0+. Dans des modèles alternatifs, nous avons testé l'hypothèse d'un conditionnement de la survie par la taille au stade tacon 0+, que ce soit par un effet global indépendamment du choix de smoltification ou par des effets distincts en fonction du statut des individus (futurs tacons 1+ vs. futurs smolts 1+). Les estimations textita posteriori de ces effets de la taille se sont révélées largement distribuées de part et d'autre de la valeur nulle (cf. Figure 13). L'avantage de survie en faveur des futurs smolts 1+ n'est donc pas le résultat d'une confusion avec une survie hivernale des tacons 0+ taille dépendante.

Ces résultats sont en accord avec certaines études qui n'ont pas clairement démontré que la taille influençait le taux de survie hivernale des juvéniles de salmonidés (Zabel & Achord, 2004 ; Zabel et al., 2005). Nous notons néanmoins un faible effet négatif de la taille sur la survie hivernale pour les futurs tacons 1+ (i.e. les résidents, cf. Figure 14). Les plus petits tacons 0+ auraient une meilleure survie que les plus grands.

Une survie hivernale dépendante du choix de smoltification ?

Dès le printemps et l'été de la première année de vie, les futurs smolts 1+ et les futurs tacons 1+ sont engagés dans des voies de développement bien distinctes (Metclafe, 1998) avec des stratégies d'allocation des ressources différentes (Morgan, 2002). Les futurs smolts 1+ ont tout intérêt à maintenir une croissance durant l'hiver si l'on considère l'existence d'une survie en mer dépendante de la taille des individus à la smoltification (Økland et al., 1993 ; Thorpe & Metcalfe, 1998 ; Thériault & Dodson, 2003). En outre, la smoltification est un processus coûteux en énergie qui exige un rendement métabolique élevé et une acquisition importante en ressources (Metcalfe & Thorpe 1992 ; Metcalfe et al. 1995). Huntingford (1992) a montré en milieu contrôlé que les futurs smolts (smolts 2+ dans son cas) avaient une croissance plus forte durant l'hiver comparée aux résidents. Les futurs

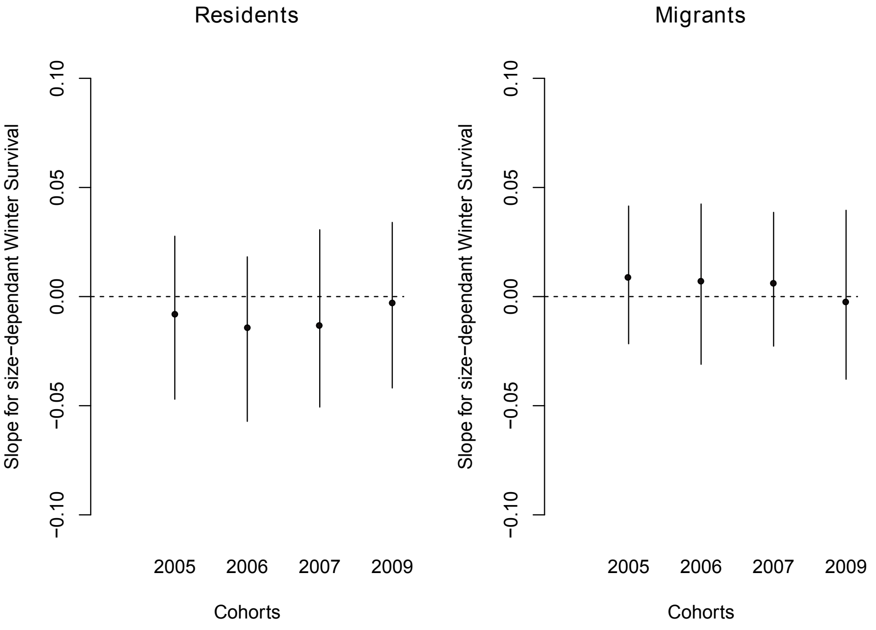

Figure 13: Distributions *a posteriori* des pentes pour la survie hivernale taille-dépendante de la première année de vie pour les résidents (futurs tacons 1+) et les migrants (futurs smolts 1+) pour les quatre cohortes suivies. La valeur médiane est représentée par un point. Les segments représentent l'intervalle de crédibilité à 95%.

smolts montrent un comportement agonistique (agressifs et dominants) vis-à-vis des individus ayant choisis de rester une année supplémentaire en eau douce, ce qui leur permet d'accéder aux sites les plus favorables pour l'acquisition de ressources trophiques (Hardwood et al., 2003), et en retour leur confère un haut rendement métabolique et un taux de croissance élevé (Nicieza & Metcalfe, 1999 ; Cutts et al., 1999 ; Finstad et al., 2007). Cependant, le maintien d'une forte croissance durant l'hiver peut engendrer des coûts pour les futurs smolts (Nicieza & Metcalfe, 1999 ; Vollestad & Quinn, 2003) notamment au niveau énergétique à travers une activité plus intense pour acquérir les ressources en nourriture (Enders et al., 2005) et par une exposition plus élevée au risque de prédation (Nicieza & Metcalfe, 1999). Les bénéfices d'une croissance continue pourraient alors être contrebalancés par le coût pour l'acquisition des ressources (Girard et al., 2005). Il existerait ainsi un compromis entre le maintien d'une forte croissance et les coûts associés (Martin-Smith & Armstrong, 2002).

Par ailleurs, les individus appelés à résider un année supplémentaire en eau douce ont un niveau d'activité réduit en hiver et adoptent un comportement cryptique (Thorpe et al., 1992 ; Metcalfe, 1998 ; Metcalfe et al., 1999). Par ce biais, ils tentent de maximiser leur survie hivernale en (i) minimisant le risque de prédation (Valdimarsson & Metcalfe, 1998) et (ii) en évitant de puiser dans leurs réserves énergétiques (Whalen & Parrish, 1999 ; Parrish et al., 2004 ; Millidine et al., 2006), alors que la sévérité des conditions hivernales conduit à une limitation des ressources trophiques disponibles et que la déplétion des réserves énergétiques est une cause de mortalité en hiver (Hutchings et al., 1999 ; Olsen & Vollestad, 2001a ; Finstad et al., 2004 ; Naesje et al., 2006). Ces bénéfices contrebalanceraient le coût lié à leur acquisition très réduite de ressources trophiques (Metcalfe & Thorpe, 1992 ; Metcalfe et al., 1999).

Variabilité inter-cohortes pour les compromis ?

Nos résultats montrent que le bilan des compromis propres à chacune des deux options d'histoire de vie choisies par les tacons 0+ automnaux reste favorable en matière de survie hivernale aux futurs smolts 1+ par rapport à leurs congénères futurs tacons 1+ pour les cohortes 2005 et 2006 (cf. Figure 15). En revanche, nos résultats n'indiquent pas de différentiel de survie entre les futurs smolts 1+ et les futurs tacons 1+ pour les cohortes 2007 et 2009. Les futurs tacons 1+ montrent des probabilités de survie hivernale plus élevées pour les cohortes 2007 et 2009 (0.52 [0.29 ; 0.84] et 0.38 [0.08 ; 0.79] respectivement) que les cohortes 2005 et 2006 (0.24 [0.06 ; 0.36] et 0.15 [0.02 ; 0.38] respectivement). Cela pourrait être expliqué par des conditions environnementales plus favorables que pour les deux premières cohortes suivies conduisant par exemple à de meilleures conditions individuelles avant l'hiver et/ou des conditions hivernales moins sévères.

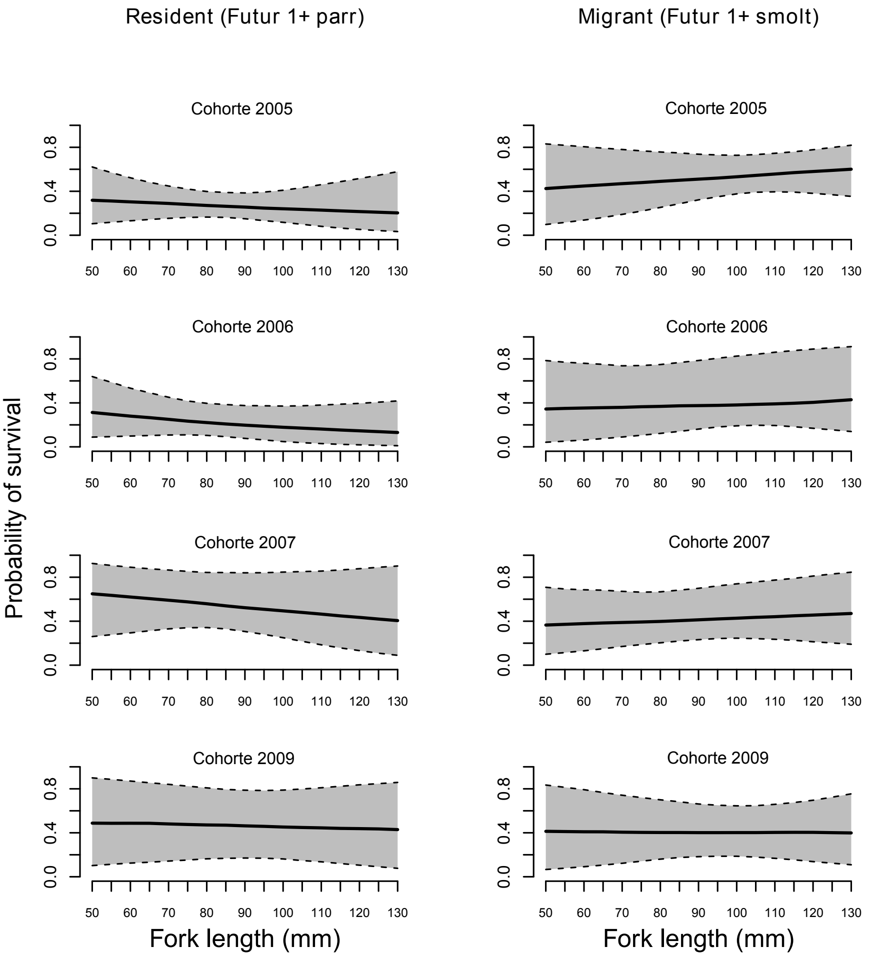

Figure 14: Survie hivernale taille-dépendante lors de la première année de vie pour les résidents (futurs tacons 1+) et les migrants (futurs smolts 1+) pour les quatre cohortes suivies. La courbe en trait plein indique la médiane de la distribution *a posteriori* de la probabilité de survie pour une taille donnée. Les courbes en tirets indiquent l'intervalle de confiance à 95%.

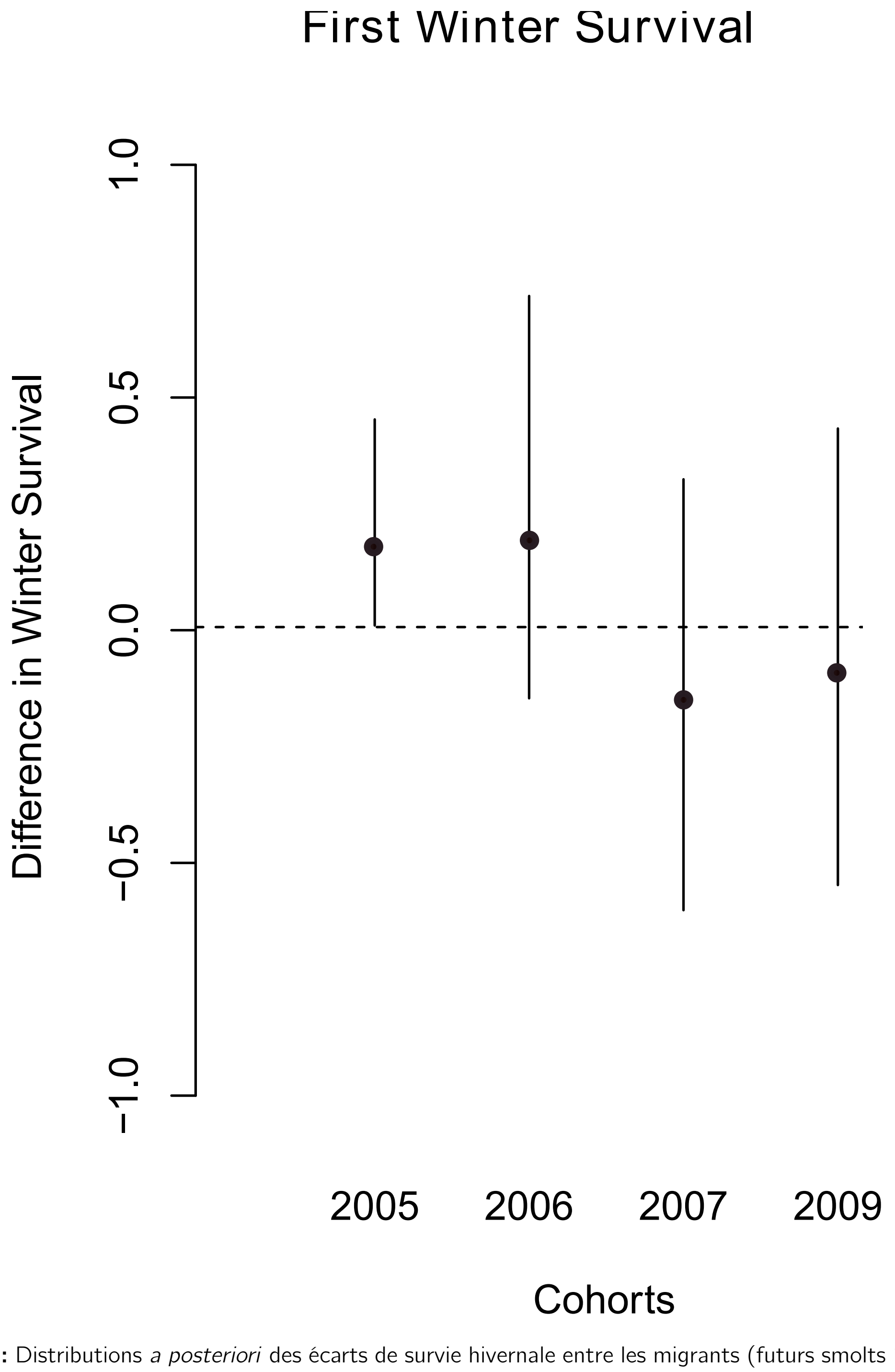

Figure 15: Distributions *a posteriori* des écarts de survie hivernale entre les migrants (futurs smolts 1+) et les résidents (futurs tacons 1+) pour les quatre cohortes suivies. La valeur médiane est représentée par un point. Les segments représentent l'intervalle de crédibilité à 95%.

ANNEXE 5

Étude du déterminisme génétique des traits d'histoire de vie chez le saumon atlantique par approche de génétique quantitative

Mise en place d'un programme de suivi génétique à long-terme d'une population de Saumon Atlantique (Salmo salar) sur le Scorff

Collaborations :

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Questions scientifiques

Le suivi à long terme d'une population permet d'étudier son évolution démographique sous l'effet de l'hétérogénéité temporelle de son environnement. En adoptant une approche phénotypique et génétique (par un suivi individuel), il nous permet d'améliorer notre compréhension de son fonctionnement et de déterminer :(1) Quels sont les rôles des facteurs écologiques et génétiques dans la structuration des populations ? (2) Quels sont les rôles de la plasticité phénotypique et des traits d'histoire de vie dans l'adaptation et le maintien des populations ?

- Comment les populations naturelles font-elles face aux changements de leur environnement ? La survie d'une population dépend de sa capacité d'adaptation. S'adapter permet l'utilisation du nouvel environnement. Il existe deux façons de s'adapter :
  • en maintenant la capacité des organismes à modifier leurs caractères phénotypiques (physiologiques, comportementaux et traits d'histoire de vie) en fonction des conditions environnementales ce qui permet une adaptation à court terme (au temps écologique) (Nussey et al., 2007). C'est la plasticité phénotypique ;
  • et/ou en opérant des changements évolutifs profonds par une adaptation génétique (en fixant les caractères optimaux) ce qui permet de répondre à la sélection naturelle au temps évolutif.

- La plasticité est-elle un caractère en tant que tel ? A-t-elle son propre déterminisme génétique ? Lorsque l'environnement est variable et prévisible et que la plasticité apporte un avantage en termes de valeur sélective (capacité d'un individu d'un certain génotype à se reproduire), la sélection naturelle devrait favoriser la plasticité. Elle est alors dite adaptative. Dans ce cas, la plasticité doit avoir une base génétique pour être maintenue et transmise aux générations suivantes.

- Pourquoi connaître la base génétique de ces caractères est-il important ? Déterminer la base génétique des caractères nous renseigne sur leurs potentiels évolutifs. Ainsi, combiner des connaissances sur le déterminisme génétique des caractères (i.e., la base de la génétique quantitative) avec une étude de la sélection qui s'opère sur ces traits permet de prédire leur réponse à la sélection naturelle. Comment ces traits sont-ils maintenus ? Comment évoluent-ils en réponse à la sélection naturelle ? In fine, une meilleure compréhension de ces traits permet de mieux appréhender la réponse de la population aux changements de leur environnement et donc son potentiel adaptatif.

Description du projet

Dans un contexte d'environnement changeant, comprendre comment les populations peuvent répondre à ces changements dans une échelle de temps écologique et évolutive et identifier les mécanismes évolutifs en jeu constituent des enjeux majeurs. La capacité adaptative d'une population est favorisée par la variabilité des traits phénotypiques (physiologie, comportements et traits d'histoire de vie) et permettent une réponse évolutive à la sélection naturelle. Mais comment cette variabilité est-elle maintenue ? Comment prédire la réponse à la sélection ?

La réponse à la sélection d'un trait considéré est déterminée par sa variabilité génétique, son expression (i.e. la variabilité phénotypique en interaction avec l'environnement) et l'intensité de la sélection. Tandis que l'expression différentielle d'un caractère (i.e., la plasticité) permet une réponse adaptative au temps écologique, sa base génétique permet une réponse évolutive. Pour comprendre et prédire ces changements évolutifs et les conséquences démographiques sur la population, il est donc nécessaire d'identifier (1) l'intensité de la sélection qui agit sur la distribution des phénotypes et

(2) l'héritabilité génétique afin que ces changements soient transmis aux générations suivantes. En d'autres termes, le suivi démographique permet l'analyse des pressions de sélection sur les traits tandis que la génétique quantitative analyse la part génétique de la variabilité phénotypique qui renseigne sur le potentiel évolutif d'un trait face à la sélection (Stearns 1992). La génétique quantitative permet ainsi de comprendre comment les traits d'histoire de vie peuvent répondre à la sélection.

L'analyse de la variabilité phénotypique dans la population et sa composante génétique requiert (1) une mesure quantitative de la variabilité phénotypique et (2) une analyse de la covariance phénotypique entre individus apparentés donnant une indication de la base génétique d'un trait i.e. la variance génétique du trait. Leurs estimations en milieu naturel soulèvent de nombreuses difficultés. La première réside dans le fait que le suivi exhaustif au cours du temps de toute la population n'est pas réalisable. La seconde est que la relation d'apparentement entre individus (i.e., le pedigree) doit être connue. Cela nécessite d'une part l'acquisition de données (via prélèvements génétiques) et d'autre part leurs analyses en laboratoire afin de reconstituer ce pedigree.

Les suivis à long terme de populations naturelles permettent ainsi de mesurer la variabilité phénotypique de la population et d'appliquer la génétique quantitative à l'étude de la réponse évolutive de la population à la sélection en milieu naturel (pour revue, Hill 2010 ; Kruuk & Hill 2008 ; Pemberton 2008). A ce jour, ce type de suivi et d'acquisition de données génétique est encore relativement rare surtout en ce qui concerne les poissons (Kruuk & Hill 2008). Enfin, les progrès constant de la génétique moléculaire permettent une reconstruction de plus en plus précise du pedigree grâce à l'utilisation de marqueurs microsatellites. L'acquisition du pedigree nous permet alors d'estimer la variabilité génétique d'un trait considéré dans la population (sa base génétique) et en déduire l'héritabilité de ce dernier (sa capacité à être transmis aux générations suivantes). L'héritabilité constitue une mesure des contributions relatives des gènes et de l'environnement à la variation phénotypique.

Contexte

Du fait de la complexité et de la diversité des histoires de vie qu'il exprime, le saumon atlantique (Salmo salar) constitue un modèle biologique pertinent pour l'étude du déterminisme de la plasticité phénotypique et des traits d'histoire de vie. Espèce anadrome et philopatrique (Gueguen & Prouzet 1994), son cycle de vie se sépare entre l'eau douce (phase dulçaquicole), où se déroulent la reproduction et l'élevage de jeunes, et l'océan, où les individus entreprennent des migrations de grande amplitude (plusieurs milliers de kilomètres) vers les aires de croissance maritimes. En Bretagne, la reproduction a lieu au mois de décembre et les jeunes de l'année émergent des graviers des sites de reproduction au début du printemps suivant. Dès leur première année de vie en eau douce, les juvéniles alors appelés tacons (stade tacons 0+), doivent opter entre différentes tactiques alternatives d'histoire de vie : maturation sexuelle précoce (pour les mâles uniquement), migration vers la mer au printemps suivant (stade smolt 1+) ou résider une année supplémentaire en eau douce (stade tacon 1+). Pour les mâles restant en eau douce, un second choix est à faire entre la maturation sexuelle précoce ou rester immature lors de leur seconde année de vie en eau douce (au stade tacon 1+). Qu'ils aient pu se reproduire préalablement ou non, les individus survivants à l'âge de deux ans migrent tous (à quelque rares exceptions près) vers la mer au printemps (stade smolt 2+ pour « plus de deux ans »).

Maturation précoce et migration ne sont donc pas des tactiques mutuellement exclusives. Quel que soit l'âge, la migration vers la mer s'accompagne d'une transformation physiologique et comportementale que l'on appelle la smoltification. Le processus de smoltification prépare les individus à un changement de milieu et une adaptation au milieu marin (en particulier à travers l'osmorégulation) (Duston & Saunders 1997 ; Thorpe et al. 1998 ; Thorpe & Metcalfe 1998).

Le retour des adultes dans leur rivière natale intervient l'année suivant leur migration vers la mer ou l'année d'après. Le séjour en mer permet un accroissement de taille important, ce qui procure un avantage en termes de succès reproducteur (notamment en ce qui concerne les femelles dont la production d'œufs est étroitement liée à la taille (Fleming, 1996, 1998). Cependant, l'anadromie engendre un coût de migration en termes de survie (forte mortalité en mer) et une mortalité post-reproduction accrue. La résidence en eau douce conduirait à un succès reproducteur nettement inférieur à celui des anadromes mais bénéficie de taux de survie bien supérieurs à celui des anadromes. En particulier, la mortalité post-reproduction est proche de 100% pour les individus anadromes alors qu'elle est notablement plus faible pour les mâles atteignant la maturité en tant que tacon.

La croissance, par l'accumulation de réserves énergétiques, joue un rôle majeur pour le choix entre les différentes options d'histoire de vie (Hutchings & Jones 1998 ; Prevost et al. 1992 ; Thorpe et al. 1998) et la survie (Johnston et al. 2005). Selon le cadre conceptuel proposé par Thorpe et al. (1998) et Mangel & Satterthwaite (2008), les « décisions » entre les différentes tactiques d'histoire de vie (maturation précoce et migration) dépendent de l'énergie accumulée par l'individu et de l'énergie nécessaire aux processus de maturation et smoltification. Il existerait donc des valeurs seuils (énergétique) à atteindre à des périodes bien précises (« fenêtres de décision ») pour déclencher ces processus. Ces valeurs seuils seraient individuelles et auraient une base génétique c'est-à-dire qu'elles seraient héritables. Ainsi, pour faire face aux changements de milieu, le saumon atlantique s'appuie sur une plasticité phénotypique favorisant son adaptation au nouvel environnement et conduisant à une diversité de tactiques alternatives d'histoire de vie. La mise en évidence du potentiel adaptatif du saumon atlantique en milieu naturel nécessite de ce fait (1) d'évaluer la plasticité des traits phénotypiques observés (traits morphologiques et traits d'histoire de vie) et (2) de connaître le déterminisme génétique de ces caractères.

Les questions biologiques que l'on souhaite aborder sont :

– Les caractères tels que la maturation sexuelle précoce, la migration (âge à la migration et temps de séjour en rivière/mer) ou la croissance sont-ils déterminés génétiquement et transmissibles (héritables) ?
– Ces caractères sont-ils plastiques et si oui, cette plasticité est-elle héritable ?
– L'héritabilité de ces caractères fluctue-t-elle en fonction des conditions environnementales ? dans le temps ?

Un travail sur l'analyse de la structure de conditionnement des stratégies d'histoire de vie du saumon atlantique à partir de données de capture-marquage-recapture (CMR) a été entrepris sur le Scorff (ORE PFC) dans le cadre d'une collaboration avec l'U3E (Inra Rennes), UMR Ecobiop (Inra St Pée s/ Nivelle) et le CEFE (UMR CNRS). Ce suivi individuel par CMR permet d'observer et d'étudier les variations phénotypiques dans la population. Coupler ces données de capture-marquage-recapture (CMR) avec les relations d'apparentement entre les individus marqués à travers les méthodes récentes en génétique et en dynamique des populations, permettra d'étudier les bases génétiques des traits d'histoires de vies et de mieux appréhender la réponse de la population aux changements de leur environnement. Cela nécessite la mise en place d'un programme de suivi génétique à long terme en parallèle au programme CMR sur la population de saumon du Scorff et l'analyse de ces données par les méthodes de génétique moléculaire (permettant de reconstituer le pedigree à partir de leur ADN grâce aux marqueurs microsatellites) et par approche de génétique quantitative (estimation de l'héritabilité des caractères).

In fine, l'ambition de ce projet est la mise à jour des relations entre génotype, phénotype et démographie chez le saumon atlantique en condition naturelle et d'étudier l'évolution temporelle et spatiale de la diversité génétique et des traits phénotypiques en lien avec la valeur sélective.

Autres perspectives

Étudier les décisions d'histoire de vie sexe-dépendantes

Il apparaît nécessaire de tenir compte explicitement du sexe dans le processus dynamique d'histoire de vie chez le saumon atlantique, et ce dès la phase juvénile (le stade tacons 0+). En effet, les tacons femelles matures sont très rarement observées (Bagliniere & Maisse, 1985). On peut donc considérer que pour elles, l'accès à la reproduction est peu probable en restant en eau douce d'autant que leur valeur sélective (mesurée par la production et la taille des oeufs) est étroitement liée à leur taille (Fleming & Gross, 1990). Considérant le fait que les femelles doivent obligatoirement migrer en mer pour atteindre la maturité sexuelle (peu d'observations de femelles tacons matures) et en tenant compte des coûts en termes de survie de la phase eau douce, nous prédisons un fort gradient de sélection pour une croissance en eau douce rapide dés la première année de vie pour les femelles (les contraintes et les coûts liés à cette croissance restent à être identifier). Une sélection dans la même direction doit opérer chez les mâles mais ces derniers ont la possibilité de se reproduire en eau douce sans migration (maturation sexuelle précoce). Le gradient de sélection pour la migration dés la première année de vie devrait donc être moins fort pour les mâles que pour les femelles. Pour vérifier ces hypothèses et étudier les décisions de tactiques d'histoire de vie sexe-dépendantes, il est donc nécessaire de déterminer le sexe des individus. Or, pour le moment nous ne pouvons connaître le sexe des individus que par observation direct dans le cas où ceux-ci sont maturants (les mâles uniquement), sont capturés au stade adulte ou bien lorsqu'ils sont morts (observation des gonades). Le contrôle moléculaire du déterminisme du sexe et de la différenciation sexuel chez les poissons est encore peu connu (pour revue, Volff et al. 2007). Afin de mieux comprendre la base moléculaire et évolutive de la variabilité du déterminisme du sexe chez les poissons, il est nécessaire d'identifier les gènes contrôlant le dimorphisme sexuel. La mise en évidence d'un tel déterminisme permettrait vraisemblablement à terme l'identification précoce du sexe des individus par analyse des échantillons génétique prélevés.

Étudier la contribution relative des tacons mâles sur la taille efficace de la population

Le programme de suivi génétique permettrait d'étudier la relation entre la taille de la population et la contribution des tacons mâles sur la taille efficace. Pour cela l'estimation du succès reproducteur individuel est nécessaire ainsi que la variance de ce succès. L'échantillonnage des individus reproducteurs étant partiel, il est nécessaire de résoudre le problème d'estimation de la taille efficace à partir de données manquantes (suivi non exhaustif).

Procédure d'échantillonnage

L'objectif est d'identifier les géniteurs et leur descendance. Pour cela, nous devons réaliser un prélèvement génétique (un morceau de nageoire pelvienne) systématique sur :

1. les géniteurs potentiels :
   a. l'ensemble des adultes anadromes de l'année t ;
   b. les tacons spermiants de l'année t ;

2. et sur les descendants potentiels :
   a. les tacons 0+ de l'année suivante (année t+1) ;
   b. les tacons 1+ de l'année d'après (année t+2) ;
   c. les tacons 2+ de l'année d'après (année t+3).

En ce qui concerne les adultes anadromes, les prélèvements seront effectués lors de leur capture au moment de la montaison (capture au Moulin des princes) et lors des captures hivernales sur les frayères. Tandis que les prélèvements sur les tacons seront effectués lors des pêches automnales (en parallèle à la campagne de marquage par PIT-tag).

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[3] **Buoro M.**, Prévost E. & O. Gimenez. Investigating Evolutionary Trade-Offs in Wild Populations of Atlantic Salmon (*Salmo Salar*) : Incorporating Detection Probabilities and Individual Heterogeneity. *Evolution*, 64-9 : 2629–2642, 2010.

[4]**Buoro M.**, Gimenez O. & E. Prévost. Explicit modelling of proximate mechanisms for revealing life-history trade-offs in wild conditions. En préparation.

[5] Papaix J., Cubaynes S.,**Buoro M.**, Charmantier A., Perret P. & O. Gimenez. Combining capture recapture data and pedigree information to assess heritability of demographic parameters in the wild. *Journal of Evolutionary Biology*, 23(10) :2176-84, 2010

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Article 1

Why using complex hierarchical models to investigate evolutionary processes in the wild ?

Mathieu Buoro, Etienne Prévost et Olivier Gimenez

Soumis à *Methods in Ecology and Evolution* (Octobre 2011)

SUMMARY

1. The growing interest for studying questions in the wild requires acknowledging that eco-evolutionary processes are complex, hierarchically structured and often observed partially or with measurement error. These issues have long been ignored in evolutionary biology, which might have led to flawed inference when addressing evolutionary questions.

2. Hierarchical modelling (HM) has been proposed as a generic statistical framework to deal with complexity in ecological data and account for uncertainty. HMs allows the translation of complicated models in terms of simple components by distinguishing 3 levels: observations at hand, underlying processes of interest and parameters governing these processes. However, to date, HM has seldom been used to investigate evolutionary mechanisms possibly underlying observed patterns. Here, we contend the HM approach offers a relevant approach for the study of eco-evolutionary processes in the wild by confronting formal theories to empirical data through proper statistical inference.

3. Studying eco-evolutionary processes requires considering the complete and often complex life histories of organisms. We show how this can be achieved by combining sequentially all life histories components and all available sources of information through HM. We demonstrate how eco-evolutionary processes would have been poorly inferred or even missed without using the full potential of HM. As a case study, we used the Atlantic salmon and data on wild marked juveniles. We assessed a reaction norm for migration and two potential trade-offs (selective survival according to migration decision and a survival cost of reproduction).

4. We discuss wider implications of HM in ecology and evolution as well as its advances and constraints. HM has a great potential to address evolutionary questions and investigate important process that could not previously be assessed in laboratory or short time-scale studies.

Key-words: Atlantic salmon; Bayesian modelling; Evolutionary processes; Hierarchical modelling

INTRODUCTION

Investigation of eco-evolutionary processes is challenging due to their complex nature, their interactions as well as the difficulty in collecting relevant data in the wild. In particular, life histories are complex combinations of various eco-evolutionary processes. Addressing the interplay between life-history traits and associated plasticity remains crucial to understand the evolution of life histories, how their variations influence population dynamics (Roff 1992; Proaktor et al. 2008), and to assess the ability of individuals to adapt to environmental change (Stearns 1992; Clutton-Brock 1998; Roff et al. 2006).

Theoretical and manipulative approaches have provided useful information about, e.g., state-dependent life history decisions, reaction norms and evolutionary trade-offs. However, the patterns highlighted in such studies constitute ‘potential’ evolutionary processes. Working in a controlled environment or isolating part of the process (e.g. life history stage) does not capture interactions between ecological and evolutionary processes themselves (Stearns 1992). Evolutionary studies in the wild are necessary to reveal processes occurring in natural conditions that cannot be easily mimicked in laboratory conditions. However, individual lifetime fitness components need to be assessed through continual monitoring of individuals from birth to death, which raises methodological issues, especially in wild animals.

First, the exhaustive monitoring of individuals over time is almost impossible in the wild. The observation of an individual is often a random process, with a probability of detection less than 1 (i.e., the probability to observe an individual that is alive and present in the study area). Consequently, life histories and traits are only partially observed: if an individual goes undetected, is it dead or alive? If alive, is it breeding or not? This issue of uncertain detection has long been ignored in evolutionary biology (Clobert 1995; Cam 2009; Conroy 2009), which might have led to flawed inference when addressing evolutionary questions (Gimenez et al. 2008; Hadfield 2008; Nakagawa & Freckleton 2008). Second, uncertainty in the observation process may be irreducible when some individual traits cannot be fully observed (e.g., reproductive state) or precisely measured (e.g., size; Catchpole et al. 2008; Hadfield 2008; King et al. 2008). Hence, field data provide only a noisy or partial measure of the underlying eco-evolutionary processes.

Sound statistical methods, dealing with complex phenomena and uncertainty, are thus needed for addressing eco-evolutionary questions. Hierarchical modelling (HM) has been increasingly recognized as a powerful approach for analysing complex biological phenomena (Clark et al. 2005; Royle & Dorazio 2008; Cressie et al. 2009; Link & Barker 2010; Kéry &

Schaub 2011). In HM, complicated models can be decomposed into simpler components, some of which representing the underlying processes of ultimate interest and others generating the observed data. On one hand, explicit modelling of the observation process allows accommodating uncertainties in the data collection and dealing with multiple sources of data. On the other hand, HM offers a clear distinction between the biological processes and their observation, hence a focus on the questions of interest.

There has been growing interest in the HM approach for ecological studies (Fig. 1), e.g., to estimate abundance and assess spatio-temporal variation in species distribution (Dauphin et al. 2010; Brun et al. 2011; Mordecai et al. 2011). However, despite the flexibility of HM its use in evolutionary ecology is still very limited. Reasons are unclear but we hypothesize that evolutionary studies often used theoretical and/or experimental approaches involving organisms that are relatively easy to monitor. In contrast, ecological studies require monitoring organisms in natural conditions implying numerous constraints in the data collection.

In this paper, we argue that studying eco-evolutionary processes requires considering the complete life histories of organisms and accommodating uncertainty arising from data collection. With this aim in view, we demonstrate that HM is a relevant approach to address eco-evolutionary questions in the wild as it combines several important ingredients within a single framework: (1) Modelling complex phenomena such as complete life histories and associated transitions between states (e.g., alive / dead, breeding / not breeding, migrating / resident); (2) Integrating underlying evolutionary processes of interest; and (3) Accounting for uncertainty in data collection. We illustrate our purpose with a case study dealing with life histories of stream-dwelling juvenile Atlantic salmon (*Salmo salar*) in the Scorff River (Southern Brittany, France). Atlantic salmon has a complex life cycle and exhibits a variety of life histories that have to be modelled in a unique framework if one wants to understand their variations. First, we describe the HM framework to analyse longitudinal data collected at the individual level. Second, we model the size-dependent reaction norm for seaward migration and two potential trade-offs, namely a survival cost of migration and a survival cost of reproduction. By integrating step-by-step various components of the life cycle and the observation process, we show how eco-evolutionary processes would have been poorly inferred or even missed without integrating all life history events and sources of available information through HM.

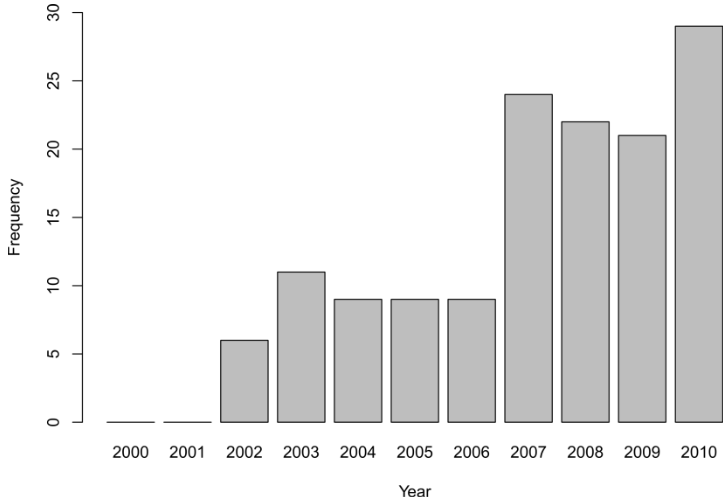

Figure 1: Time series of the number of papers using or addressing hierarchical modelling in ecology and evolutionary ecology over the past decade (using ISI web of knowledge citation report; terms employed "Hierarchical modeling" and "Multilevel" in subject areas ecology, evolutionary biology, genetics & heredity and biology). There were no paper on hierarchical modelling in ecology studies until 1992; and the number of papers on hierarchical modelling was remarkably small until 2000, whereafter it increased constantly.

MATERIAL & METHODS

1. Hierarchical modelling framework

HM framework is a natural approach to deal with hierarchically structured data: "observable outcomes [are] modelled conditionally on certain parameters, which themselves are given a probabilistic specification in terms of further parameters" (Gelman et al, 2004). HM distinguishes 3 levels: the data at hand, the underlying processes of interest and the parameters governing these processes (Cressie et al. 2009). First, that observed data Y are assumed to have some distribution (measurement error) dependent on an unobserved process X and a set of parameters θ_Y governing the uncertainty in the relationship between Y and X: $[Y \mid X, \theta_Y]$. We use the notation $[A \mid B]$ to denote a set of random variables A distributed conditionally on a set of variables B. Second, some distribution is assumed for the process X itself, governed by a set of parameters θ_X: $[X \mid \theta_X]$. Combining these two assumptions, HM allows modelling both the randomness in the data (the observation process) and in the underlying process via the joint conditional distribution of Y and X given the set of associated parameters θ_Y and θ_X:

$$\left[Y, X \mid \theta_Y, \theta_X\right] = \left[Y \mid X, \theta_Y\right] \times \left[X \mid \theta_X\right] \quad \text{(eqn 1)}$$

This formulation is quite generic, the hidden (i.e. not readily observable) process of interest X standing for eco-evolutionary processes in our case.

2. Longitudinal data at the individual level

One often relies upon individual mark–recapture (MR) protocols (Lebreton et al. 1992) for estimating important fitness components, e.g. survival, dispersal and reproduction (Gimenez et al. 2008). MR data result from the partial observation (detection or not) of events that are generated from a sequence of life stages. HM has been proposed as a flexible framework to deal with MR data (Rivot & Prévost 2002; Gimenez et al. 2007; Schofield et al. 2009). For the sake of illustration, we first go through a simple example with survival while coping with imperfect detection. Let us focus on the case of an individual i between two sampling occasions t - 1 and t (Fig. 2). Conditional on its state at time t - 1 (alive or dead), this individual may be alive or dead at the following sampling occasion with some probability. Formally, we denote $X_{i,t}$ a binary random variable corresponding to the state of the individual i at time t, which takes value 1 if the individual is alive at t, and 0 otherwise. Then, $X_{i,t}$ given $X_{i,t-1}$ is distributed according to a Bernoulli distribution with probability depending on the survival probability ϕ (Gimenez, 2007; Royle, 2008). Note that the survival probability ϕ corresponds to the associated parameters θ_X in equation (1). This leads to the state equation:

$$\left[X_{i,t} \mid X_{i,t-1}, \phi_{i,t-1}\right] \sim Bernoulli\left(X_{i,t-1} \times \phi_{i,t-1}\right) \quad \text{(eqn 2)}$$

When individual i is alive at t ($X_{i,t} = 1$), it can be observed or not, while when dead ($X_{i,t} = 0$), it necessarily goes undetected. We denote $Y_{i,t}$ a binary random variable corresponding to the observation of the individual i at time t, which takes value 1 if the individual is observed and 0 otherwise. Given the state $X_{i,t}$, $Y_{i,t}$ is distributed according to a Bernoulli distribution with probability p_t depending on the detection probability at time t (Gimenez et al. 2007; Royle & Dorazio 2008). Note that the detection probability p_t corresponds to the associated parameters θ_Y in equation (1).

$$[Y_{i,t} \mid X_{i,t}, p_t] \sim Bernoulli(X_{i,t} \times p_t) \qquad \text{(eqn 3)}$$

Besides the estimation of transition probabilities between the demographic states, HMs allow inferring the state (e.g. survivor, migrant or breeder) of any individual at a given time while acknowledging that they may be only partially observed. By extension to the full eco-evolutionary process (e.g. life history transitions) the associated life history of every individual can be estimated. In what follows, we extend the simple example above to a real case study and show how building increasingly complex and comprehensive HMs can limit the risk of flawed inference in eco-evolutionary studies. We focus on the study of phenotypic plasticity and selective survival in the juvenile phase of Atlantic salmon life cycle using MR data.

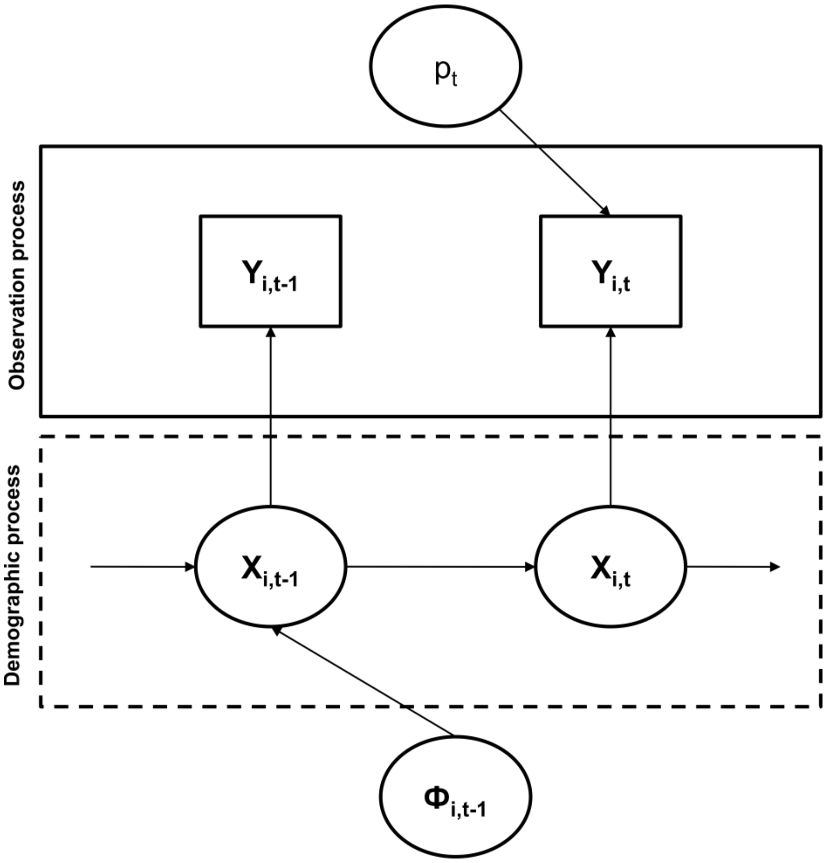

Figure 2: Graphical representation of a hierarchical mark-recapture model for an individual *i* between two sampling occasions $t - 1$ and t (see eqns 2 and 3). The first component is a demographic process (dashed box) characterized by a succession of hidden states (solid circles), also called latent states. The demographic process depends on parameters

corresponding to transitions probabilities between successive states (solid ellipses). Each quantity in the model corresponds to a node (e.g., latent states or parameters) and links between nodes show direct dependence. Rectangular nodes and elliptical nodes denote known and unknown quantities (i.e. quantities that require a distributional assumption) respectively. The unknown state of individual i at time t ($X_{i,t}$) is drawn from a Bernoulli distribution depending on its state at time $t - 1$($X_{i,t-1}$) and the probability of transition between these two states (e.g., the survival probability $\phi_{i,t-1}$). The observational data (solid square) through the observation process (solid box) are the visible part of the demographic process. Observations are also obtained conditionally on latent states and the parameters of the observation process associated (solid ellipses). The observation or not of individual i at time t ($Y_{i,t}$) is drawn from a Bernoulli distribution that depends on the detection probability p_t at time t and conditional on individual i being alive at time t ($X_{i,t} = 1$). This formulation separates the nuisance parameters (detection probabilities) from the parameters of interest for example survival probability, the latter being involved exclusively in the state equation. The resulting HM is a combination of a demographic process and an observation process.

3. Hierarchical modelling of juvenile Atlantic salmon MR data

i. Atlantic salmon life cycle

Atlantic salmon is an anadromous fish species. Its life cycle unfold both in freshwater and in the ocean (Webb et al. 2007). The juvenile phase takes place in freshwater. In Brittany, it lasts 1 or 2 years (Fig. 3). Thereafter, the fish migrate to the ocean. Migration to the ocean is accompanied by a smolting process preparing individuals for seawater life. Fish return after 1 or 2 years to their native stream to breed. Males may breed before undertaking their seaward migration. During the juvenile phase of the life cycle, individuals adopt alternative life history tactics. First, they have to decide whether to migrate to the ocean after their first year of life or to reside in the freshwater an additional year. Second, they have to decide whether to mature or not before migrating to the ocean. The latter choice involves only males during their second year in freshwater. These life history tactics depend on, and modify, the way energy is acquired, stored and used by individuals (Thorpe et al. 1998). Evolutionary trade-offs are thus expected in this species.

In the following, we use the term “0+” for individuals of less than one year of age in freshwater, “1+” for those of more than 1 year of age and “2+” for those of more than 2 years of age. Juveniles are named “parr” if resident in freshwater and “smolts” when they migrate to the sea.

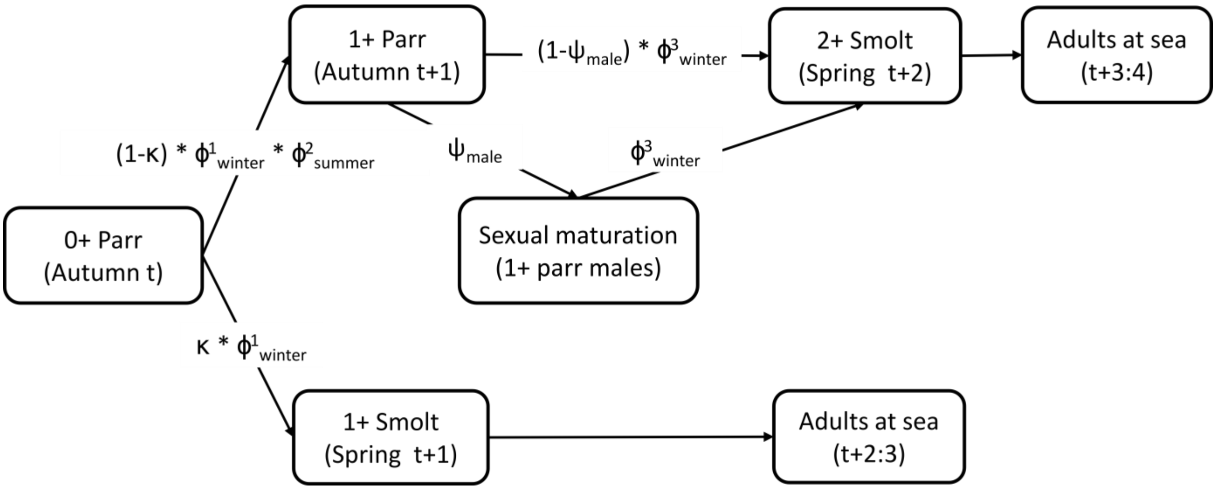

Figure 3: Life cycle of the Atlantic salmon in the Scorff, Brittany (France). Reproduction occurs in freshwater in December and eggs are buried in the river bed gravel. Fry emerge from the spawning in early spring. After a few months of life, juveniles, then called “0+ parr,” choose between migrating to sea the following spring (1+ smolt stage) with a probability κ or staying another year in freshwater (1+ parr) with a probability $1 - \kappa$. The probability of winter survival of the 0+ parr between the first autumn and the following spring is $\phi_1$winter. The probability of summer survival of the 1+ parr is ϕ_2 summer. Some of the males remaining in freshwater become sexually mature at the 1+ parr stage with a probability of maturing ψ. The probability of winter survival of the 1+ parr between the second autumn and the following spring is $\phi_3$winter. Virtually all surviving juveniles (previously mature or not) will migrate to the sea in the following spring (2+ smolt). Migration to the sea is accompanied by physiological, morphological, and behavioural changes (i.e., smolting process), which prepares individuals for seawater life

ii. Study site and MR data collection

The Scorff river is a small coastal river of Southern Brittany (France). Atlantic salmon colonization is essentially restricted to the main river over a 50 km stretch.

In autumn 2005, 0+ parr were sampled by electrofishing at 39 stations along the main course of the Scorff. Every fish captured was measured (fork length) and individually marked with a Passive Integrative Transponder (PIT) for subsequent identification. In spring 2006, downstream migrating 1+ smolts were captured at two successive traps located at the lower end of the river system below all sites where juveniles were marked. Untagged fish caught at the upstream trap (Leslé Mill) were marked by removing a small piece of a pelvic fin. At the second trap (Princes Mill) situated downstream all individuals previously fin-clipped were identified. In autumn 2006, the 1+ parr were sampled by electrofishing. Marked fish were identified and untagged fish were PIT tagged. Sexually maturing and already spermating males were detected by pressing their belly. In spring 2007, the 2+ smolts were trapped, checked for PIT tags, and fin-clipped if unmarked. These data are summarized in Appendix 1. More details on the MR data protocol can be found in Buoro et al. (2010).

iii. Statistical models

Our analyses combine a demographic process model and an observation model. Both are made up of several components, each corresponding to a life history transition or a source of information. Life history events are binary and modelled as random variables with Bernoulli distribution (see equations 1 and 2 above; Table A2 in Appendix 2). To illustrate the usefulness of increasing complexity and comprehensiveness of HM, we incorporate the different parts in four steps (noted A to D) sequentially and compare the results with those obtained at the previous steps.

Each model was represented in two ways. First we opted for directed acyclic graphs (DAG) that are convenient to display HM conditioning structure (Lunn et al., 2000). Second, we provided the corresponding equations needed to describe the model based on extensions of equations 2 and 3.

Model A: 0+ Parr to 1+ smolt stage transition

Demographic process

We started with model A focusing on the first two life history events in the first year of life of Atlantic salmon juveniles (Fig. 3): (1) the decision taken in the first autumn of either smolting the following spring at one year of age or to stay an additional year in freshwater (1+parr) and (2) the survival of the 0+ parr between the first autumn and the following spring (winter survival). The DAG of model A is displayed in Fig. 4 while equations are given in Appendix 2.

First, we assumed that age at smolting depends positively on growth during the first months of life in freshwater (Baglinière et al. 1993; Thorpe & Metcalfe 1998). Using the conceptual framework of probabilistic reaction norms (Heino 2002), we used a logit-linear relationship to represent the link between the individual *i* probability of smolting at age 1+ (κ_i) and size at the 0+ parr stage:

$$logit(\kappa_i) = \alpha_1 + \alpha_2 \times Fl_i \qquad \text{(eqn 4)}$$

where Fl_i is the individual fork length (mm) centred on the sample mean. We used a logit link function to ensure that probabilities lie on [0, 1]. Parameter α_2 controls the influence of size at 0+ parr stage on smolting and corresponds to the selection gradient of the probabilistic reaction norm for smolting. We expect the relationship to be positive, to reflect a positive size-dependent relationship of smolting at age 1+.

Second, we assumed the decision of smolting at age 1+ modified survival. During the first winter, future migrants adopt a very different behaviour from those intended to reside an additional year in the river as they try to maximize their growth (Metcalfe & Thorpe 1992; McCormick et al. 1998). We modelled this differential survival at the individual level by linking the probabilities of winter survival to the smolting decision.

$$logit(\phi_{1,i}) = \beta_1 + \beta_2 \times Parr_{0,i}^{smolt} \qquad \text{(eqn 5)}$$

where $\phi_{1,i}$ stands for the probability of first winter survival (0+ parr) of an individual *i* , $Parr^{Smolt}_{0,i}$ is the smolting indicator taking value 1 if individual *i* is smolting and 0 otherwise. Parameter β_2 reflects the influence of the decision of smolting on winter survival at 0+ parr stage. For instance, if β_2 is negative, then the winter survival $\phi_{1,i}$ of a smolting 0+ parr

(*$Parr^{Smolt}_{0,i}$* =1) is lower than that of a resident 0+ parr (*$Parr^{Smolt}_{0,i}$*), revealing a survival cost of smolting.

Observation process

Captures of tagged fish occurred at each stage of the life history of PIT-tagged individuals. The first recapture event after tagging was the trapping of the 1+ smolts (spring 2006) both at the Leslé Mill with probability pL_1 and at the Princes Mill with probability pP_1. At the individual level, capture was modelled as a Bernoulli distribution (Appendix 2) with associated probability of capture assumed fixed across individuals.

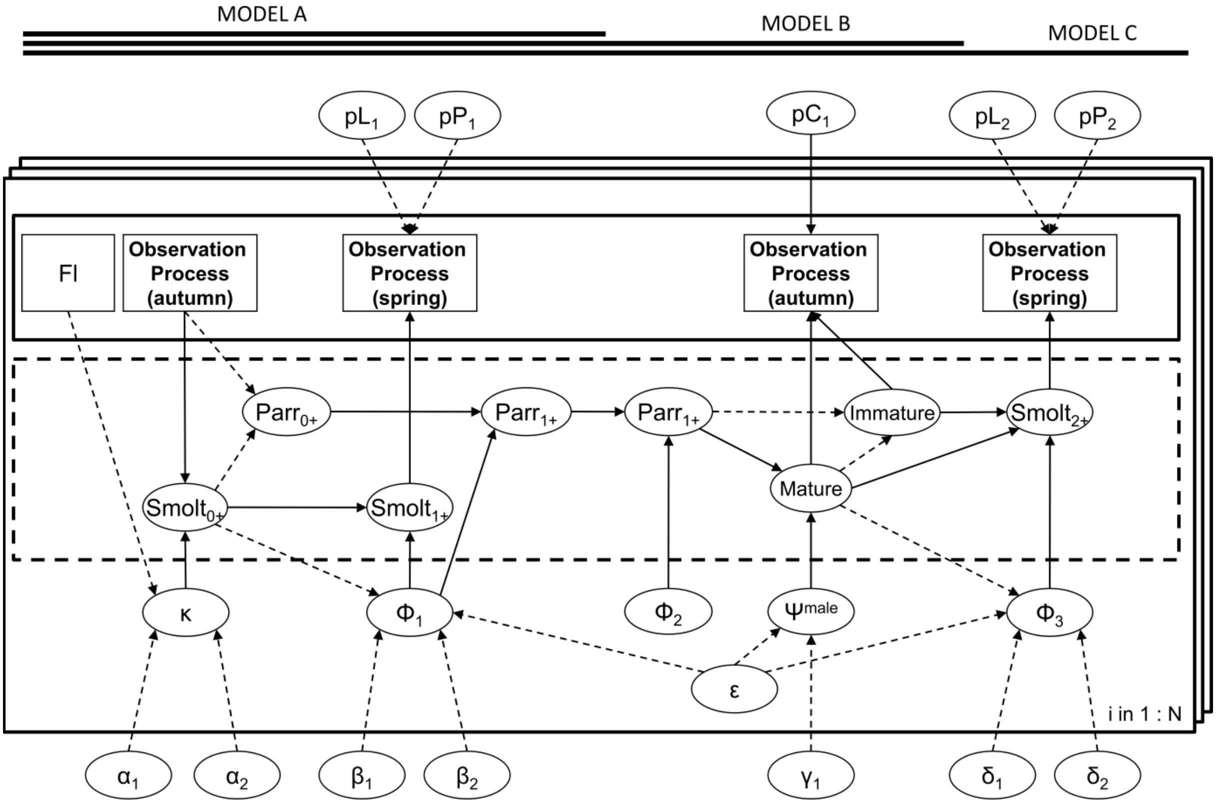

Figure 4: Graphical representation (DAG) of hierarchical mark-recapture models for life histories of Atlantic salmon juvenile for models A, B and C. Model D were not include as it corresponds to the same observation models than model C with additional data. Notations are given in the text. As seen in the Fig. 2, we distinguished the demographic process (dashed box) from the observation process (solid box) and hidden states (solid ellipses) from observational data (solid rectangular). Observations are also obtained conditionally on latent

states and the parameters of the observation process associated (solid ellipses). Each quantity in the model corresponds to a node (e.g., latent states or parameters) and links between nodes show direct dependence. Rectangular nodes and elliptical nodes denote known and unknown quantities (i.e. quantities that require a distributional assumption) respectively. Stochastic dependence and deterministic dependence are denoted by single arrows and dashed arrows respectively. Repetitive structures, such as the loop *i* from 1 to N, are represented by overlapping frames.

Model B: Incorporating summer survival and maturation process at 1+ parr stage

Demographic process

To extend the life cycle, summer survival and maturation decision of the 1+ parr needs to be modelled (Fig. 4, model B). Survival of resident 1+ parr between their initial marking in autumn 2005 and their first recapture in autumn 2006 is made of two successive survival events: winter survival (from autumn 2005 to spring 2006) and summer survival (from spring 2006 to autumn 2006). The explicit distinction of these two survival events allows assessing the first winter survival probability of the future 1+ parr, despite the absence of recaptures for 1+ parr in spring 2006.

Fisrt, we assumed that summer survival of 1+ parr was higher than previous winter survival in the Scorff river (Baglinière et al. 1994). We incorporated this information by specifying summer survival probability $\phi_{2,i}$ conditionally on winter survival $\phi_{1,i}$ as

$$\phi_{2,i} = \phi_{1,i} + (1 - \phi_{1,i}) \times \mathit{\Delta}_{survival} \qquad \text{(eqn 6)}$$

where $\mathit{\Delta}_{survival}$ is an unknown parameter between 0 and 1 which determines the survival difference between first winter and summer.

As survival is energy demanding, higher survival potential should be related to higher energy storage and a more efficient use of available energy. From this model B, we introduced an additive random effect ε_i in equation 5, to account for individual heterogeneity in survival due to unknown causes. ε_i is normally distributed with 0 mean and unknown standard deviation σ_ε. In accordance to Cam et al. (2002), this unobservable individual survival potential affected every subsequent survival event. By this way, for a given individual, having a higher survival probability during the first winter reveals a better chance to stay alive during the following survival events (i.e., summer survival and second winter survival (see model C)).

Second, we assumed that males 1+ parr have to decide to mature or not prior to ocean migration during this summer transition (Thorpe et al. 1998). Maturation state is only observed for male 1+ parr captured in autumn and detected as spermating. To define maturation state for every 1+ parr, whether marked in autumn 2005 as 0+ parr or in autumn 2006 as 1+ parr, we modelled sexual maturation of males at the 1+ parr stage using a Bernoulli distribution with probability of maturing at 1+ parr stage being the product of the probabilities of sexual maturation for a male and of being a male. We assumed that the probability for a 1+ parr to be a male was 0.5 (balanced sex-ratio). The probability of sexual maturation for a male ψ_i^{male} was assumed to depend on unobserved individual quality reflected by the survival potential:

$$logit\left(\psi_i^{male}\right) = \gamma_1 + \varepsilon_i \qquad \text{(eqn 7)}$$

A male having a high survival potential ε_i, i.e. with a high level of energy storage, should in turn have a higher probability of maturing at the 1+parr stage. Indeed, sexual maturation of males at the 1+parr stage depends on the accumulation of energy reserves in the spring of the second year of life (Prévost et al. 1992; Duston & Saunders 1997).

Observation process

The 1+ parr remaining in freshwater (autumn 2006) were captured by electrofishing with probability pC_1 (Table A2 in Appendix 2). Sampling by electrofishing was conducted in the same sites each year. There is evidence of site fidelity in Atlantic salmon parr (Stickler et al., 2008). In our study, almost all the 1+ parr recaptured were caught at the same station where they were marked at 0+ stage. We considered that the probability of capture for 1+ parr in 2006 was higher than the probability of capture for 0+ parr in 2005, and specified the probability of detection of 1+ parr in autumn 2006, pC_1, conditionally on the probability of detection of 0+ parr in autumn 2005, pC_0:

$$pC_1 = pC_0 + (1 - pC_0) \times \Delta_{capture} \qquad \text{(eqn 8)}$$

where $\Delta_{capture}$ is un unknown parameter between 0 and 1 which determines the difference between pC_1 and pC_0.

Model C: Incorporating 2+ smolts stage and cost of reproduction for survival

Demographic process

Sexual maturation and reproduction of resident males in freshwater is energy demanding (Rowe et al. 1991; Fleming 1996; Arndt 2000). Combined with the exposure to the agonistic behaviour of the large anadromous males on the spawning grounds (Hutchings & Myers 1987; Fleming 1996), this should lead to reduced survival (Myers 1984; Fleming & Reynolds 2004). We modelled this cost of reproduction at the individual level by linking the probabilities of the second winter survival to the state indicator of the decision of maturation ($Parr_{1,i}^{mature}$) (Fig. 4, model C):

$$logit(\phi_{3,i}) = \delta_1 + \delta_2 \times Parr_{1,i}^{mature} + \varepsilon_i \qquad \text{(eqn 9)}$$

where $\phi_{3,i}$ stands for the probability of second winter survival (1+ parr) of individual i. $Parr_{1,i}^{mature}$ is the maturing indicator taking value 1 if individual i is mature and 0 otherwise. Parameters δ_2 reflects the influence of the decision of maturing on winter survival at the 1+ parr stage. If δ_2 is negative, then the winter survival $\phi_{3,i}$ of a maturing male 1+ parr ($Parr_{1,i}^{mature}$ =1) is lower than that of a immature 1+ parr ($Parr_{1,i}^{mature}$ = 0), suggesting a survival cost of reproduction.

Observation process

The 2+ smolts (spring 2007) were trapped at the Leslé Mill with probability pL_2 and at the Princes Mill with probability pP_2 according to same protocol used for the 1+ smolt the previous year (see "*Observation process*" section in model A).

Model D: Incorporating additional information

Additional information about life history events and smolt trapping probabilities were available. First, the 1+ parr sampled by electrofishing in autumn 2006, but untagged at 0+ parr stage, were also PIT tagged. We assumed that sexual maturation and second winter survival were the same whether 1+ parr had been tagged or untagged at the 0+ parr stage. As a consequence, we used the same equations (7) and (9) with common parameters as presented before (models B-C). Second, we took advantage of ancillary fin-clipping data collected at the smolt traps in 2006 and 2007 (see "Study site and MR data collection" section; Appendix 1) to improve estimation of smolt trapping probabilities. We assumed that the probability of capture at both traps were the same for PIT-tagged, fin-clipped and untagged smolts.

4. Statistical inference in a Bayesian framework

To fit HM to data, we adopted a Bayesian approach using Markov chain Monte Carlo (MCMC). The Bayesian approach to statistical inference combines the likelihood (information available in the data) and prior distributions for parameters of interest (knowledge available before the data collection) to obtain the joint posterior probability distribution of all the model unknowns, i.e. individual states, transition probabilities between states and random effects, observation probabilities and additional parameters (see Gelman (2004), Ellison (2004) and McCarthy (2007) for more details about the Bayesian statistical modelling approach).

Besides handling the complexity of our model, the Bayesian approach made the combination of multiple sources of information possible for improving estimation of model parameters. In our case, apart from observed data generated by the PIT tagging program, ancillary sources of information could be incorporated as well (see previous section). We also used informative prior probability distributions of model parameters to improve the precision of parameter estimates and reduce model complexity (McCarthy 2005). Prior information was available either from the literature or from additional data. For example, in agreement with what was known about the species biology, we considered the probability of surviving in freshwater as being neither null nor equal to 1 between two consecutive stages. Consequently, we chose parameters of the prior distribution such that less importance was given to extreme values of survival probabilities (see "Choice of prior distribution" section in Appendix 3 for more details). Data were also used to elicit informative priors. The probability of capture of 0+ parr in autumn 2005 could be assessed from the smolt trapping data in 2006. We summarize this available information by assigning a Beta prior distribution to pC_0 (eqn 8) whose parameters are the number of smolts marked in the previous autumn and captured at smolt traps (Leslé Mill and Princes Mill), and the number of untagged smolts captured at smolt traps. Note that the data used here were different from the observations used elsewhere in the model and resulting from the observation process or the ancillary data described above. For all the other parameters we used non-informative priors (Appendix 3).

The joint posterior distribution of all the model unknowns was derived by means of MCMC sampling as implemented by the OpenBUGS software (Lunn et al., 2009). The OpenBUGS codes of models are available at http://www.cefe.cnrs.fr/biom/zips/Models_Buoro et al 2011_MEE.txt. OpenBUGS uses a programming syntax similar to the popular R software, which should make our code self-reading for familiar users. We ran 3 parallel MCMC chains and retained 50000 iterations after an initial burn-in of 10000 iterations for each model. Convergence of MCMC sampling was assessed by means of the Brooks-Gelman-Rubin diagnostic (Brooks 1998).

RESULTS

In the following, medians and 95% credible intervals from the posterior distribution were reported for parameters of interest (Table 1). We also provided the probability for a parameter of being positive calculated as the proportion of sampled values higher than zero ($\Pr([\theta|Y] > 0)$) with θ a given parameter and Y the observed data). Results for the probabilities of sexual maturation and winter survival were given considering a random effect ε_i equal to 0 (eqn 5, 7, 9).

Parameter	Definition	Model	Posterior distribution		$\Pr([\theta \mid Y] > 0)$
			Median	**95% credible interval**	
Demographic Process					
α_1	Intercept of the size-dependent probabilistic reaction norm for smolting (Eqn 4)	A	-2.23	[-2.98 ; -1.33]	0
		B	-2.10	[-2.82 ; -1.35]	0
		C	-1.83	[-2.55 ; -1.13]	0
		D	-1.91	[-2.56 ; -1.24]	0
α_2	Selection gradient of the size-dependent probabilistic reaction norm for smolting (Eqn 4)	A	0.13	[0.09 ; 0.19]	0.99
		B	0.14	[0.10 ; 0.19]	0.99
		C	0.16	[0.11 ; 0.21]	0.99
		D	0.16	[0.12 ; 0.21]	0.99
β_1	First winter survival for futures 1+ parr (Eqn5)	A	0.02	[-3.68 ; 3.78]	0.50
		B	-2.04	[-4.53; 0.46]	0.07
		C	-2.05	[-4.53; -0.63]	0
		D	-1.53	[-2.80; -0.73]	0
β_2	Effect of the decision of smolting at 1 year of age on the first winter survival (Eqn 5)	A	0.51	[-3.60 ; 4.96]	0.60
		B	2.29	[-1.07 ; 5.63]	0.90
		C	1.84	[-0.20 ; 5.44]	0.95

		D	1.64	[0.43 ; 3.56]	0.99
δ_1	Second winter survival for immature 1+ parr (males and females; Eqn 9)	A	-	-	-
		B	-	-	-
		C	0.55	[-2.06 ; 4.18]	0.66
		D	-0.49	[-2.29 ; 0.53]	0.19
δ_2	Effect of the decision of maturing on the second winter survival (cost of reproduction for survival; Eqn 9)	A	-	-	-
		B	-	-	-
		C	-1.28	[-5.87 ; 3.52]	0.28
		D	-1.51	[-3.12 ; -0.28]	0.01

Table 1: Summary of posterior distributions (medians, 95% posterior credible intervals and probability to be positive) for demographic process parameters of interest (i.e., probabilistic reaction norm and selective survival).

1. Observation probabilities

Detection probabilities were *a posteriori* well estimated (Fig. 5) in comparison with their non-informative prior distributions (see Appendix 3). Using ancillary data (model D), uncertainty on detection probabilities estimates was most significantly reduced compared to PIT-tag data only (models A, B and C). Smolt trap efficiencies varied from 2006 (pL_1 and pP_1) to 2007 (pL_2 and pP_2) due to the high sensitivity to hydrological conditions (Rivot & Prévost 2002).

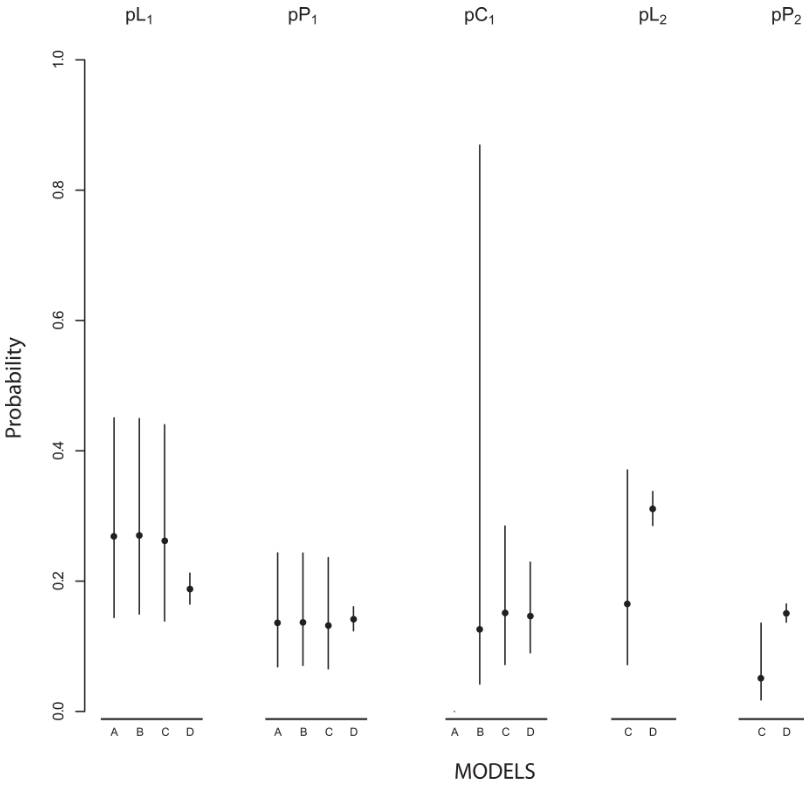

Figure 5: Posterior distributions of the probabilities of capture for each models (also noted from "A" to "D"; based on 50000 MCMC samples). Notation: pL and pP are the probabilities of capture at Leslé Mill and Princes Mill respectively at both occasions (1: spring 2006 and 2: spring 2007) and pC is the probability of capture in autumn at 1+ parr stage. The median (black point) and the 95% PPI (Posterior Probability Interval (PPI); solid lines) are displayed.

2. Choice between alternative life-history tactics

The gradient of the probabilistic reaction norm for age at smolting was strictly positive (Pr ($\alpha_2 > 0$) ≈ 100%) (Table 1). The decision of smolting at 1 year of age was strongly size dependent (Fig. 6). The estimation of the reaction norm was little affected by increasing model complexity. Using the full model D, uncertainty in the reaction norm parameters in model D was slightly reduced compared to the simplest model A considering the 1+ smolt stage only (Table 1). At the same time, the gradient α_2 was somewhat larger and the parameter α_1 was somewhat smaller. As a consequence, the size at the 0+ parr stage for which the probability of becoming a 1+ smolt is 0.5 was smaller in model D than in model A (88 mm [84; 95] vs. 95 mm [93; 103] respectively).

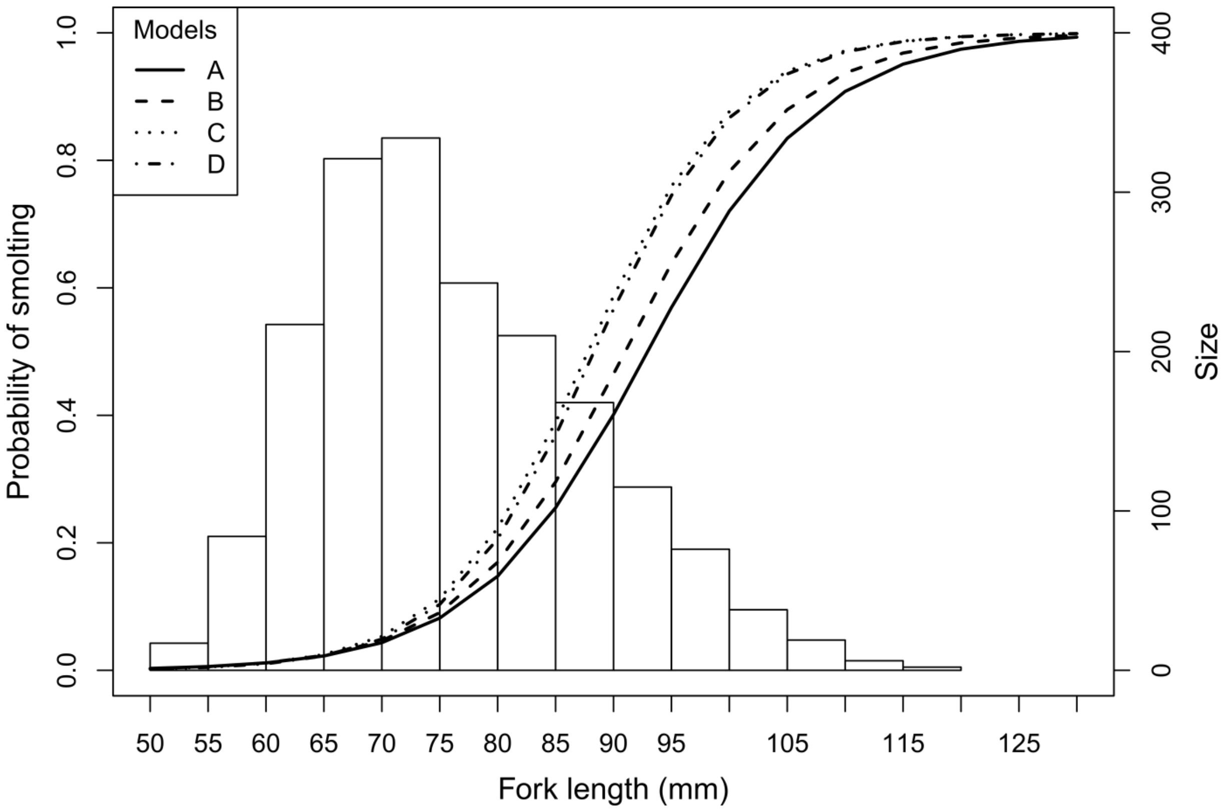

Figure 6: Probabilistic reaction norms for the age at smolting for each models (noted from A to D). The posterior medians of the probability of smolting at 1 year of age are functions of fork length. A histogram of the size distribution of the 0+ parr sampled in autumn 2005 is also displayed.

The probability of sexual maturation for a male at the 1+ parr stage was high for both models C and D but poorly estimated while the uncertainty was marginally reduced in model D (0.72 [0.14; 0.99] vs. 0.58 [0.19; 0.91] for model C and D respectively).

3. Selective survival and cost of reproduction

Parameter β_2 was estimated positive in all models (Table 1). Its 95% posterior probability interval included 0 except in model D combining all life histories events and sources of data, thus revealing a selective survival in first winter in favour of 0+ parr that decided to smolt at 1 year of age the following spring (0.53 [0.32; 0.83] versus 0.19 [0.07; 0.33] for future 1+ parr staying in freshwater under model D). The difference of winter survival between future migrants and future residents was clearly positive (0.35 [0.09; 0.68]) (Fig. 7A).

Using PIT-tag data only (model C), parameter δ_2 was estimated negative with probability 0.72 (Table 1). Combining additional sources of data (model D), parameter δ_2 was unambiguously estimated negative with probability 0.99, thus showing a selective survival depending on the sexual maturation status of the 1+ parr, i.e. a cost of reproduction on the second winter survival (Fig. 7B). Winter survival of a male previously mature at the 1+ parr stage was 0.14 [0.02; 0.35] versus 0.39 [0.12; 0.62] for an immature (males and females together) 1+ parr.

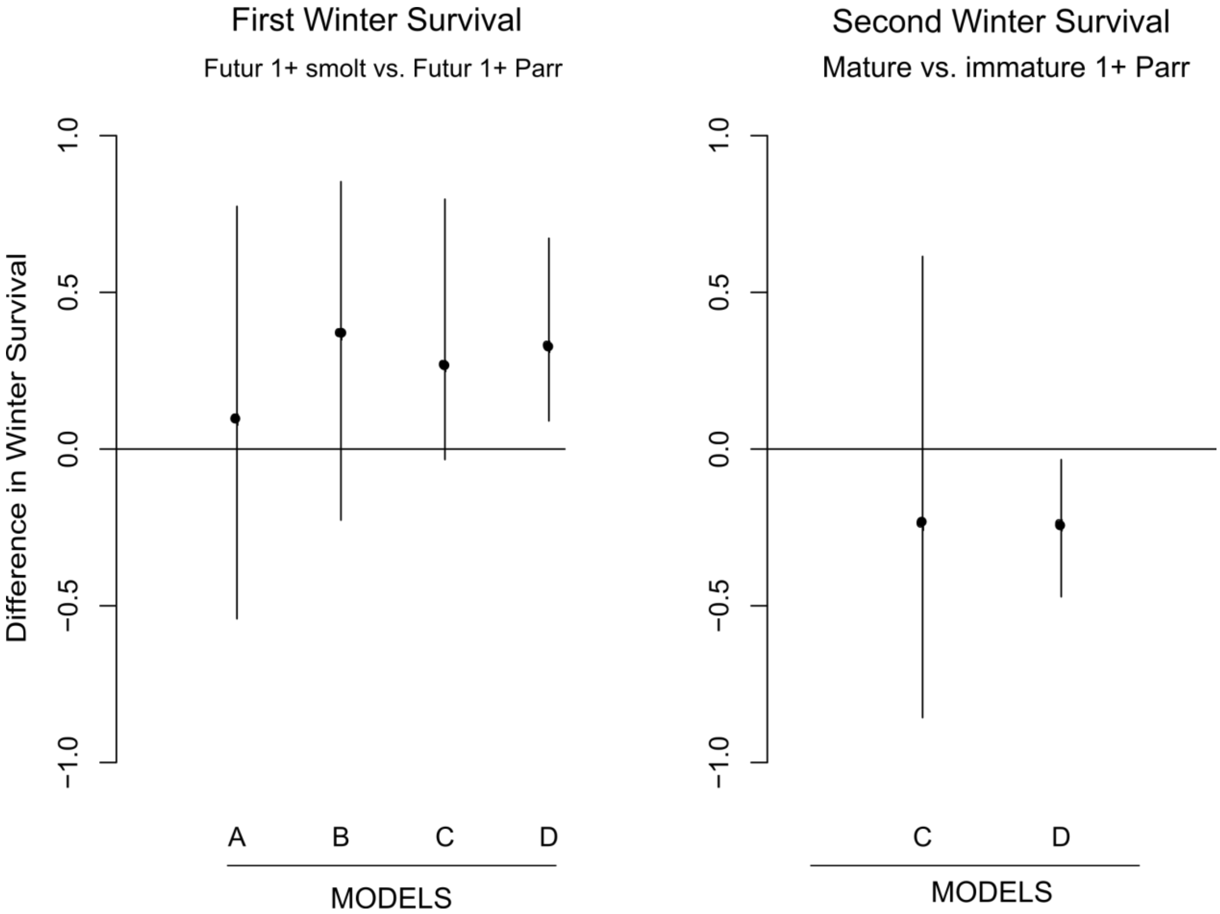

Figure 7: Posterior distributions of the difference in survival probability (considering zero random effect as null) for each models (also noted from “A” to “D”) for (A) future 1+ smolts

versus future 1+ parr during the first winter and (B) mature 1+ parr versus immature 1+ males during the second winter (cost of reproduction for survival). The median (black point) and the 95% PPI (Posterior Probability Interval (PPI); solid lines) are displayed.

DISCUSSION

There is growing interest in studying eco-evolutionary processes in the wild (Schoener 2011). The two main challenges are to take into account a) their rather complex nature involving various life histories traits (and stages) and their associated interactions, and b) the fact they are partially observed and/or with measurement error. We contend that the HM approach offers a generic framework for taking up these challenges. By explicitly distinguishing the observation process from the ecological process, HM is a powerful way to deal with uncertainties inherent in data collection and hence to focus on the underlying complex eco-evolutionary mechanisms. We illustrated the HM framework by studying eco-evolutionary processes in Atlantic salmon using data collected at the individual level on marked juveniles. We jointly modelled the “hidden” demographic process (individual life histories) and the observation process (captures of fish at each stage of their life history). By explicitly handling the dynamics of life history stages, we assessed evolutionary processes: size-dependent probabilistic reaction norm for smolting, selective survival of future smolts and cost of reproduction (evolutionary trade-offs). Finally, adopting a step-to-step approach, we demonstrated that increasing complexity of models improved estimation accuracy and highlighted eco-evolutionary processes of interest not revealed with simpler models.

Modelling complex eco-evolutionary processes using HM

We showed how HM allows the incorporation step-by-step of successive life-history stages of Atlantic salmon juveniles as simple components of a more complex life-history model. This helps combining several life-history decisions (i.e., migration and maturation decisions) resulting from evolutionary processes (i.e., phenotypic plasticity, selective survival, cost of reproduction) at once. Adopting a HM framework has also the advantage of treating parameters and latent states similarly as unknown quantities to be estimated. This adds to the flexibility of HM since an unknown state can be used as a covariate in a model. Taking advantage of these features, we were able to explore the effect of migration decision on winter survival, despite this decision could not be observed at the onset of the winter transition. Indeed, migration is decided before the first winter by 0+ parr but it was only partially observed in the following spring through the recapture at smolts stage during their downstream migration. Thus, migration decision was an unknown to estimate for any fish not recaptured at the smolt stage (or later on). Taking advantage of the probabilistic reaction norm for migration, we estimated the unknown latent state indicator for migration decision before first winter, which was used in turn as a covariate in a model to highlight a selective winter survival. By combining two eco-evolutionary processes (life-history decision and potential evolutionary-trade-off), our analysis revealed a positive relationship between the first winter survival of the 0+ parr and their decision of smolting the following spring. We used the same approach combining the life-history decision for maturing with second winter survival event to highlight a survival cost of reproduction. HM allowed the estimation of the maturation state of all 1+ parr tagged even though it was only observable for the spermating males captured at the 1+ parr stage in autumn 2006. Our results showed mature male 1+ parr had a lower probability of winter survival (post-reproductive survival) than their immature counterparts (Myers 1984; Baglinière et al. 1993; Whalen & Parrish 1999). In addition, selective first winter survival and cost of reproduction could not be detected without extending the model beyond the life stages involved in the corresponding demographic transitions (Fig. 7). Increasing complexity of our model was necessary to reveal these eco-evolutionary processes.

Dealing with various sources of available information

In line with Cressie et al. (2009), we showed HM is a powerful approach to deal with various sources of information within a unique framework, hence improving our ability to study complex eco-evolutionary processes (Ogle 2009). In our Atlantic salmon case study, we considered sequentially the use of additional sources of data (1+ parr untagged at 0+ parr stage and smolt fin-clipping data). This resulted in a significant improvement in the estimation of parameters related to the observation process (detection probabilities) and more importantly to the process of ultimate interest (e.g. cost of reproduction). Our results showed that selective survival and cost of reproduction could not be detected without integrating all sources of information (Fig. 7). The flexibility of HM facilitates the increase in model complexity required to combine various sources of information. The Bayesian treatment of HM facilitates also the use of ancillary sources of information, through prior probability distributions of model parameters, to improve the precision of parameter estimates and reduce model complexity (McCarthy, 2005). In our study, we incorporated prior information based on information available either from the literature or from additional independent data (see Appendix 3 for more details).

Advances and constraints of HM

Missing data, complex multilevel structures or measurement errors are inherent difficulties in eco-evolutionary field studies. There has been a long tradition among ecologists to resort to HM to cope with these issues (Clark & Gelfand 2006). In contrast, evolutionary processes have traditionally been addressed by theoretical studies or controlled experiments in laboratory (Roff 1992). Experimental studies allow assessing life histories traits and fitness for every individual while safely ignoring the above limitations of field studies. Confronting theoretical or experimental results with empirical data collected in the field is more challenging. Empirical data often include noisy measures or partial observation with unknown levels of uncertainty (Cressie et al. 2009). It is important to account for this measurement error uncertainty in evolutionary studies since ignoring it may lead to flawed inference (Gimenez et al. 2008; Nakagawa & Freckleton 2008). HM allows distinguishing the measurement uncertainty from the underlying signal, thus making the processes of interest amenable to proper statistical inference from empirical data.

The flexibility of HM does not come without costs. With the rapid development of statistical software such as BUGS (Lunn et al. 2009) and the increase in computer power, one might be tempted to incorporate more and more details, hence increasing model complexity. This raises several issues. First, model specification is not straightforward for users without programming skills. Solutions can be found by making BUGS codes publicly available, by fostering collaborations between statisticians and evolutionists, and by training in hierarchical modelling (Ogle et al. 2009). Second, there is a risk of over-parameterized models with non-estimable parameters. Rather than fitting the complete model at first, incorporating the different relevant components, piece by piece, starting with a simple model then increasing complexity is a good practice (Craigmile et al., 2009; Brun et al., 2011). Third, to cope with complexity, one often resorts to a Bayesian approach using MCMC algorithms to fit HM to data. Despite being very flexible, these computational methods require sufficient training to be applied correctly. Besides, comparing hierarchical models via model selection is not easy although several alternatives exist (O'Hara & Sillanpää 2009; Brun et al. 2011). ABC methods might be most promising for fitting complex HMs (Beaumont 2010). As an alternative to the Bayesian approach, several approaches are being developed (Lele et al. 2007, 2009; De Valpine 2009, 2011) that deserve further exploration.

Overall, the costs associated to HM are compensated by their ability both to comprehensively integrate various life history events and to combine multiple sources of available information. These two features are key for drawing accurate statistical inference about eco-evolutionary processes in the wild from field data.

HM as a generic framework for studying evolutionary processes in the wild?

Eco-evolutionary processes operating at the level of individuals, populations and communities generate and maintain biodiversity (Pressey et al. 2003). Evolutionary processes and individual variation, raw material for natural selection, have ecological consequences and vice versa (Bolnick et al. 2001), hence a growing interest in integrating ecological and evolutionary tools and concepts. HM holds great promise by offering a generic framework to jointly address empirical and theoretical backgrounds and explore eco-evolutionary dynamics (Pelletier et al. 2009; Ezard et al. 2009; Carlson et al. 2011). For example, introducing quantitative genetics into eco-evolutionary models would help understanding the evolution of traits and their ecological consequences (Ozgul et al. 2009; Coulson et al. 2010). Besides, long-term individual-based studies are becoming more frequent providing a unique opportunity to address evolutionary questions in the wild and illustrate processes that could not previously be assessed in laboratory or with short time-scale studies (Clutton-Brock & Sheldon 2010). This requires dealing with models of increasing complexity and data of various kinds for which HM provides a relevant, flexible and reliable inference framework.

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APPENDIX 1

Table A1: Summary of tag/recapture data for each observation events and each method of tagging (PIT and Fin-clipping) for one cohort of Atlantic salmon.

Tag		**Capture-recapture at each stage of life**			
		0+ Parr	**1+ Smolt**	**1+ Parr**	**2+ Smolt**
Passive Integrated transponder (PIT)	Tagged at the 0+ parr stage	1829	67	29	39
	Tagged at the 1+ parr stage			281	55
Fin-clipping	Captured and tagged at Leslé Mill		1291		1751
	Captured at Princes Mill (untagged at Leslé Mill)		820		594
	Captured at Princes Mill (tagged at Leslé Mill)		179		262

APPENDIX 2

Table A2: States (indicators), transition probabilities (life history traits of ultimate interest) and equations of the demographic process accounting for the sequence of events corresponding to the life history of Atlantic salmon from the 0+ parr stage in autumn to the migration to the ocean in the second year of life. Equations defining individual specific transition probabilities are given in the text.

States	Definitions	Associated probabilities	Modeling
	Demographic Process		
Smolt0	0+ Parr in autumn / futurs 1+ smolts	κ_i : Probability to smoltify at 1 year of age (Eq. 3)	$Parr_{0,i}^{Smolt} \sim Bernoulli\left(\kappa_i\right)$
Smolt1	Surviving 1+ smolts in spring	$\phi_{1,i}$: Probability of 1st winter survival in the (Eq. 4)	$Smolt_{1,i} \sim Bernoulli\left(\phi_{1,i} \times Smolt0_i\right)$
Parr1	Surviving 1+ parr in spring		$Parr_{1,i} \sim Bernoulli\left(\phi_{1,i} \times 1 - Smolt0_i\right)$
Parr1.1	Surviving 1+ parr in autumn	$\phi_{2,i}$: Probability of summer survival (Eq. 5)	$Parr_{1.1,i} \sim Bernoulli\left(\phi_{2,i} \times Parr1_i\right)$
Parr1.mat	Mature males 1+ parr in autumn	ψ_i^{male} : Probability of maturing for males (Eq. 6)	$Parr_{1,i}^{mature} \sim Bernoulli\left(0.5 \times \psi_i^{male} \times Parr_{1.1,i}\right)$
Smolt2	Surviving 2+ smolts in spring	$\phi_{3,i}$: Probability of winter survival in the 2nd year of life (Eq. 8)	$Smolt_{2,i} \sim Bernoulli\left(\phi_{3,i} \times Parr_{1,i}\right)$
	Observation Process		

$S_{L,i}$	Smolts 1+ captured at Leslé Mill in spring	pL_1 : Probability of capture at Leslé Mill	$S_{L,1,i} \sim Bernoulli\left(pL_1 \times Smolt1_i\right)$
$S_{LP,i}$	Smolts 1+ captured at Leslé Mill and Princes Mill in spring	pP_1 : Probability of capture at Princes Mill	$S_{LP,1,i} \sim Bernoulli\left(pP_1 \times Smolt1_i\right)$
$S_{P,i}$	Smolts 1+ uncaptured at Leslé Mill but captured and Princes Mill in spring		$S_{P,1,i} \sim Bernoulli\left(pP_1 \times 1 - Smolt1_i\right)$
$Parr1_{,i}$	Parr 1+ captured in autumn	pC_1 : Probability of capture by electrical fishing in autumn	$Parr1_i \sim Bernoulli\left(pC_1 \times Parr1.1_i\right)$

APPENDIX 3

Choice of prior distributions

A Bayesian analysis requires specifying prior probability distributions for the unknown parameters in our model. These parameters and their corresponding prior distributions are listed in Table A1. The choice of the prior distribution is based on knowledge available before the experiment (McCarthy & Masters 2005). The parameters of our model are mainly probabilities ranging from 0 to 1. For such parameters, the natural choice is a beta probability distribution governed by two parameters (Fig. A1). An uninformative (or vague) prior corresponding to a uniform distribution between 0 and 1 amounts to a beta distribution governed by two parameters equal to 1. Different levels of information can be introduced in the form of weakly informative to very informative priors.

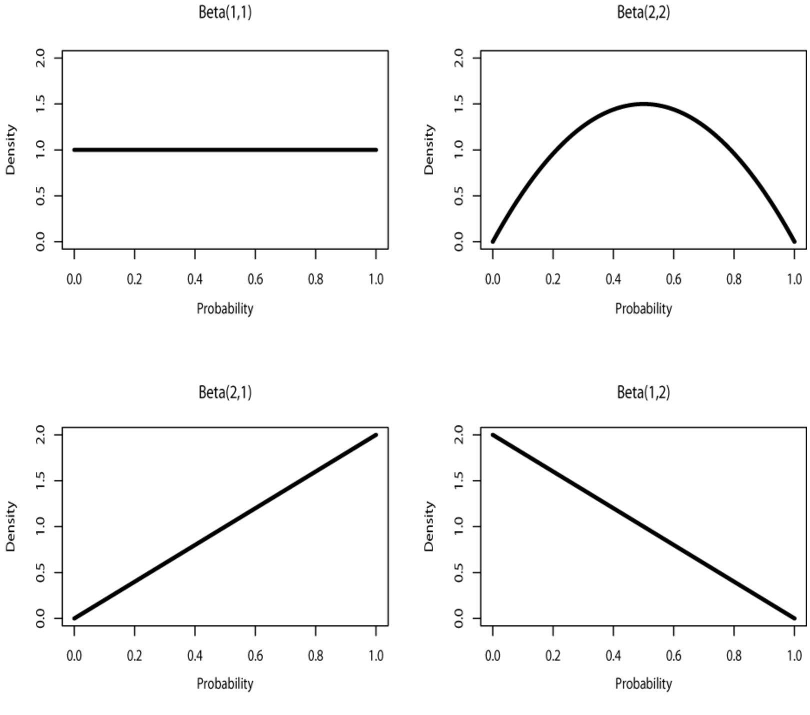

Figure A1: Plot of the *Beta probability* density function for 4 different sets of parameters. Beta(1, 1) is the uniform prior between 0 and 1. Beta(2, 2) is a slightly more informative probability distribution centered on 0.5 and giving a zero probability for values close to 0 and 1. Beta(1, 2) or Beta(2, 1) are triangular distributions giving a zero probability for values close to respectively 0 or 1.

In our study, all priors were weakly informative while integrating the knowledge available on the biology of the species. This ensures that posterior distributions reflect mainly the information from the data. For instance, the probability of sexual maturation for an “average” 1+ male parr (i.e., random effect is equal to zero, eqn. 6) is assumed uniform:

$$\psi_{mean}^{male} \sim Beta(1,1) \tag{A1}$$

For logistic models (eq. 3, 4 and 8), using non-informative priors (e.g. uniform distribution or normal distribution with large variance) on the regression parameters lead to an informative prior on the associated probability giving a high probability respectively for extreme values close to 0 and 1. This an undesirable consequence of the non linear scale change corresponding to the logit transformation which can significantly affect posterior inference, especially in the case of weakly informative data (Gelman 2006; Van Dongen 2006). To cope with this issue, we worked directly on transition probabilities between life history stages (probabilities of smolting, survival and maturation) for two given values of the covariates. We considered two cases according to the covariates included in the logit-linear relationships: a) the covariate is a binary (1 or 0) i.e. relationships representing the trade-offs (eq. 4 and 8) and b) the covariate is continuous, (i.e., size in the probabilistic reaction norm for smolting (see eq. 3).

5. Trade-offs (binary covariate)

Considering the first winter survival (eq. 4) of an average individual noted a ($\varepsilon_a = 0$) that will not smoltify ($Smolt0_a = 0$), we assumed that:

$$logit(\phi_{1,a}) = \alpha_1 \text{ i.e. } \alpha_1 = logit(\phi_{1,a}) \tag{A2}$$

where $\phi_{1,a}$ stands for the probability of first winter survival of an average future 1+ parr. In the case of an average future 1+ smolt, noted b, then $Smolt0_b = 1$ and $\varepsilon_b = 0$:

$$logit(\phi_{1,b}) = \alpha_1 + \alpha_2 \text{ i.e. } \alpha_2 = logit(\phi_{1,b}) - \alpha_1 \text{ or } \alpha_2 = logit(\phi_{1,b}) - logit(\phi_{1,a}) \tag{A3}$$

where $\phi_{1,b}$ stands for the probability of first winter survival of an average future 1+ smolt. Because there exists a one to one transformation between ($\varphi_{1,a}$, $\varphi_{1,b}$) and (α_1, α_2), setting a prior distribution on parameters $\phi_{1,a}$ and $\phi_{1,b}$ leads to specify a prior on the regression parameters (α_1, α_2) as well. In accordance with previous work on the survival of juvenile salmon in French rivers (Baglinière et al. 1993; Baglinière et al. 1994; Dumas & Prouzet 2003; Baglinière et al. 2005), we considered that prior knowledge available allowed to set that the probability to survive is not null nor equal to 1 between two consecutive stages and we used a beta distribution with both parameters set to 2 to summarize this knowledge (Table A1). The same approach was followed to specify priors on the parameters of the logit-linear relationship for the winter survival of the second year of life (eq. 4).

6. Probabilistic reaction norm (continuous variable)

We assumed that age at smolting is positively influenced by size in the first autumn in freshwater (eq. 3). We worked directly on the probability of smolting for extremes of the size range observed at 0 + parr stage, i.e. 50 and 120 mm (respectively Lfc_{50} and Lfc_{120}, the fork length centered on the sample mean). From the logit-linear relationship between the probability of smolting κ, the regression parameters β can be expressed as a function of the extreme sizes probabilities (eq. A4 and A5):

$$logit(\kappa_{50}) = \beta_1 + \beta_2 Lfc_{50} \tag{A4}$$

$$logit(\kappa_{120}) = \beta_1 + \beta_2 Lfc_{120} \tag{A5}$$

where κ_{50} and κ_{120} are probabilities of smolting at one year of age for a fish of 50 mm and 120 mm respectively.

We then obtain:

$$\beta_2 = \frac{logit(\kappa_{120})Lfc_{50} - logit(\kappa_{50})Lfc_{120}}{Lfc_{50} - Lfc_{120}} \tag{A6}$$

$$\beta_1 = \frac{logit(\kappa_{50}) - \beta_2}{Lfc_{50}} \quad \text{which gives} \quad \beta_1 = \frac{logit(\kappa_{50}) - logit(\kappa_{120})}{Lfc_{50} - Lfc_{120}} \tag{A7}$$

Setting priors on κ_{50} and κ_{120} determines a resulting priors on regression parameters β_1 and β_2 (eq. A6 and A7).

Previous studies have shown that the decision to smoltify is size-dependent (Nicieza et al. 1991; Berglund et al. 1992; Fangstam et al. 1993; Thorpe et al. 1998). Prior distributions were selected according to this available knowledge:

$$\kappa_{50} \sim Beta(1,2) \text{ and } \kappa_{120} \sim Beta(2,1) \tag{A8}$$

We thus assumed that a 0+ parr of 50 mm was *a priori* more likely to have lower probability of smoltifying at 1 year of age than a fish of 120 mm, without totally excluding the opposite assumption.

Summer survival

We assumed that summer survival was higher than first winter survival. We incorporated this information by specifying the probability of summer survival $\phi_{2,i}$ of an individual i conditionally on winter survival $\phi_{1,i}$ (eq. 5). We assumed that $\Delta_{survival}$ determines the difference between the probability of first winter survival and summer survival of 1+ parr. $\Delta_{survival}$ is an unknown parameter between 0 and 1 and considered as constant between individuals. Considering that summer survival has a low probability of being equal to the winter survival or to 1, $\Delta_{survival}$ was assigned a beta distribution with both parameters set up to 2.

Variance of the random effect

Gelman (2006) analyzes the consequences (sometimes undesirable) of the choice of different uninformative priors for the variance of the random effect in the case of a hierarchical linear model. Among the options he proposed, we chose a chi-square distribution with 1 degree of freedom for the variance of the random effect

Table A3: List of prior distributions assigned to unknown quantities of our model.

Parameters	Descriptive	Prior distributions
κ_{50}	Probability of smolting for 0+ Parr of 50mm FL	$\kappa_{50} \sim Beta(1,2)$
κ_{120}	Probability of smolting for 0+ Parr of 120mm FL	$\kappa_{120} \sim Beta(2,1)$
$\phi_{1,a}$	First winter survival for a future 1+ parr (0 random effect)	$\phi_{1,a} \sim Beta(2,2)$
$\phi_{1,b}$	First winter survival a future 1+ smolt (0 random effect)	$\phi_{1,b} \sim Beta(2,2)$
$\phi_{3,a}$	Second winter survival for an immature 1+ parr (0 random effect)	$\phi_{3,a} \sim Beta(2,2)$
$\phi_{3,b}$	Winter survival of the second year of life for a mature 1+ parr (0 random effect)	$\phi_{3,b} \sim Beta(2,2)$
ψ_{mean}^{male}	Probability of maturation for a male 1+ parr (0 random effect)	$\psi_{mean}^{male} \sim Beta(1,1)$
$\Delta_{survival}$	First winter survival and summer survival differential	$\Delta_{survival} \sim Beta(2,2)$
σ_{ε}	Variance of the individual random effect	$\sigma_{\varepsilon} \sim \chi^2_{1ddl}$
pL_1	Detection probability at the Leslé Mill in 2006.	$pL_1 \sim Beta(1,1)$
pP_1	Detection probability at the Princes Mill at the 1+ smolt stage in 2006.	$pP_1 \sim Beta(1,1)$
pL_2	Detection probability at the Leslé Mill at the 2+ smolt stage in 2007.	$pL_2 \sim Beta(1,1)$
pP_2	Detection probability at the Princes Mill at the 2+ smolt stage in 2007.	$pP_2 \sim Beta(1,1)$

pA_1	Detection probability of adults (1 year at sea) in 2007.	$pA_1 \sim Beta(1,1)$
Δ_{capt}	Detection probability in autumn of 0+ parr in 2005 and detection probability of 1+ parr in 2006 differential	$\Delta_{capt} \sim Beta(1,1)$

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Article 2

Assessing adaptive phenotypic plasticity by means of conditional strategies from empirical data : the latent environmental threshold model.

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ASSESSING ADAPTIVE PHENOTYPIC PLASTICITY BY MEANS OF CONDITIONAL STRATEGIES FROM EMPIRICAL DATA: THE LATENT ENVIRONMENTAL THRESHOLD MODEL

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Conditional strategies are the most common form of discrete phenotypic plasticity. In a conditional strategy, the phenotype expressed by an organism is determined by the difference between an environmental cue and a threshold, both of which may vary among individuals. The environmental threshold model (ETM) has been proposed as a mean to understand the evolution of conditional strategies, but has been surprisingly seldom applied to empirical studies. A hindrance for the application of the ETM is that often, the proximate cue triggering the phenotypic expression and the individual threshold are not measurable, and can only be assessed using a related observable cue. We describe a new statistical model that can be applied in this common situation. The Latent ETM (LETM) allows for a measurement error in the phenotypic expression of the individual environmental cue and a purely genetically determined threshold. We show that coupling our model with quantitative genetic methods allows an evolutionary approach including an estimation of the heritability of conditional strategies. We evaluate the performance of the LETM with a simulation study and illustrate its utility by applying it to empirical data on the size-dependent smolting process for stream-dwelling Atlantic salmon juveniles.

KEY WORDS: **Bayesian modeling, conditional strategies, environmental threshold model, phenotypic plasticity, quantitative genetics.**

The ability of organisms to adapt to rapidly changing environmental conditions is becoming of applied importance for understanding how they persist (Gienapp et al. 2008; Reed et al. 2010). Phenotypic plasticity (i.e., the ability of a given genotype to produce variable phenotypes, dependent upon environmental conditions) is the most immediate, and potentially adaptive, response of individuals to environmental change (Ghalambor et al. 2007; Gienapp et al. 2008). Its evolution can accelerate phenotypic evolution, which, in turn, can facilitate persistence in new environment (Lande 2009; Chevin and Lande 2010). It can be maintained (i.e., adaptive phenotypic plasticity) in variable environments when reliable cues allow organisms to match their phenotypes to encountered conditions (Ghalambor et al. 2007; Reed et al. 2010). Anthropogenic disturbances and/or climate change can reduce the reliability of cues as indicators of optimal life-history decisions, rendering previously adaptive plastic responses suboptimal in new environmental contexts.

In the case of phenotypic plasticity with discrete traits (e.g., maturation at given age, polymorphism in defensive structures, or alternative mating tactics), the concept of conditional strategies (Gross 1996) has become a popular framework (Roff 2011). Tomkins and Hazel (2007) defined a conditional strategy as a genetically determined decision rule containing a conditional clause. For example, with binary traits, that is, traits with two possible categorical phenotypic states (also known as tactics), the phenotype expressed by an individual may depend on an environmental cue and the choice between phenotypes may result from a physiological "comparison" between the cue and a threshold (or switch point; Oliveira et al. 2008).

Hazel et al. (1990; see also Hazel et al. 2004 and Tomkins and Hazel 2007) developed the environmental threshold model (ETM) for representing a conditional strategy as an environmentally cued threshold trait (Roff 1996). In the ETM, the individual status is determined by the environmental cue, which is compared to the threshold. Thresholds vary among individuals and exhibit additive genetic variance. By incorporating environmental and genetic influences, the ETM encapsulates both phenotypic plasticity and evolutionary change in a unique framework (Tomkins and Hazel 2007). Specifically, changes in the cue distribution directly translate into a change in the phenotype proportions, thereby reflecting phenotypic plasticity. Similarly, evolutionary changes shift the threshold distributions (Hazel et al. 1990) and modify the phenotypic proportions, potentially independently of changes in the distribution of the cue.

Under conditions of sustained directional change, the costs and limits of phenotypic plasticity (DeWitt et al. 1998) require genetic variation in order for populations to continue to adapt to the new conditions by means of natural selection (Pigliucci 2005). With respect to conditional strategies, the ability of the ETM to accommodate both phenotypic plasticity and evolution within a single framework is appealing for assessing the evolution of conditional strategies in the wild (Tomkins and Hazel 2007; Roff 2011). However, for the ETM to be useful in real case studies, its various components (alternative phenotypes, environmental cues, individual genetic effects on the thresholds, and their related distributional parameters) must be quantified. The ETM was initially formalized mathematically (Hazel et al. 1990; Hazel et al. 2004) but statistical tools are needed to draw inferences from empirical data. Here, we make the distinction between "observables" (i.e., those variables that can be directly measured) and "non-observables" (i.e., those variables that can only be inferred, typically the thresholds). Empirical data often produces noisy measures of underlying traits, and it is thus important to account for this uncertainty (or measurement error). We introduce a new statistical modeling framework, which embeds the ETM to make it amenable to proper statistical inference on empirical data.

In the ETM, as the individual thresholds and the parameters of their distribution are conceptual and unknown quantities, they represent non-observable quantities. In contrast, the phenotypes expressed by individuals are observable. Whether the environmental cue is observable is often more complex. The choice of a single and observable environmental feature (e.g., ambient temperature), although logistically tractable, is necessarily to some extent arbitrary as the ways in which organisms perceive their environment is undoubtedly multifactorial (Price and Schluter 1991; Merilä and Sheldon 1999). We follow Dieckmann and Heino (2007) such that "it is more practical to let the organisms themselves do the integration over time and environmental effects." In fish, growth rate and/or size at a given age are known to be strongly influenced by the environment and are thus considered as integrating various environmental factors (Hutchings 2004; Dieckmann and Heino 2007). Rather than considering observable phenotypes as a determinant of the biological process (i.e., size-determining maturation process), we take the alternate approach in assuming that they are a manifestation of an underlying process. We argue that this assumption is biologically more realistic.

Regardless of which way the investigator chooses to measure the environmental cue, be it as an external environmental variable or a biological trait, the proximate mechanism by which the organism assesses its environment will most often remain unknown (Metcalfe 1998; Tufto 2000; Thorpe 2007; Tomkins and Hazel 2007). Therefore, we argue that this source of uncertainty should be explicitly incorporated in a statistical framework to assess conditional strategies by means of the ETM. We propose to split the environmental cue of the ETM into two distinct but related quantities: the *proximate cue* which is to be compared with a threshold that would trigger the phenotype expressed by an individual and an *observable cue* which can be readily measured. Although the proximate cue is unobservable (e.g., underlying physiological mechanisms such as hormones; see Willmore et al. 2007; Aubin-Horth and Renn 2009; McNamara and Houston 2009), it should be correlated with the observable cue (e.g., morphology such as body size or growth; see Fairbairn and Yadlowski 1997). The threshold versus proximate cue comparison is now a fully hidden process as it involves two unobservable variables. This process combines both an environmental effect, through the proximate cue, and a genetic effect, through the threshold. In a modeling context, both aspects need to be distinguished in a model so that they can be interpreted separately. For this reason, we further assume that the threshold is purely genetically determined, in keeping with Roff's (1994) statement that "the critical assumption of the ETM is that there is a single and unique switch point (threshold) for each genotype."

We describe a new statistical model, the Latent ETM (LETM) and highlight its connections with statistical models in quantitative genetics. The LETM structure makes the variation in the additive genetic component of the conditional strategy (the variance of the threshold distribution) relatively easy to estimate. This feature is crucial because the genetic variance of the threshold is a key element for assessing the evolutionary potential of a conditional strategy (Hazel et al. 1990; Hazel et al. 2004; Tomkins and Hazel 2007). In addition, we show that the use of genetic relatedness between individuals is required for the estimation process by separating the threshold genetic variance from random noise in the proximate versus observable cue relationship. Finally, we illustrate our approach with a case study on the size-dependent smolting process for stream-dwelling juvenile Atlantic salmon in the Scorff River (Southern Brittany, France). Overall, the LETM approach can be fruitfully applied whenever the conditional strategy framework is relevant, pending the availability of individual data for at least the alternative phenotypes involved and a related observable cue.

The Latent Environmental Threshold Model

We use the notation $A|B \sim Dist(f(B))$ to denote a set of random variables A distributed conditionally on the set of variables B according to a probability distribution *Dist* with parameters that are a function f of B. Observable quantities are denoted with capital Roman letters and unknowns with Greek letters.

FROM THE ETM TO THE LETM

For an individual i, the threshold modeling framework stipulates that if the value of a cue η_i is larger (respectively lower) than a threshold θ_i, then it triggers the expression of a phenotype, say migrant (respectively resident). If Y_i is the binary variable indicator of the phenotype (e.g., 1 for migrant and 0 for resident), then we have:

$$Y_i = \left\{ \begin{array}{l} 1 \text{ if } \eta_i \geq \theta_i \\ 0 \text{ if } \eta_i < \theta_i \end{array} \right\}. \tag{1}$$

The cue η_i varies among individuals as a function of the environment, whereas the threshold θ_i is considered an intrinsic property of the individuals, independent of η_i. The threshold θ_i also varies among individuals and is a polygenic quantitative trait that is normally distributed with mean μ_θ and standard deviation σ_θ, as typically assumed in quantitative genetics (Hazel et al. 1990; Lynch and Walsh 1998; Tomkins and Hazel 2007):

$$\theta_i \mid \mu_\theta, \sigma_\theta \sim N(\mu_\theta, \sigma_\theta). \tag{2}$$

Equations (1) and (2) and their associated assumptions correspond exactly to the ETM (Hazel et al. 1990). Equation (1) represents the putative proximate mechanism explaining the phenotypic expression. In this mechanism, the phenotype Y_i is observable, whereas the threshold θ_i is not; it is a conceptual variable referred to as a latent variable in statistical terminology (Congdon 2007).

We introduce two additional assumptions in the specification of the LETM. First, we assume that the proximate cue η_i is unobservable. By doing so, we explicitly recognize that often little biological knowledge is available regarding the proximate mechanism influencing the expression of the phenotype (Metcalfe 1998; Thorpe 2007; Tomkins and Hazel 2007). Although η_i is not observable, an observable proxy X_i can be measured which is correlated with η_i. The distribution of the unknown proximate cue η_i can be expressed conditionally on the observable proxy X_i with some residual error ε_i:

$$\eta_i = F(X_i) + \varepsilon_i, \tag{3}$$

where F is a function, for example, a linear relationship, summarizing the link between the proximate and the observable cue. The residual error ε_i is assumed normally distributed with mean 0 and standard deviation σ_η:

$$\varepsilon_i \sim N(0, \sigma_\eta). \tag{4}$$

Note that equations (3) and (4) correspond to the Berkson measurement error model in the statistical literature (Congdon 2007). This formulation has the advantage of being assumption free regarding the distribution of the X_i. Consequently, the statistical analysis is made more flexible as it is independent of the procedure used for collecting the X_i observations. They can come either from field sampling or from controlled experiments.

The second assumption is in line with Roff's (1994) statement that there may be a unique threshold for each genotype. Specifically, we consider the threshold θ_i as being completely genetically determined which implies that the standard deviation σ_θ in equation (2) is a measure of genetic variability. This was also proposed by Hazel et al. (1990) to show the effect of the selection on the threshold distribution. By doing so, the various components involved in the model are clearly distinguished, hence making the inference process easier: the environment, the proximate mechanisms triggering the phenotype expression (conditionally on the environment), and the genetic control on this mechanism.

The statistical model defined by equations (1)–(4) considers the ETM as a latent structure connecting the observed environment with the observed phenotypes. We, therefore, refer to it as the LETM. The conditional structure of the LETM can be summarized by a directed acyclic graph (Fig. 1).

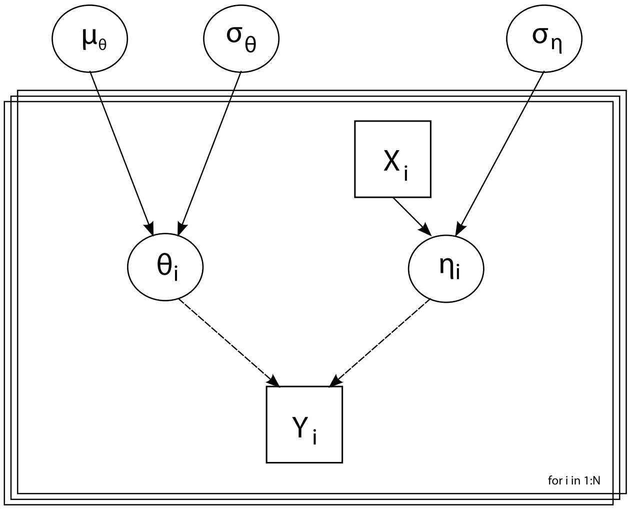

Figure 1. **Directed acyclic graph of the latent environmental threshold model. Squares represent observable data and circles represent unknown quantities to be estimated. For an individual *i*, the threshold θ_i is normally distributed with mean μ_θ and standard deviation σ_θ. The proximate cue η_i is normally distributed with a mean of the observable cue X_i and standard deviation σ_η. Finally, Y_i is a binary indicator variable of the observed phenotype and is modeled as a function of the threshold and the proximate cue at the individual level, with $Y_i = 1$ when $\theta_i < \eta_i$. Solid and broken arrows represent stochastic and logical dependence, respectively. The model is fit to observations of phenotyped individuals, hence the boxes denoting a loop over $i = 1, 2, \ldots, N$ individuals.**

ALTERNATIVE FORMULATION OF THE LETM

Equation (1) can be reformulated as:

$$Y_i = \begin{Bmatrix} 1 \text{ if } z_i \geq 0 \\ 0 \text{ if } z_i < 0 \end{Bmatrix}, \tag{5}$$

where z_i is the difference (η_i - θ_i) between the proximate cue and the individual threshold. Taking the proximate versus observable distinction into account (eq. 3), z_i is given by:

$$z_i = X_i - \theta_i + \varepsilon_i, \tag{6}$$

where ε_i and θ_i, are independent and normally distributed (eqs. 2 and 4), hence z_i is normally distributed with mean ($X_i - \mu_\theta$) and variance $\sigma_P^2 = \sigma_\theta^2 + \sigma_\eta^2$.

From equations (5) and (6), the LETM can be seen as a threshold model often used in quantitative genetics to model binary traits (Falconer 1981; Gianola 1982; Sorensen et al. 1995). In a threshold model, Y_i is distributed as a Bernoulli distribution with probability p_i, where

$$p_i = \Pr(Y_i = 1) = \Pr(z_i \geq 0) = \Phi\left(\frac{X_i - \mu_\theta}{\sqrt{\sigma_\theta^2 + \sigma_\eta^2}}\right), \tag{7}$$

where ϕ is the cumulative distribution function of a standardized normal distribution.

In this framework, z_i is a latent variable often called a liability. Equation (6) is analogous to a standard "animal model" (Kruuk 2004; Wilson et al. 2010) and splits z_i into three terms: X_i the observed cue is a fixed effect, θ_i the threshold is a random additive genetic effect (also called the genetic value or the breeding value for individual *i*), and ε_i is a residual error term. In the animal model, σ_P^2 is the total phenotypic variance and the ratio of the additive genetic variance (σ_θ^2) to the total phenotypic variance (σ_P^2) is the heritability (h^2) of the latent trait z_i. It is also considered as the heritability of the associated conditional strategy (Lynch and Walsh 1998).

IDENTIFIABILITY ISSUES

The animal model is known to be prone to identifiability issues (i.e., difficulty in distinguishing variance components in the estimation process) as it combines several unobservable random effects (Kruuk 2004; Wilson et al. 2010). Regarding the LETM, the issue lies in the separation of the genetic effects represented by the threshold θ_i from the residual error term ε_i. When data are available only for the observable cue X_i and the alternative phenotypes Y_i, there is potential confusion between the genetic variance σ_θ^2 and the residual error variance σ_η^2. As a consequence, only the total phenotypic variance (σ_P^2) is identifiable, whereas the proportion of total variance explained by the variability in the threshold—that is, the heritability $h^2 = \sigma_\theta^2/\sigma_P^2$—is not. To circumvent this issue, additional information is required. To make the animal model identifiable, pedigree data on individual relatedness are used and the individual phenotypes are considered as nonindependent because related individuals share genes. More specifically, the individual additive genetic effects covary and the structure of the covariance matrix depends on the relatedness between individuals. In the case of the LETM, we assume that the individual thresholds θ_i covary according to the individual relatedness, equation (2) therefore becomes:

$$\theta_i \mid \mu_\theta, \sigma_\theta^2, A \sim \text{MVN}(\mu_\theta, G), \tag{8}$$

where MVN is the multivariate normal distribution, θ is the vector of thresholds (i.e. additive genetic effects), and G is the variance–covariance genetic matrix. The matrix G is given by $G = A \times \sigma_\theta^2$, where A is the additive genetic relationship matrix and σ_θ^2 is the additive genetic variance. The additive genetic relationship matrix A contains all the pairwise values of relatedness (two times the coefficient of coancestry, i.e., 0.5 for parent–offspring pairs and full siblings, 0.25 for half siblings, and 0.125 for first cousins; see Wilson et al. 2010 for more details).

BAYESIAN STATISTICAL INFERENCE

Bayesian approaches using Markov chain Monte Carlo (MCMC) algorithms provide a flexible framework for analyzing latent variables models and their conditional structure (Clark 2004). We therefore adopted this approach to fit the LETM to data. Specifically, the Bayesian approach combines the likelihood (i.e., information derived from the observed data) and the prior distribution of the unknown quantities (i.e., knowledge available before the data were observed) to produce a joint probability distribution of all model unknowns, conditionally on the observed data (the so-called joint posterior distribution; see Gelman et al. 2004; Ellison 2004 and McCarthy 2007; for more details about the Bayesian statistical modeling). If the (noninformative) prior and the posterior distributions of a given parameter largely overlap, then there is not enough information in the data to estimate this parameter. The joint posterior distributions of all the model unknowns, that is, the parameters (μ_θ, σ^2_θ, σ^2_η), the individual thresholds, and the proximate cues (θ_i, η_i), were obtained by means of MCMC sampling as implemented in the OpenBUGS software (Lunn et al. 2009). The code of the LETM as well as an example of data are available at (http://www.cefe.cnrs.fr/biom/zips/LETM.txt). We ran two parallel MCMC chains and retained 25,000 iterations after an initial burn-in of 5000 iterations. Convergence of MCMC sampling was assessed by means of the Brooks-Gelman-Rubin diagnostic (Brooks and Gelman 1998).

A Bayesian analysis requires specifying prior probability distributions for the model parameters, that is, the unknown quantities that are not conditioned by any other quantity in the model (μ_θ, σ_θ, σ_η; Fig. 1). In our study, all priors were noninformative or weakly informative (e.g., priors on threshold and proximate cue variance). The prior on the mean of the threshold distribution μ_θ was specified as a normal distribution with mean 0 and a large variance (1000). To make the assessment of identifiability issues easier, priors on the standard deviations σ_θ and σ_η were not defined directly but rather on the total phenotypic variance and the heritability h^2. Note that because there is a one-to-one transformation relating (σ^2_P, h^2) to (σ^2_θ, σ^2_η), assigning a prior to (σ^2_P, h^2) induces a prior on (σ^2_θ, σ^2_η) as well (Gelman et al. 2004). We used a uniform distribution between 0 and a large value (100) for σ_P as recommended by Gelman (2006) and a uniform distribution between 0 and 1 for h^2.

Simulation Study

We evaluated the performance of the LETM for statistical inference, with simulated data. The simulation model was the LETM itself with known parameter values and including three common genetic structures for the θ_i's, that is, full siblings, half siblings, and a mixture of both. The covariation in the θ_i's according to their relatedness (eq. 8) was explicitly included in the simulation model. Note that clonal genetic structure can be used (coefficient of relatedness equal to 1; see Ostrowski et al. 2000 for an illustration of such an experimental protocol) but we believe our approach is more realistic regarding data at hand for ecologists and evolutionists. Statistical inference was then derived from the simulated data to check whether the LETM provided accurate estimates of the parameters (μ_θ, σ^2_θ, σ^2_η) and of the individual latent variables (the thresholds θ_i and proximate cues η_i). Genetic information regarding the θ_i's was incorporated in the fitting process.

We generated 20 datasets consisting of 400 individuals and structured as 20 batches of 20 individuals. Within each batch individuals were either full sibling, half sibling, or a mixture of both, whereas between batch, individuals were unrelated. First, the threshold values were generated from the multivariate normal distribution with mean $\mu_\theta = 0$ and a genetic variance–covariance matrix G. The matrix G is the product of an additive genetic relationship matrix A and genetic variance (eqs. 2 and 8). The additive genetic relationship matrix A was generated according to each of the three designs: (1) with values of relatedness of 0.5 between individuals within a batch in the case of the "full sibling design," (2) 0.25 for the "half sibling design," and (3) a mixture of both in the "mixture design." In the latter case, we simulated a pedigree for each batch from the R package "GeneticsPed" (Bioconductor). First, we sampled the number of potential breeders in a Poisson distribution with parameter set to 2 for both sexes (i.e., generating two potential breeders on average for each sex). GeneticsPed generated pedigree from potential breeders allowing the reconstruction of kin groups (mixtures of full siblings and half siblings and sometimes higher degrees of relatedness such as cousins if required) and the associated additive genetic relationship matrix A. The threshold (i.e., genetic) variance was fixed to 0.5. Second, we generated an observed cue X_i value for each individual i from a normal distribution with mean 0 and standard deviation 1. For each individual i, given the value of the observed cue X_i, we generated its proximate cue η_i from a normal distribution with mean X_i and variance $\sigma^2_\eta = 0.5$ (eq. 3). Thus, the "actual" total phenotypic variance is 1 and the "actual" heritability of the conditional strategy is 0.5 in the data simulation model. Finally, given the values of the proximate cue η_i and that of the threshold θ_i, we assigned the phenotype indicator values Y_i (eq. 1). Note that simulated data are more variable in the proximate cue than in their threshold, as it should often be the case with real data (Tomkins and Hazel 2007).

Application to Alternative Life-History Tactics in the Atlantic Salmon

The Atlantic salmon is an anadromous species that occupies both freshwater and the ocean during its life cycle (Verspoor et al.

2007). In Brittany, the juvenile phase in freshwater lasts one or two years (Baglinière et al. 1993). Thereafter, fish migrate to the ocean and return after one or two years to their native stream to breed. Atlantic salmon are conditional strategists with state-dependent choice among alternative life-history tactics (Hutchings and Myers 1994; Gross 1996; Thorpe et al. 1998; Garant et al. 2003; Hutchings 2004; Hutchings 2011). During their first year of life in their natal river, young of the year (YOY; i.e., individuals less than one year old) can either migrate to the ocean the next spring or reside in freshwater for an additional year (Thorpe et al. 1998). The choice between the migrant versus the resident alternative tactics (i.e., phenotypes) is related to the size of the individuals in their first autumn (Nicieza et al. 1991; Thorpe et al. 1998; Thorpe and Metcalfe 1998).

Although size is an observable cue, it is probably best considered as a proxy for energetic status (Thorpe et al. 1998), that is, likely a more proximate cue, which is to be compared to a threshold for triggering seaward migration the next spring (Thorpe et al. 1998; Mangel and Satterthwaite 2008; Satterthwaite et al. 2010). The individual energetic status influences this life-history choice (Jonsson and Jonsson 2005) because migration to the ocean is preceded by the smolting process, which is an energetically costly process of preparing individuals for seawater life (McCormick and Hansen 1998; Thorpe et al. 1998). The energetic status reflects the way that energy is acquired, stored, and used; and is strongly influenced by the environmental conditions experienced by each individual (e.g., food availability, temperature regime, or density of conspecifics; Elliott and Hurley 1997; Forseth et al. 2001; Jones et al. 2002; Imre et al. 2005; Murphy et al. 2006; Finstad et al. 2010). Under the LETM, we consider migrant versus resident (at one year of age) as alternative phenotypes and size in autumn of YOYs as an observable cue indicative of the individual energetic status (i.e., the proximate cue triggering phenotype expression).

DATA COLLECTION

In autumn 2006, YOY juveniles were sampled by electrofishing at 39 stations along the main course of the Scorff. Every fish captured was measured (fork length, to the nearest 1 mm) and individually marked with a passive integrative transponder (PIT) tag (11 mm long, 2.2 mm in diameter) inserted into the peritoneal cavity according to the protocol described in Acolas et al. (2007). One-year old seaward migrating juveniles (smolts) previously PIT tagged were identified during their downstream migration in the spring of 2007. They were captured at two successive traps located at the lower end of the river system below all sites in which YOY were marked. At both facilities, their individual PIT tags were identified. Eventually, PIT-tagged anadromous salmon were recaptured in 2008 and 2009 when returning into the Scorff river after one or two years at sea. They were sampled at the Princes Mill facility in a trap designed to catch upstream migrating adults. PIT tagged resident juveniles, that is, future two years old smolts, were identified in autumn 2008 using sampling by electrofishing according to same protocol used for the YOY the previous year. Two-year old smolts were also recaptured the following spring (2009) and identified by their PIT tags.

Here, we considered the set of YOY juveniles marked in autumn 2006 and recaptured later on ($n = 104$). For each of them, we recorded both its phenotype (migrant vs. resident) and its observable cue (fork length at first autumn).

MODELING

For each individual i, the proximate cue η_i (energetic status) was assumed to be normally distributed with the mean of its fork length at first autumn $\mathrm{Fl_i}$ (the observable cue) and standard deviation σ_η (eq. 3). The alternative phenotype indicator Y_i (eq. 1) takes the value 1 if individual i migrates to sea at one year of age, and 0 if it stays an additional year in fresh water.

As YOY juveniles tend to stay close to their natal spawning nest (Beall et al. 1994; Einum et al. 2008; Foldvik et al. 2010), we assumed that YOY captured in the same station in autumn could be all brothers and sisters (i.e., full-siblings' genetic structure) or half brothers and half sisters (i.e., half-siblings' genetic structure) or, a mixture of both (i.e., mixtures' genetic structure). These assumptions were made to illustrate the greater genetic similarity of YOY salmon within, than between, sites. The mixture design is probably the most realistic option because of complex mating patterns in Atlantic salmon with both sexes having several partners (Thériault et al. 2007). In the mixture design, we assumed that the number of potential breeders was low at each sampling stations and that males outnumbered females (Jordan and Youngson 1992; Grimardias et al. 2010). As the pedigree of the fish sampled is unknown, we generated 20 mixtures' genetic structure (i.e., additive genetic relationship matrix A) according to the same protocol as in the simulation study (see "Simulation study" section above) with each station corresponding to a batch made of a mixture of full siblings, half siblings (and first cousins if required).

Results

SIMULATION STUDY

Whatever the genetic structure considered, the comparison of posterior and prior distributions showed that the information contained in the data led to considerable updating of the prior distributions. The LETM properly estimated the threshold mean μ_θ and the total phenotypic variance; the posterior medians of these parameters were close to their true value (Fig. 2). The posterior distributions of σ^2_θ and σ^2_η were well estimated too indicating that these parameters were identifiable. The heritability h^2

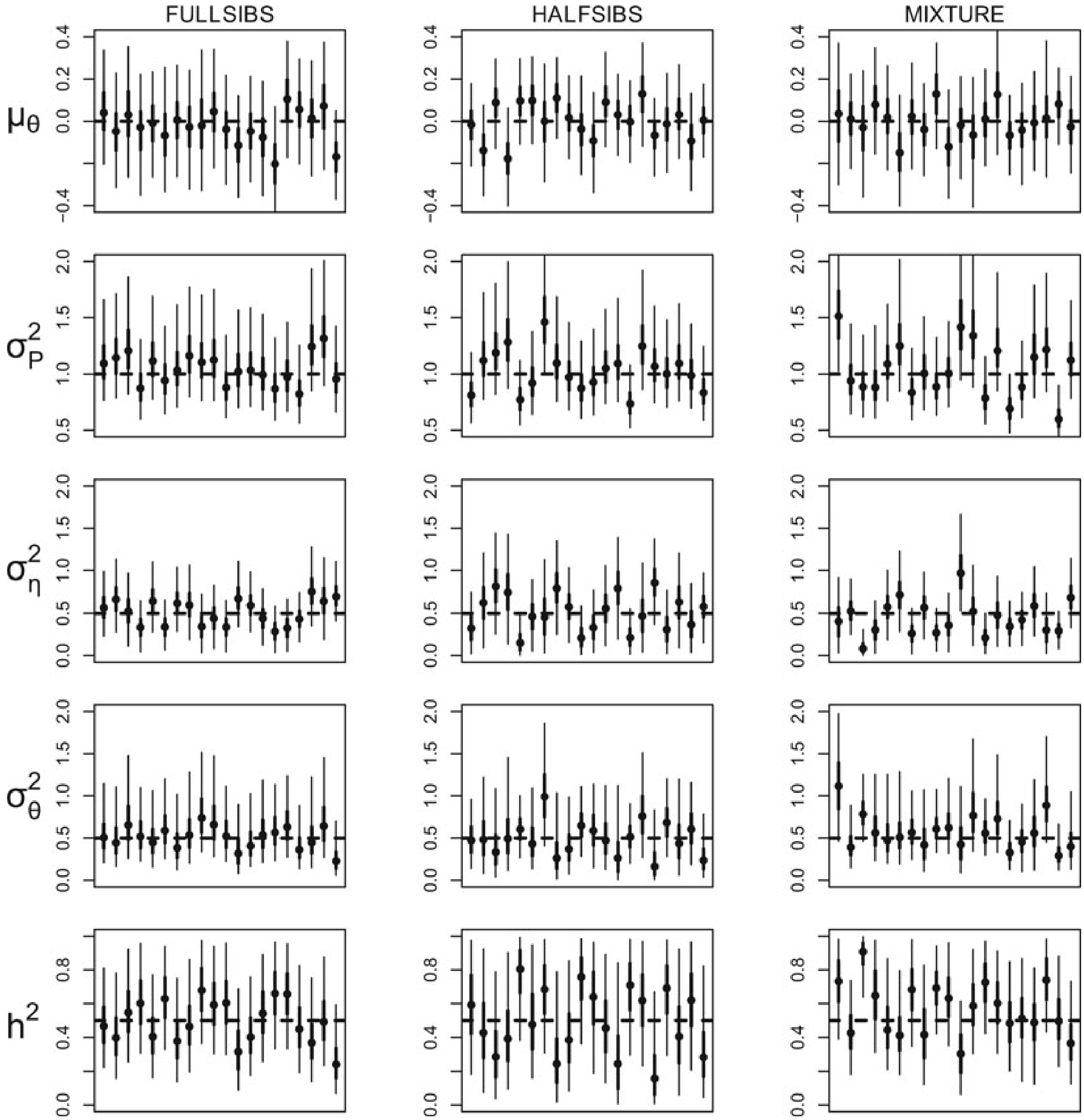

Figure 2. Posterior distributions of the latent environmental threshold model parameters for each genetic structure (full siblings, half siblings, and mixture) and for 20 replicate datasets. The median (black point) and the 95% posterior probability interval (solid lines) are displayed based on 25,000 Markov chain Monte Carlo samples. The actual values are also displayed (dashed lines).

could therefore be estimated: its posterior distribution was much narrower than its prior and the actual value was very close to the posterior median (Fig. 2). In fullsibs design, uncertainty was smaller than in halfsibs design confirming that the power to infer from half-sibling families is less than from full-sibling families (Roff 1997). Uncertainty in the mixture design was intermediate.

At the individual level, the proximate cue η_i and the threshold θ_i were estimated without systematic bias and the actual simulated values fell in most instances within the 95% posterior probability interval (PPI, also called credible interval, which is defined as the interval between the 2.5 and 97.5 percentiles of the posterior distribution; Fig. 3).

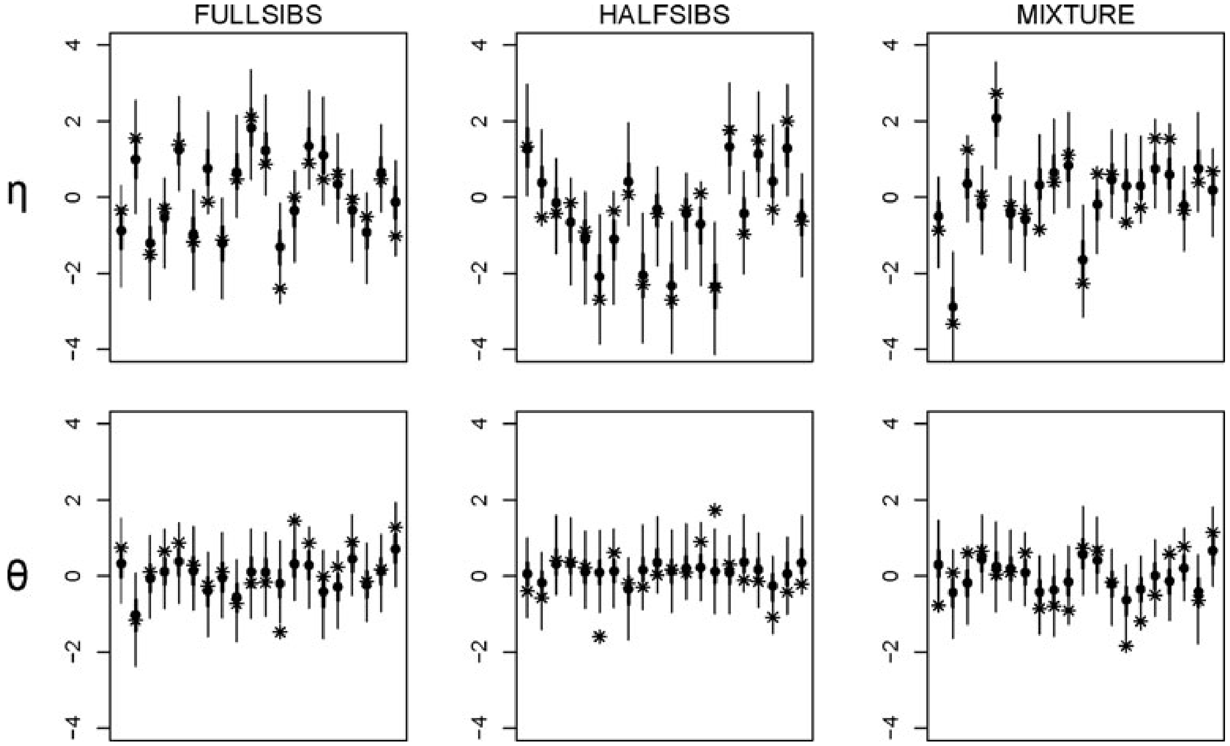

Figure 3. Posterior distributions of proximate cue η_i and threshold θ_i for the latent environmental threshold model for one randomly chosen individual in each of the 20 batches of 1 (out of 20) replicate datasets. The median (black point) and the 95% and 50% posterior probability interval (solid lines and bold lines, respectively) are displayed based on 25,000 Markov chain Monte Carlo samples. The actual values are also displayed (stars).

CASE STUDY

Using the LETM framework, we were able to obtain precise estimates of the mean latent threshold μ_θ and the total phenotypic variance whatever the genetic structure considered (Fig. 4). The posterior distribution of the heritability h^2 showed the information contained in the data led to substantial updating of the prior distribution, indicating that σ^2_θ and σ^2_η could be identified. h^2 posterior distribution favors a high heritability value with a posterior mean of approximately 0.77. In agreement with the simulation study, results were very similar between genetic designs. In fullsibs design, uncertainty was smaller than in halfsibs design whereas mixture design was intermediate depending on proportions of fullsibs and halfsibs.

Estimates of the proximate cue and of the threshold at the individual level were also obtained (Fig. 5). Again, results were very similar between genetic designs. YOY salmon appeared much more variable in the proximate cue than in their threshold. The proximate cue is a conceptual quantity and, as such, its scale is arbitrary. Here, given the measurement error structure of the LETM (eq. 3), its scale is the same as that of the observed cue. For example, a proximate cue 90 can be interpreted as the mean energetic status of a YOY with a 90-mm-long fork in autumn. For the same reason, the mean threshold μ_θ can be either interpreted as the energetic status (proximate cue; eq. 5) or the fork length in autumn (observed cue; eq. 6) of a YOY salmon having an equal probability of becoming migrant or resident.

Discussion

Conditional strategies are the most common form of discrete phenotypic plasticity within species (Gross 1996). Understanding how plasticity, in general, and these strategies, specifically, evolve and are maintained by natural selection is crucial for our understanding of phenotypic and life-history evolution (Pigliucci 2005). The ETM accounts for both genetic variation and environmental cues that affect phenotypic expression. For this reason, in their review of the theoretical models that have been proposed to understand the evolution of phenotypic plasticity in the conditional strategy framework, Tomkins and Hazel (2007) argued that the ETM is "the best model available currently for understanding the evolution and maintenance of conditional strategies." Nonetheless, the ETM has rarely been applied to the study of adaptive phenotypic plasticity both in the wild (Edeline 2007 refers to it but in a rather qualitative way) and under

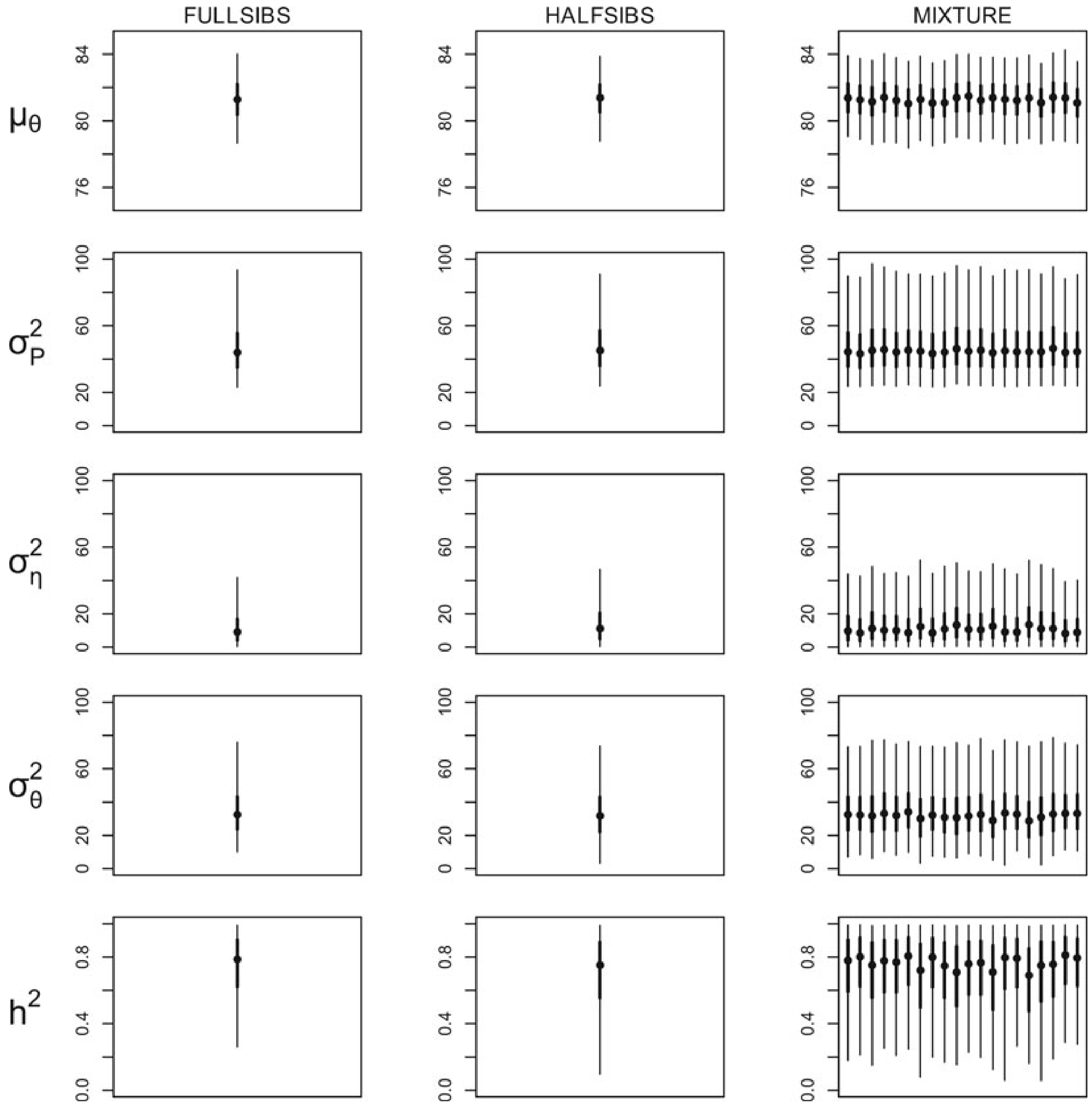

Figure 4. Posterior distributions of the latent environmental threshold model parameters for Atlantic salmon data from the Scorff. Parameters for each genetic structure, that is, full siblings, half siblings, and mixture is shown. For the later, 20 putative mixtures are represented. The median (black point) and the 95% and 50% posterior probability interval (solid lines and bold lines, respectively) are displayed.

controlled experimental conditions (Ostrowski et al. 2000). We believe this is because the ETM was not conceived as a statistical tool to deal with observed data. Here, we developed a statistical model, the LETM that includes the ETM as its core theoretical process.

Several methods exist to estimate heritability (see Roff 1997 for a review). However, most of them are not appropriate for assessing heritability of conditional strategies with empirical data, especially when collected in the wild. Indeed, they have been developed to analyze data obtained in controlled/laboratory conditions involving no environmental variations and perfect knowledge of the pedigree, including sometimes parents' phenotype. Our approach does not suffer from these restrictions and can be applied with only relatedness data although the parents of the observed individuals are unknown. The "Fullsibs'method" (i.e., an analysis of variance based approach) is the only classical method

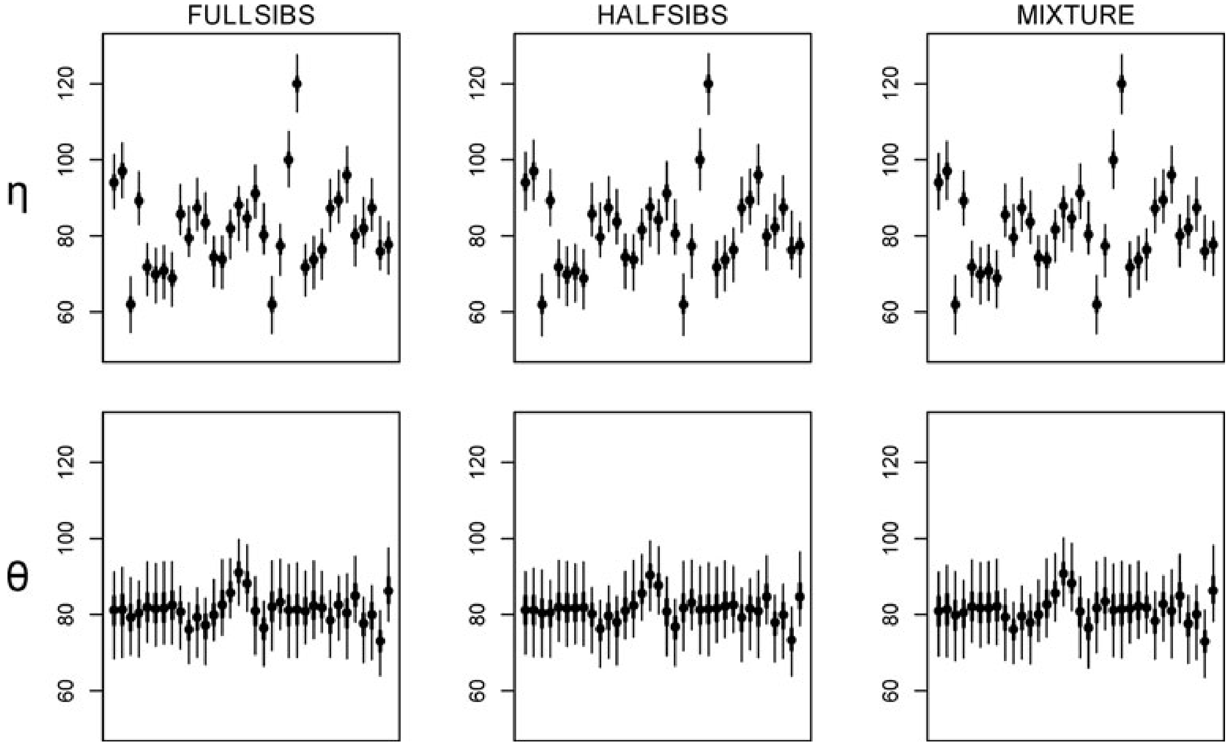

Figure 5. Posterior distributions of proximate cue η_i and threshold θ_i for the latent environmental threshold model for one individual randomly picked in each station along the main course of the Scorff and for each genetic structure, full siblings, half siblings, and mixture. For the later, one mixture was randomly picked out of the 20 putative mixtures. The median (black point) and the 95% and 50% posterior probability interval (solid lines and bold lines, respectively) are displayed.

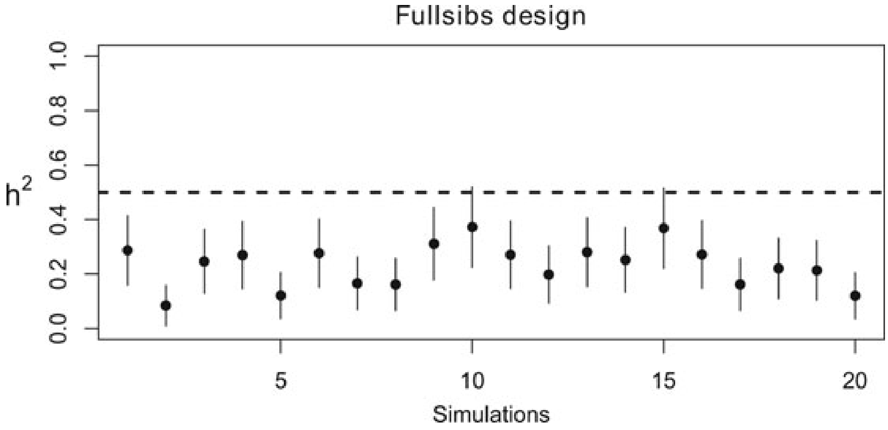

Figure 6. Mean and standard deviation of the heritability estimates calculated using the classical "Fullsibs methods" (see Roff 1997) for the 20 replicated datasets used to test the latent environmental threshold model. The actual value is also displayed (dashed lines).

listed in Roff (1997) that can be applied to our data. We used it (see usual formulas in Roff, 1997) to analyze our simulated datasets (fullsibs design). In contrast with our LETM, this method systematically underestimates heritability of conditional strategies (Fig. 6).

The originality of our approach lies in the observable versus proximate cue distinction, with the latter being unobservable but effectively triggering the phenotypic expression. As a consequence, the ETM becomes a fully embedded process within the LETM, linking the observable environment to the observable phenotype. We take advantage of this feature to explicitly separate the genetic component from the environmental component involved in a conditional strategy. The LETM allows the estimation not only of the parameters of the threshold distribution, but also of the proximate cue and the threshold at the individual level. As the LETM is a statistical model inspired by quantitative genetics, individual relatedness data can be used to circumvent the identifiability issue affecting the heritability of the conditional strategy. The accuracy of the genetic threshold variance estimates, a key parameter for assessing the evolutionary potential of a conditional strategy (Tomkins and Hazel 2007), is subsequently improved. When data are only available for the alternative phenotypes and the observable cue, the LETM is not fully identifiable.

The proposed distinction between observable and (unobservable) proximate cues is supported by Ostrowski et al.'s (2000) study on the snail *Bultinus truncatus*. They tested the ETM in a set of experiments in which both the genotype and the environment were controlled. In contrast with what was expected under the ETM, they observed significant random variation in the phenotypic expression for any environment × genotype combination they used. They hypothesized that microenvironmental, uncontrolled variation in the threshold explained this residual random variation. We contend the proximate versus observable cue dichotomy is a more sensible alternative hypothesis. In the case of Ostrowski et al. (2000)'s study, it would mean that the organisms assess temperature—the observable environmental cue that is experimentally controlled—through an unknown proximate mechanism with some random "measurement error." The proximate cue would then only be correlated with temperature.

Despite the introduction of the proximate versus observable cue distinction, the LETM is still a relatively simple model in the version we presented here. This transpires from its formulation as specific case of an animal model (eq. 6; see Kruuk 2004; Kruuk and Hill 2008; Wilson et al. 2010). Building upon the LETM outlined here to incorporate more complex structures could allow further improvements in parameter estimation. When biological traits are used as an observable environmental cue, the latter can have a genetic component (Gienapp and Merilä 2010), which could be correlated to the genetic threshold. For example, in salmonids, fish size is considered as an observable environmental cue, but it has also a genetic basis and is heritable (Garant et al. 2003; Thériault et al. 2007; Carlson and Seamons 2008; Serbezov et al. 2010; Varian and Nichols 2010). There is no theoretical reason to restrain the complexity of the animal model within the LETM framework for improving its biological realism. The statistical ecologist working with empirical data, however, might be constrained by identifiability issues, given the information available in the data in hand. This is especially true for the LETM due to its threshold structure. Indeed, for the variable z_i (eq. 6), we have only censored information through the observation of the phenotype (i.e., z_i is positive or negative, eq. 5) and not an exact measurement as is usual when the quantitative trait is readily observable. This difficulty is illustrated in the simulation experiment and the salmon case study. With a large number of simulated individuals, reasonably precise heritability estimates could be obtained, indicating that the model was identifiable. In contrast, less precise estimates of heritability were obtained from our case study data (posterior mean $h^2 = 0.77$, $\mathrm{SD} = 0.18$ for fullsibs design), which was based on a much smaller number of individuals ($n = 104$) suggesting identifiability issues. Using an experimental setting of common rearing of half-sibling families (866 individuals), Páez et al. (2010) had also low precision in heritability estimates for a binary "propensity to migrate" in Atlantic salmon ($h^2 = 0.77$, $\mathrm{SD} = 0.33$). Similar results were obtained from a simulation with 20 groups each made of five brothers and sisters with heritability fixed to 0.8 (results not shown). The presence of additive genetic variance suggests that life-history tactic for migration can respond to selection, whether natural and/or human induced, through evolution of the threshold (Hutchings 2011; Páez et al. 2010). At the same time, in our case study the additive genetic variance of the threshold (σ^2_θ) is low compared to the total variance of the proximate cue, that is, the sum of the empirical variance of the observed cue ($\sigma^2_X = 168.7$) and σ^2_η. This is consistent with the conditional strategy framework for phenotypic plasticity, which implies the adoption of a tactic (i.e., a phenotype) is primarily due to environmental influence.

Although many theoretical approaches have been proposed for studying evolution of phenotypic plasticity and its consequences on adaptation and persistence capacities of population (see Lande 2009; Reed et al. 2010), there is still a paucity of ecological empirical studies assessing the evolution of phenotypic plasticity in the wild (Nussey 2005; Nussey et al. 2007; Charmantier et al. 2008), and more particularly of conditional strategies (but see Ostrowski et al. 2000 under controlled conditions; Piché et al. 2008 and Páez et al. 2010). The LETM opens up interesting prospects for the study of phenotypic plasticity using observational data. It is a generic tool that could be applied to a wide range of taxa and to different forms of conditional strategies, for example, the induction of defenses against predators (Hammill and Rogers 2008), polyphenic traits in insects (Moczek 2010; Tomkins and Moczek 2009), filial cannibalism (Takeyama et al. 2006), and alternative reproductive tactics (Gross 1996; Piché et al. 2008; Pitnick et al. 2009). By incorporating cues that allow organisms to match their phenotypes to the conditions encountered, it improves our ability to predict how populations will respond to environmental changes (Reed et al. 2010). It also facilitates the quantification of patterns of quantitative genetic variation and heritability of conditional strategies. Although full-siblingship and/or half-siblings genetic structure was assumed both in our simulated data and in our illustrative salmon case study, the LETM can be applied to any other pedigree structure, keeping in mind that "the power of a quantitative genetic analysis (also) depends crucially on the pedigree structure" (i.e., its connectedness; Wilson et al. 2010).

In the context of rapid and global environmental change, both evolution and plasticity are likely to prove critical for species adaptation (Gienapp et al. 2008). The joint appraisal of both phenomena from observational data is required, for which the use and further developments of the LETM should help.

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Article 3

Investigating Evolutionary Trade-Offs in Wild Populations of Atlantic Salmon (Salmo Salar) : Incorporating Detection Probabilities and Individual Heterogeneity

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INVESTIGATING EVOLUTIONARY TRADE-OFFS IN WILD POPULATIONS OF ATLANTIC SALMON (*SALMO SALAR*): INCORPORATING DETECTION PROBABILITIES AND INDIVIDUAL HETEROGENEITY

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Evolutionary trade-offs among demographic parameters are important determinants of life-history evolution. Investigating such trade-offs under natural conditions has been limited by inappropriate analytical methods that fail to address the bias in demographic estimates that can result when issues of detection (uncertain detection of individual) are ignored. We propose a new statistical approach to quantify evolutionary trade-offs in wild populations. Our method is based on a state-space modeling framework that focuses on both the demographic process of interest as well as the observation process. As a case study, we used individual mark–recapture data for stream-dwelling Atlantic salmon juveniles in the Scorff River (Southern Brittany, France). In freshwater, juveniles face two life-history choices: migration to the ocean and sexual maturation (for males). Trade-offs may appear with these life-history choices and survival, because all are energy dependent. We found a cost of reproduction on survival for fish staying in freshwater and a survival advantage associated with the "decision" to migrate. Our modeling framework opens up promising prospects for the study of evolutionary trade-offs when some life-history traits are not, or only partially, observable.

KEY WORDS: **Bayesian inference, cost of reproduction, life-history theory, selective survival, state-space model.**

Life-history theory seeks to explain the complexity of life cycles and diversity of living organisms through the action of natural selection on evolutionary mechanisms (Stearns 1992). Life histories are marked by the expression of traits that are closely related to fitness such as age, fertility, or longevity. The evolution of life-history traits (e.g., demographic parameters such as survival probability or number of offsprings produced), and associated plasticity, can affect population dynamics (Roff 1992; Proaktor et al. 2008) as well as determine the ability of individuals to adapt to environmental change (Roff 1992; Stearns 1992; Clutton-Brock 1998; Roff et al. 2006).

If life-history traits were independent, individuals would simply tend to optimize each trait to maximize individual fitness. Because resources (time, space, energy) are limited, individuals must allocate resources among the various functions essential to survival and reproduction (Van Noordwijk and De Jong 1986). When life-history traits are positively dependent on the same resource, they are negatively related to each other. This interdependence is called an evolutionary trade-off (Van Noordwijk and De Jong 1986; Roff 1992; Stearns 1992). The trade-off can be optimized by natural selection as it ultimately influences fitness (Roff 1992; Stearns 1992; Roff et al. 2006).

Stearns (1992) defines 45 kinds of trade-offs between life-history traits, of which the costs of reproduction (trade-offs between reproduction and survival, current, and future reproduction or growth) are the most often studied (Stearns 1992; Roff and Fairbairn 2007). Trade-offs are considered one of the most critical factors in the evolution of life-history traits and therefore play a key role in the life-history theory (Stearns 1992; Clutton-Brock 1998). Interest in studying life-history trade-offs and their consequences under natural conditions is growing (Clark and Martin 2007; Harshman and Zera 2007; Townsend and Anderson 2007), with particular emphasis on accounting for individual quality (Bonenfant et al. 2003; Proaktor et al. 2008; Weladji et al. 2008; Hamel et al. 2009).

The study of evolutionary trade-offs has long been limited by inappropriate methods and affected by many confounding factors (Townsend and Anderson 2007). To highlight trade-offs, individual fitness components need to be assessed. This suggests tracking an individual for all, or part of, its life history. Manipulative approaches to studying trade-offs has revealed much useful information (Zera and Harshman 2001; Harshman and Zera 2007). However, the patterns highlighted through such studies are only "potential" trade-offs (Viallefont et al. 1995; Townsend and Anderson 2007) because studying evolutionary trade-offs in a controlled environment does not take environmental interactions into account (Stearns 1992).

The study of evolutionary processes under natural conditions raises methodological issues. First, the exhaustive monitoring of individuals over time is often impossible in the wild. The detection of an individual is often a random process, with a probability of detection less than 1. Consequently, two important components of fitness—survival and reproduction—are only partially observed: if an individual goes undetected, is it dead or alive? If alive, is it breeding or not? This issue of uncertain detection has long been ignored in evolutionary biology (Clobert 1995; Cam 2009; Conroy 2009), which might have led to flawed inference when addressing evolutionary questions (Gimenez et al. 2008; Hadfield 2008; Nakagawa and Freckleton 2008). Uncertainty in the observation process can also be inherent in the sampled individuals when some traits cannot be fully observed (e.g., reproductive state) or precisely measured (e.g., size; Catchpole et al. 2008; Hadfield 2008; King et al. 2008).

In addition, accounting for individual quality in trade-offs analyses has been problematic because of the inequality of individuals with regard to the acquisition of resources (Stearns 1992; Cam 2009). This variation in individual quality may interfere with identifying trade-offs (Nichols et al. 1994; Doughty and Shine 1997; Cam et al. 2002). For example, Blums et al. (2005) concludes that both reproductive and survival components of fitness are positively correlated with individual quality for females of three duck species and consequently impair the identification of a cost of reproduction. Weladji et al. (2008) in female reindeer (*Rangifer tarandus*) and Hamel et al. (2009) in ungulate populations demonstrate that the heterogeneity in individual quality overrides trade-offs between current reproduction and future performance. These recent studies concluded that individual heterogeneity should be accounted for when assessing trade-offs.

Field methods used to collect data for testing trade-off predictions rely upon mark–recapture (MR) methods that explicitly account for the detection process (Lebreton et al. 1992). The definition of groups of individuals corresponding to life cycle stages is now used in evolutionary biology investigations based on MR experiments (Brown and Thomson 2004; Cam 2009) and is widely used to investigate evolutionary trade-offs (Nichols et al. 1994; Tavecchia et al. 2001; Moyes et al. 2006; Townsend and Anderson 2007). We demonstrate extensions to go beyond this first step in accounting for individual variation by including other sources of individual heterogeneity both known and unknown (Gimenez et al. 2006; Metcalf and Koons 2007; Royle 2008). Individual heterogeneity may be of known origin, as in the studies mentioned in the previous paragraph, or of unknown origin. In the former, individual heterogeneity is incorporated into a model using covariates as fixed effects (e.g., Gimenez et al. 2009) such as size or states (e.g., breeder vs. nonbreeder), whereas in the latter, individual random effects have to be employed. Service (2000), Cam et al. (2002) and Wintrebert et al. (2005) show that considering individual heterogeneity through the use of random effects was essential to identify senescence in survival. However, these studies all assume perfect detectability, motivating the need for further developments to explicitly account for a detection probability less than 1.

Here, we develop a general framework to assess trade-offs among life-history traits in natural conditions, which addresses both the issues of detectability less than 1 and individual heterogeneity. We propose a novel approach that combines the three following components within a single framework: (1) Modeling the complete life cycle and the associated transitions between states (alive or dead, breeding or not breeding, migrating or resident); (2) Integrating individual heterogeneity of known (fixed effect) or unknown (random effect) origin potentially affecting life-history traits involved in the trade-offs of interest; and (3) Taking uncertainty in detection into account.

We adopt a state-space modeling approach to separate the demographic process of biological interest, which integrates the individual heterogeneity, from the observation process through the detection of marked individuals (Buckland et al. 2004; Rivot et al. 2004; Gimenez et al. 2007; Royle 2008).

Salmonids provide a relevant biological model to study evolutionary questions such as the evolution of life-history traits (e.g., age and size at first maturity), of philopatry, of semelparity vs. iteroparity (Crespi and Teo 2002; Hendry and Stearns 2004), of alternative breeding tactics (Gross 1996), and of life-history trade-offs (Hendry and Stearns 2004). As a case study, we analyze the MR dataset collected on the Atlantic salmon (*Salmo salar*) population of the Scorff river (Southern Brittany, France). Atlantic salmon display a complex life cycle and a variety of life histories. The choice among alternative life histories ultimately depends on their costs and benefits, that is, trade-offs.

Atlantic salmon is an anadromous species that has a life cycle in both freshwater and the ocean (Gueguen and Prouzet 1994). In Brittany (Fig. 1), the juvenile phase takes place in freshwater and lasts 1 or 2 years. Thereafter, the fish migrate to the ocean and return after 1 or 2 years to their native stream to breed. Among males, some individuals may breed before undertaking their seaward migration. We focused on young Atlantic salmon during the freshwater phase of the life cycle. During this phase, individuals may adopt different life-history tactics. First, they have to decide whether to migrate to the ocean after their first year of life or to reside in the freshwater an additional year. Migration to the ocean is accompanied by a smolting process that prepares individuals for sea water life. Second, they have to decide whether to mature or not before migrating to the ocean. The latter choice involves only males during their second year in freshwater.

Atlantic salmon can be described as a conditional strategist (sensu Gross 1996) with status-dependent choice among alternative life-history tactics (migrating to sea or not, delaying reproduction or not). These life-history tactics depend on, and modify, the way energy is acquired, stored, and used by individuals (Thorpe et al. 1998). During the first winter, future migrants (smolts) adopt a very different behavior from those intended to reside an additional year in the river (Metcalfe and Thorpe 1992; McCormick et al. 1998). Such fish try to maximize their growth and may therefore be exposed to a higher risk of predation (McCormick et al. 1998). The predation risk is increased during the downstream migration in early spring as well (Larsson 1985; Moore et al. 1995). The physiological process of smolting requires energy that may be lacking for ensuring survival (McCormick et al. 1998; Thorpe and Metcalfe 1998). Sexual maturation and reproduction of resident males in freshwater is also energetically demanding (Jonsson et al. 1991; Rowe et al. 1991; Fleming 1996; Arndt

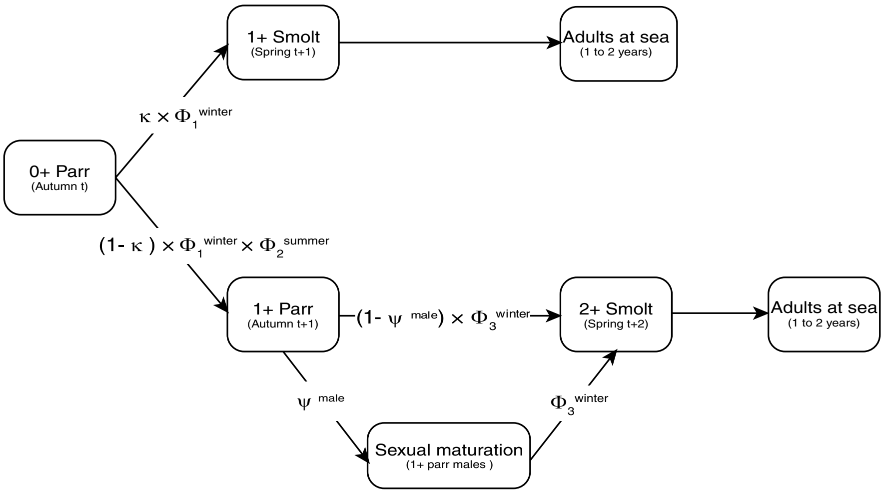

Figure 1. Life cycle of the Atlantic salmon in the Scorff, Brittany (France). Reproduction occurs in freshwater in December and eggs are buried in the river bed gravel. Fry emerge from the spawning r in early spring. After a few months of life, juveniles, then called "0+ parr," choose between migrating to sea the following spring (1+ smolt stage) with a probability κ or staying another year in freshwater (1+ parr) with a probability $1 - \kappa$. The probability of winter survival of the 0+ parr between the first autumn and the following spring is Φ_1^{winter}. The probability of summer survival of the 1+ parr is Φ_2^{summer}. Some of the males remaining in freshwater become sexually mature at the 1+ parr stage with a probability of maturing Ψ. The probability of winter survival of the 1+ parr between the second autumn and the following spring is Φ_3^{winter}. Virtually all surviving juveniles (previously mature or not) will migrate to the sea in the following spring (2+ smolt). Migration to the sea is accompanied by physiological, morphological, and behavioral changes (i.e., smolting process), which prepares individuals for sea water life. After spending between one or two years in the North Atlantic Ocean, adults return to breed in their natal river. The post-spawning mortality is close to 100% for anadromous individuals (i.e., having undertaken the oceanic migration) while mortality is lower for males having matured as parr.

2000). Combined with the exposure to the agonistic behavior of the large anadromous males on the spawning grounds (Hutchings and Myers 1987; Fleming 1996), it should lead to reduced survival (Jonsson et al. 1997; Hendry and Berg 1999; Fleming and Reynolds 2004). Consequently, both the decision to migrate to the ocean and the reproduction of males are expected to reduce survival. We propose to demonstrate the relevance of our novel state space modeling approach by quantifying two potential trade-offs in one cohort of juvenile Atlantic salmon in the wild: a survival cost of migration and a survival cost of reproduction.

Material and Methods

STUDY SITE AND MR DATA COLLECTION

The Scorff river is a small coastal river (75 km including 15 km of estuary) of Southern Brittany (France). Atlantic salmon colonization is essentially restricted to the main river over a 50 km stretch starting at the head of tide.

In the following, we use the term "0+" for individuals of less than one year of age in freshwater, "1+" for those of more than 1 year of age and "2+" for those of more than 2 years of age. Juvenile are named "parr" if residents in freshwater and "smolts" when they migrate to the sea.

In autumn 2005, 0+ parr were sampled by electrofishing at 39 stations along the main course of the Scorff. Every fish captured was measured (fork length, to the nearest millimeter) and individually marked with a PIT (passive integrative transponder) tag (11 mm long, 2.2 mm in diameter) inserted into the peritoneal cavity according to the protocol described in Acolas et al. (2007). This marking technique is known to have little effect on young salmon and a very low rate of tag loss (Gries and Letcher 2002; Letcher and Gries 2003).

In spring 2006, downstream migrating 1+ smolts were captured at two successive traps located at the lower end of the river system below all sites where 0+ parr were marked. At both facilities, all individuals previously PIT tagged were identified. In addition, untagged fish caught at the first upstream trap (i.e., the Leslé Mill) were in turn marked by removing a small piece of a pelvic fin. At the second trap (i.e., the Princes Mill), located at the head of tide 600 m downstream from the Leslé Mill, all individuals previously fin-clipped were identified. Fin-clipping data provided supplemental information for assessing the detection probabilities of the PIT tagged individuals (see section "Statistical inference in a Bayesian framework").

In autumn 2006, the 1+ parr were sampled by electrofishing according to same protocol used for the 0+ parr the previous year. Marked fish were identified and untagged fish were PIT tagged. Sexually maturing and already spermating males were detected by gently pressing their belly. In spring 2007, the 2+ smolts were trapped, checked for PIT tags, and fin-clipped if unmarked as for 1+ smolts.

Eventually, anadromous salmon could be recaptured in 2007 and 2008 when returning to the Scorff river. They were sampled at the Princes Mill facility in a trap designed to catch upstream migrating adults. PIT-tagged individuals were systematically detected.

Table 1 summarizes the data from individuals tagged at 0+ and 1+ parr stages and recaptured at each observation event, as well as from smolts captured and fin-clipped at each trap.

STATE-SPACE MODELING FRAMEWORK

The data resulted from the partial observation (detection or not) of events that were generated from a demographic process (the sequence of the life-cycle stages, Fig. 1). The need for a convenient and flexible framework to account explicitly for these two components has led to the development of state-space models (SSMs) (Clark 2003; Rivot 2003; Buckland et al. 2004). Recently, SSMs have been used for estimating animal survival (Gimenez et al. 2007) from MR data, while incorporating individual heterogeneity (Gimenez et al. 2006; Royle 2008; see also Gimenez and Choquet 2010). In SSMs, the relationship between the observation and the demographic process is governed by two sets of equations, namely the state and the observation equations (Harvey

Table 1. Summary of tag/recapture data for each observation event and each method of tagging (PIT-tag or Fin clip) for one cohort of Atlantic salmon.

	Capture–recapture at each stage of life				
Tag	0+ Parr	1+ Smolt	1+ Parr	2+ Smolt	Adults
Passive integrated transponder (PIT)					
Tagged at 0+ parr stage	1829	67	29	39	5
Tagged at 1+ parr stage			281	55	
Fin clip					
Captured and tagged at Leslé Mill		1291		1751	
Captured at Princes Mill and untagged at Leslé Mill		820		594	
Captured at Princes Mill and tagged at Leslé Mill		179		262	

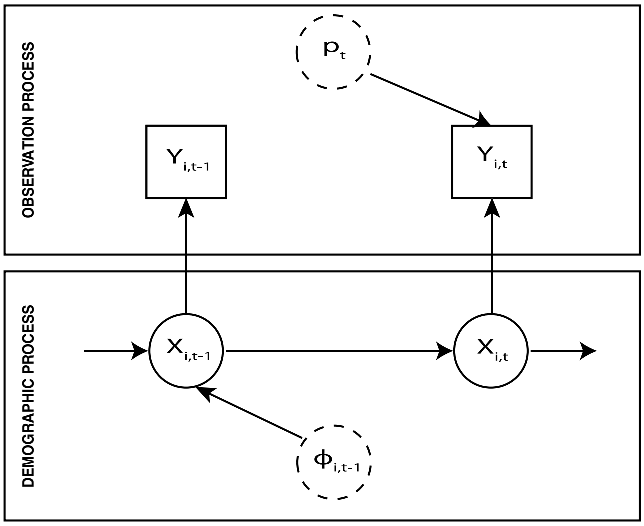

Figure 2. Graphical representation of a state-space model (SSM) for a juvenile individual *i* between two sampling occasions *t* − 1 and *t* (see eqs. 1 and 2). The first component of the SSM is a demographic process characterized by a succession of hidden states (solid circles), also called latent states. The demographic process depends on parameters corresponding to transitions probabilities between successive states (dashed circles). The unknown state of individual *i* at time *t* ($X_{i,t}$) is drawn from a Bernoulli distribution depending on its state at time *t* − 1 ($X_{i,t-1}$) and the probability of transition between these two states (e.g., the survival probability $\Phi_{i,t-1}$). The observational data (solid square) through the observation process are the visible part of the demographic process. Observations are also obtained conditionally on latent states and the parameters of the observation process associated (dashed ellipses). The observation or not of individual *i* at time *t* ($Y_{i,t}$) is drawn from a Bernoulli distribution that depends on the detection probability p_t at time *t* and conditional on individual *i* being alive at time *t* ($X_{i,t}$ = 1). This formulation separates the nuisance parameters (detection probabilities) from the parameters of interest for example survival probability, the latter being involved exclusively in the state equation. The resulting SSM is a combination of a demographic process and an observation process.

et al. 2004; Clark 2007). For the sake of illustration, we first go through a straightforward example. Let us focus on the case of a juvenile *i* between two sampling occasions $t - 1$ and t (Fig. 2). Conditional on its state at time $t - 1$ (alive or dead), this individual may be alive or dead at the next sampling occasion with some probability. Formally, we denote $X_{i,t}$ a binary random variable corresponding to the state of the individual *i* at time *t*, which takes the value 1 if the individual is alive at *t*, and 0 otherwise. Then, $X_{i,t}$ given $X_{i,t-1}$ is distributed according to a Bernoulli distribution with probability depending on the survival probability $\phi_{i,t-1}$ (Gimenez et al. 2007; Royle 2008). This leads to the state equation:

$$X_{i,t} \mid X_{i,t-1} \sim \text{Bernoulli}(X_{i,t-1} \times \phi_{i,t-1}). \tag{1}$$

When individual *i* is alive at *t* ($X_{i,t} = 1$), it can be observed or not, whereas when dead ($X_{i,t} = 0$), it necessarily goes undetected (in our case the detection of dead fish holding a PIT tag was impractical). We denote $Y_{i,t}$ a binary random variable corresponding to the observation of the individual *i* at time *t*, which takes the value 1 if the individual is observed and 0 otherwise. Given the state $X_{i,t}$, $Y_{i,t}$ is distributed according to a Bernoulli distribution with probability depending on the detection probability p_t at time *t* (Gimenez et al. 2007; Royle 2008). This leads to the observation equation

$$Y_{i,t} \mid X_{i,t} \sim \text{Bernoulli}(X_{i,t} \times p_t). \tag{2}$$

Usually with MR methods, the focus is on estimating the transition probabilities that make the link between the demographic states. By using SSMs, we can feasibly access the states of each individual while acknowledging they may be only partially observed. In what follows, we extended this simple approach to the freshwater phase of Atlantic salmon life cycle.

DEMOGRAPHIC PROCESS

The complete life history of Atlantic salmon from the 0+ parr stage in autumn to the migration to sea can be summarized by the following sequence of events (Fig. 1): (1) Decision at the first autumn of smolting at one year of age (1+ smolt) or to stay an additional year in freshwater (1+ parr); (2) Winter survival of the 0+ parr between the first autumn and the following spring (at the time of recapture of the 1+ smolts); (3) Summer survival of the 1+ parr between spring and autumn; (4) Sexual maturation of males at 1+ parr stage; and (5) Winter survival of the 1+ parr between the second autumn and the following spring (at the time of recapture of the 2+ smolts).

We assumed that sexual maturation and second winter survival were governed by the same processes for 1+ parr captured in autumn 2006 but untagged at 0+ parr stage and for the individuals tagged at the 0+ parr stage.

Each of these events is binary and was modeled as a random state variable following a Bernoulli distribution as above (Table 2). We accounted for individual heterogeneity regarding these random events by assuming the associated probabilities may vary among individuals. The modeling of this variability is a key feature in our approach and is detailed in the following.

EVOLUTIONARY TRADE-OFFS OF ULTIMATE INTEREST AND INDIVIDUAL HETEROGENEITY

Both the decision of smolting at age 1+ and the reproduction of 1+ males are expected to reduce survival. We modeled these potential trades-offs at the individual level (index *i*) by linking the probabilities of winter survival to the state

Table 2. States (indicators), transition probabilities (life-history traits of interest) and equations of the demographic process modeling the sequence of events corresponding to the life history of Atlantic salmon from the 0+ parr stage in autumn to the migration to the ocean. Equations defining individual specific transition probabilities are given in the text.

State	Definition	Associated probability	Modeling
Smolt0	0+ Parr in autumn/futurs 1+ smolts	κ_i: Probability to smoltify at 1 year of age (eq. 5)	$\text{Smolt0}_i \sim \text{Bernoulli}(\kappa_i)$
Smolt1	Surviving 1+ smolts in spring	$\phi_{1,i}$: Probability of first winter survival in the (eq. 3)	$\text{Smolt1}_i \sim \text{Bernoulli}(\phi_{1,i} \times \text{Smolt0}_i)$
Parr1	Surviving 1+ parr in spring		$\text{Parr1}_i \sim \text{Bernoulli}(\phi_{1,i} \times 1 - \text{Smolt0}_i)$
Parr1.1	Surviving 1+ parr in autumn	$\phi_{2,i}$: Probability of summer survival (eq. 7)	$\text{Parr1.1}_i \sim \text{Bernoulli}(\phi_{2,i} \times \text{Parr1}_i)$
Parr1.mat	Mature males 1+ parr in autumn	ψ_i^{male}: Probability of maturing for males (eq. 6)	$\text{Parr1.mat}_i \sim \text{Bernoulli}(0.5 \times \psi_i^{\text{male}} \times \text{Parr1.1}_i)$
Smolt2	Surviving 2+ smolts in spring	$\phi_{3,i}$: Probability of winter survival in the second year of life (eq. 4)	$\text{Smolt2}_i \sim \text{Bernoulli}(\phi_{3,i} \times \text{Parr1}_i)$

indicator of the decision of smolting (Smolt0_i) or of maturation (Parr1.mat_i):

$$\text{logit}(\phi_{1,i}) = \alpha_1 + \alpha_2 \times \text{Smolt0}_i + \varepsilon_i \tag{3}$$

$$\text{logit}(\phi_{3,i}) = \delta_1 + \delta_2 \times \text{Parr.mat1}_i + \varepsilon_i \tag{4}$$

where $\phi_{1,i}$ stands for the probability of first winter survival (0+ parr) of an individual i and $\phi_{3,i}$ for the probability of second winter survival (1+ parr). We used a logit link function to ensure that probabilities lie on [0, 1]. Smolt0_i and Parr1.mat_i are the smolting and the maturation indicators that take the value 1 if the individual is smolting or maturing respectively and 0 otherwise. Parameters α_2 and δ_2 reflect the influence of the decision of smolting or of maturing on winter survival at 0+ and 1+ parr stage, respectively. If these parameters are different from 0, then evidence exists for a trade-off. For instance, if δ_2 is negative, then the winter survival $\phi_{3,i}$ of a maturing 1+ male parr ($\text{Parr1.mat}_i = 1$) is lower than that of a nonmaturing 1+ parr (male or female, $\text{Parr1.mat}_i = 0$), suggesting a survival cost of reproduction. Negative survival differentials α_2 and δ_2 implies individual probabilities of survival over first and second winter are positively correlated with the choice of staying in freshwater and remaining immature, respectively. ε_i is a normally distributed random effect accounting for individual heterogeneity in survival due to unknown causes. We assumed that this unobservable individual survival potential is the same for each survival event of an individual's life (Cam et al. 2002; Royle 2008). Thus we make the assumption of dependence between each of the survival events in the life history of a given individual: having a high survival probability during the first winter reveals a good survival ability of the individual that is transmitted to all survival events (i.e., better chance to stay alive during the following survival events). As survival is energy demanding, higher survival potential should be related to higher energy storage and a more efficient use of available energy for growth.

The survival probabilities $\phi_{1,i}$ and $\phi_{3,i}$ are defined for every fish marked and depend on the state variables Smolt0_i and Parr1.mat_i. This approach requires in turn that the process governing smolting and maturation be modeled such that these traits are defined for every individual, whether it has been observed (i.e., recaptured) or not.

CHOICE BETWEEN ALTERNATIVE LIFE-HISTORY TACTICS

Age at smolting depends positively on growth during the first months of life in freshwater (Nicieza et al. 1991; Baglinière et al. 1993; Thorpe and Metcalfe 1998). Using the conceptual framework of probabilistic reaction norms proposed by Heino et al. (2002), we represented this relationship by a logit-linear relationship between the individual probability of smolting at age 1+ (κ_i) and the size at the 0+ parr stage

$$\text{logit}(\kappa_i) = \beta_1 + \beta_2 \times Lf_i, \tag{5}$$

where Lf_i is the individual fork length (mm) centered on the sample mean. Parameter β_2 controls the influence of size at 0+ parr stage on smolting, and corresponds to the selection gradient of the probabilistic reaction norm for smolting. We expect the relationship to be positive, to reflect a positive size-dependent relationship of smolting at age 1+.

For most individuals, maturation state is unknown. Indeed, it is only observed for male 1+ parr captured in autumn, mature and detected as spermating. To define maturation state for every 1+ parr, whether marked in autumn 2005 as 0+ parr or in autumn 2006 as 1+ parr, we modeled sexual maturation of males at the 1+ parr stage as a Bernoulli random event. The associated probability (i.e., of maturing at 1+ parr stage) is the product of the probability of sexual maturation for a male and the probability to be a male. As we considered that the life-history process before the 1+ parr stage in autumn was not sex dependent, we assumed that the probability for a 1+ parr to be a male was 0.5 (balanced sex-ratio). The probability of sexual maturation for a male ψ_i^{male} was assumed to depend on unobserved individual quality reflected by the survival potential (individual random effect on survival ε_i)

$$\operatorname{logit}\left(\psi_i^{\text{male}}\right) = \gamma_1 + \varepsilon_i. \quad (6)$$

As a male having a high survival potential ε_i should be an individual with a high level of energy storage and efficient in its use of available energy, it should in turn have a higher probability to mature at the 1+ parr stage. Indeed, sexual maturation of males at the 1+ parr stage depends on the accumulation of energy reserves and/or growth in the spring of the second year of life (Rowe and Thorpe 1990a; Prévost et al. 1992; Duston and Saunders 1997).

SUMMER SURVIVAL

To complete the life cycle, summer survival of the 1+ parr needs to be modeled. The survival of the resident 1+ parr between their initial marking in spring 2005 and their first recapture in autumn 2006 is made of two successive survival events: winter survival (from autumn 2005 to spring 2006) and summer survival (from spring 2006 to autumn 2006). The explicit distinction of these two survival events allows assessing the winter survival probability of 1+ parr, despite the absence of recapture observations for the 1+ parr in spring 2006.

Baglinière et al. (1994) showed that, in a tributary of the Scorff, summer survival of 1+ parr was higher than previous winter survival. We incorporated this information by specifying summer survival probability $\phi_{2,i}$ conditionally on winter survival $\phi_{1,i}$ as

$$\phi_{2,i} = \phi_{1,i} + (1 - \phi_{1,i}) \times \Delta_{\text{survival}}, \quad (7)$$

where Δ_{survival} is an unknown parameter between 0 and 1. Note that this formulation allows the random effect on survival ε_i to be transferred to $\phi_{2,i}$ via its dependence on $\phi_{1,i}$.

OBSERVATION PROCESS

Captures of tagged fish occurred at each stage of the life history of PIT-tagged individuals. At the individual level, capture was a binary random event modeled using a Bernoulli distribution. The associated probability was specific to each stage and capture device, but was assumed fixed across individuals. The first recapture event after tagging was the trapping of the 1+ smolts (spring 2006) both at the Leslé Mill with probability pL_1 and at the Princes Mill with probability pP_1. The 1+ parr remaining in freshwater (autumn 2006) were captured by electrofishing with probability pC_1. The 2+ smolts (spring 2007) were trapped at the Leslé Mill with probability pL_2 and the Princes Mill with probability pP_2. Finally, anadromous adults returning to freshwater (2007 and 2008) were recaptured at the Princes Mill with probability pA_1.

Among 1+ parr individuals, spermating males were systematically detected. Nonspermating fish can be females, nonmaturing males, or nonspermating maturing males. To reflect this uncertain detection of maturing males, we assumed that, for a male, the identification of its sexual maturation is random with probability *pD* (i.e., to be spermating).

STATISTICAL INFERENCE IN A BAYESIAN FRAMEWORK

To fit our SSM to MR data, we adopted a Bayesian approach using Markov chain Monte Carlo (MCMC) algorithms as recently suggested (Gimenez et al. 2007; Royle 2008). The Bayesian approach combines the likelihood (information available in the data) and prior distributions for parameters of interest (knowledge available before the experiment). From Bayes' theorem, statistical inference is conducted by combining prior information with the likelihood to obtain the posterior probability distribution of all the model unknowns, that is, individual states, transition probabilities between states and random effects, observation probabilities, and additional parameters (see Ellison 2004; Gelman 2004, and McCarthy 2007 for more details about the Bayesian statistical modeling approach).

Besides handling the complexity of our model, the Bayesian approach made the combination of multiple sources of information possible. This approach allowed us to take advantage of all sources of information available to improve the estimation of the parameters of the model. Apart from the observed data issuing from the PIT tagging program, other sources of information could be incorporated.

First, we took advantage of ancillary datasets to improve estimation of the smolt trapping probabilities. In parallel to the PIT tagging program, smolts were also marked every year by fin clipping at the Leslé Mill and recaptured downstream at the Princes Mill. We assumed that the probability of capture at both traps was the same for PIT-tagged, fin-clipped, and untagged smolts.

Second, we incorporated information through the prior probability distribution of the model parameters. Informative prior distribution can be used to improve the precision of parameter estimates and reduce the model complexity (McCarthy and Masters 2005). Prior information was available either from the literature or from additional data. For example, in agreement with what is known about the species biology, we considered the probability to survive in freshwater as being neither null nor equal to 1 between two consecutive stages. Consequently, we chose the prior distribution of parameters such that less importance was given to extreme values of survival probabilities (see Appendix S1 for more details). Note that when data were used to set informative priors, they were different from the observations corresponding to the observation process or the ancillary datasets described above. For all the other parameters we used the standard default approach of setting little informative priors.

The joint posterior distribution of all the model unknowns was derived by means of MCMC sampling. We used the OpenBUGS software for implementing MCMC sampling (Spiegelhalter et al. 2003). The OpenBUGS code of our model is available at http://www.cefe.cnrs.fr/biom/salmonOpenBUGS.txt. We ran three parallel MCMC chains and retained 50,000 iterations after an initial burn-in of 10,000 iterations. Convergence of MCMC sampling was assessed by means of the Brooks-Gelman-Rubin diagnostic (Brooks and Gelman 1998).

Results

The comparison of posterior to prior distributions suggested that the information contained in the data led to considerable updating of the prior distributions. In the following, medians and 95% credible intervals from the posterior distribution are reported (see also Table 3).

Table 3. Summary of posterior distributions (medians and 95% posterior credible intervals) for demographic process parameters and the observation process parameters.

Parameter	Definition	Posterior distribution	
		Median	95% credible interval
Demographic process			
β_2	Selection gradient of the size-dependent probabilistic reaction norm for smolting (eq. 5)	0.15	[0.111; 0.205]
α_1	First winter survival for futures 1+ parr (logit scale, eq. 3)	−1.47	[−2.64; −0.71]
α_2	Effect of the decision of smolting at 1 year of age on the first winter survival (logit scale, eq. 3)	1.66	[0.44; 3.53]
δ_1	Second winter survival for immature 1+ parr (males and females; logit scale, eq. 4)	−0.45	[−2.03; 0.48]
δ_2	Effect of the decision of maturing on the second winter survival (cost of reproduction for survival; logit scale, eq. 4)	−1.41	[−2.92; −0.20]
Δ_{survival}	Differential between first winter survival and following summer survival	0.401	[0.07; 0.86]
ψ^{male}	Mean probability of maturation for males at 1+ parr stage (eq. 6)	0.59	[0.22; 0.91]
σ_ε	Standard deviation of the random effect on survival and maturation	0.98	[0.42; 2.20]
Observation process			
pL^1	Detection probability at Leslé Mill at the 1+ smolt stage	0.19	[0.16; 0.21]
pP^1	Detection probability at Princes Mill at the 1+ smolt stage	0.14	[0.12; 0.16]
pL^2	Detection probability at Leslé Mill at the 2+ smolt stage	0.31	[0.29; 0.34]
pP_2	Detection probability at Princes Mill at the 2+ smolt stage	0.15	[0.14; 0.17]
pA_1	Detection probability of adults	0.03	[0.01; 0.05]
pC_1	Detection probability by electrofishing (in autumn) at the 1+ parr stage	0.14	[0.09; 0.23]
pD	Detection probability of males maturation	0.82	[0.62; 0.97]

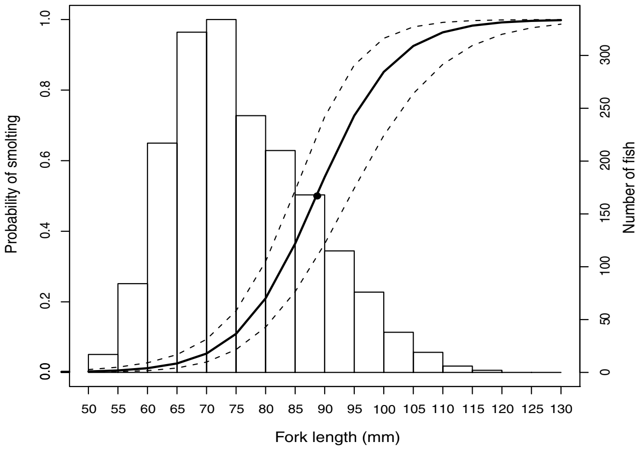

Figure 3. **Probabilistic reaction norm for the age at smolting. The posterior median (solid line) and the 95% posterior probability (dashed lines) of the probability of smolting at 1 year of age are functions of fork length. A histogram of the size distribution of the 0+ parr sampled in autumn 2005 is also displayed. Posterior distributions are based on 50,000 MCMC samples.**

OBSERVATION PROBABILITIES

Capture probabilities at traps varied from 0.12 to 0.34 in our study ("Observation process" in Table 3). Because of the use of ancillary data, detection probabilities were well estimated in comparison with noninformative prior distributions (see Appendix S1; Table 1), except for the probability of capture in autumn 2006 of the 1+ parr tagged in 2005 (0.14 [0.09; 0.23]). Smolt trap efficiencies varied from 2006 to 2007; they are known to be very sensitive to hydrological conditions (Rivot and Prévost 2002; E. Prévost, unpubl. data). The probability of detection of sexual maturation among the males at the 1+ parr stage was high (0.82 [0.62; 0.97]). The probability of detection of adults returning to freshwater was low (0.03 [0.01; 0.05]), but it reflected the combination of the survival at the ocean, and the probability of capture at Princes Mill.

AGE AT SMOLTING AND MATURATION

The gradient of the probabilistic reaction norm for the age at smolting was strictly positive (Pr $[\beta_2 > 0] \approx 100\%$). The decision of smolting at 1 year of age was strongly size dependent (Fig. 3). Fish smaller than 90 mm at the 0+ parr stage had an average probability of becoming a 1+ smolt below 0.5. This probability was very low for individuals smaller than 65 mm and close to 1 for individuals larger than 115 mm. Given the size distribution of the 0+ parr sampled and marked in 2005, the probability to become a 1+ smolt of an average individual was 0.14 [0.07; 0.23].

The probability of sexual maturation for a male at the 1+ parr stage (considering zero random effect) was high (0.59 [0.22; 0.91]).

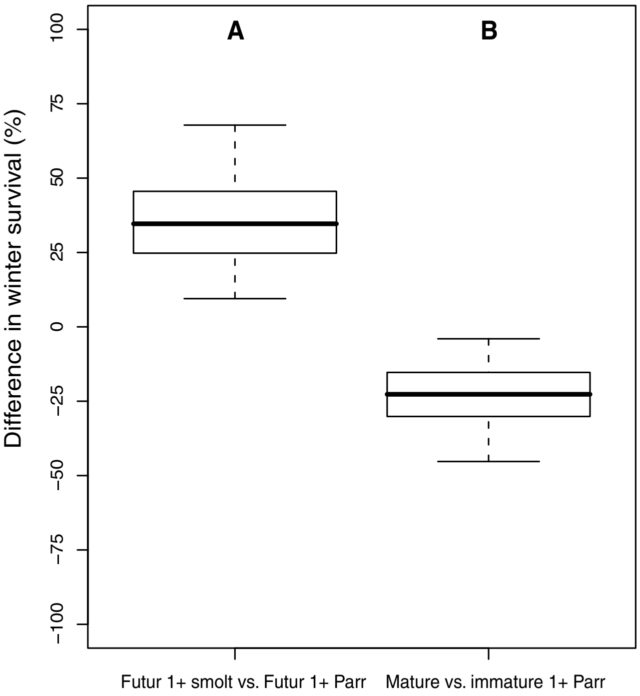

Figure 4. **Posterior distributions of the difference in survival probability (considering zero random effect as null) for (A) future 1+ smolts versus future 1+ parr during the first winter and (B) mature 1+ parr versus immature 1+ males during the second winter (cost of reproduction for survival). Posterior distributions are based on 50,000 MCMC samples. The 2.5 (lower bound of the 95% credible interval), 25, 50 (median), 75, 97.5 (upper bound of the 95% credible interval) percentiles are displayed.**

First winter survival and age at smolting

Parameter α_2 was estimated positive with probability >0.99 (1.44 [0.66; 3.53]; on the logit scale), revealing a selective survival in the first winter in favor of the 0+ parr that decided to smolt at 1 year of age the following spring. The difference of winter survival between future migrants and future residents was positive (0.35 [0.09; 0.68] considering zero random effect) (Fig. 4A). Winter survival of future migrants (1+ smolt) was 0.53 [0.32; 0.83] versus 0.19 [0.07; 0.33] for future 1+ parr staying in freshwater (considering zero random effect).

Cost of reproduction on second winter survival

Parameter δ_2 was estimated negative with probability >0.97 (-1.41 [-2.92; -0.20], logit scale) suggesting the existence of a selective survival depending on the sexual maturation status of the 1+ parr, that is, a cost of reproduction on the second winter survival. The difference in winter survival of mature and immature 1+ parr was negative (-0.23 [-0.04; -0.45] considering zero random effect) (Fig. 4B). Winter survival of a male previously mature at the 1+ parr stage was 0.14 [0.02; 0.35]) versus 0.39 [0.12; 0.62] for an immature (males and females together) 1+ parr (considering zero random effect).

Individual heterogeneity

Averages of the random effect for survival calculated over individuals surviving at each stage increased as the life cycle unfold. The average random effect was zero by definition at the 0+ parr stage, 0.53 [0.11; 2.36] for individuals surviving the first winter, 0.82 [0.16; 3.41] for those surviving till the 1+ parr stage in the fall, and 1.13 [0.23; 4.11] for surviving 2+ smolts. This increase suggests a selection over time of fish that were the most suited to survive in freshwater.

Discussion

Our Bayesian state space modeling approach allowed us to represent the whole life-history process of Atlantic salmon and to identify potential evolutionary trade-offs. This was achieved despite individual heterogeneity in life-history traits, and despite the fact that the life-history traits involved were only partially observed, due to detection probabilities less than one.

OBSERVATION PROCESS AND DETECTION PROBABILITIES

Studies of elements involved in potential selection processes under natural conditions, such as trade-offs and reaction norms, using MR experiments, have long ignored the issue of detectability less than one (Clobert 1995; Cam 2009). Gimenez et al. (2008) shows that directional selection on body mass of social weaver (*Philetairus socius*) is detected when detection probability is assumed to be one, while a stabilizing selection is found when this assumption is relaxed. Yoccoz et al. (2002) suggests that the variability in the detection process affects their ability to detect potential costs of reproduction in the Common Eider (*Somateria mollissima*). These results motivated the integration of detection probabilities in our approach for reliable inference about life-history traits. In our study, except for sexual maturation of males at 1+ parr stage, detection probabilities were much lower than 1, ranging from 0.12 to 0.34 depending on the observation process and the life-history stage considered (Table 3).

EVOLUTIONARY TRADE-OFFS AND INDIVIDUAL HETEROGENEITY

There is a growing interest in accounting for individual heterogeneity in demographic models for evolutionary studies (Cam et al. 2002; Conroy et al. 2002; Blums et al. 2005; Wintrebert et al. 2005; Royle 2008). Indeed, the assumption that individuals are equal in their ability to get resources or in the way they use them is not reasonable. Our modeling framework is flexible and offers several options for integrating individual heterogeneity in a single model. When the cause of the individual heterogeneity was identified and known, observed covariates were used, for example when incorporating the effect of the known size of the 0+ parr on the smolting decision by means of a probabilistic reaction norm. When the cause was identified but not or partially observable, unknown or partially known states were used as covariates, for example when modeling the potential evolutionary trade-offs by conditioning individual survival probabilities by partially observed traits. Last, when the cause was unknown, random effects were used to reflect variation in the individual ability to survive or to mature. Incidentally, we also note that the latter approach led to the classical conclusion that recurrent survival events tend to select over time the individuals with highest ability for survival (Cam et al. 2002; Wintrebert et al. 2005).

A cost of freshwater residency for survival?

Our analysis revealed a positive relationship between the first winter survival of the 0+ parr and their decision of smolting the following spring. This differential winter survival in favor of the 0+ parr having decided to smolt the following spring may be seen as a cost of staying an extra year in freshwater. This result is in contradiction with our initial prediction of a survival cost of migration. To our knowledge, this is the first time this result has been found in the wild, although this was shown under artificial rearing conditions (Pickering and Pottinger 1988). Baglinière et al. (1993) also showed a difference in winter survival under natural conditions between two size groups of 0+ parr, with the difference being in favor of the larger fish, and that larger fish are more likely to smolt at one year of age.

Our unexpected result should be taken with caution as it was derived from a single cohort analysis. Nevertheless, finding a positive correlation between life-history traits when negative correlation (i.e., trade-offs) is expected is not uncommon (Van Noordwijk and De Jong 1986; Glazier 1999; Brown 2003). Van Noordwijk and De Jong (1986) provide an explanation for some of these unanticipated results, which most likely applies to our study. They propose a model in which two traits (e.g., smolting and survival) compete for the same resource at the individual level, and where individuals differ both in their ability to acquire a resource (e.g., energy) and in the allocation of the latter to the traits at stake. Under this scheme, the amount of resource available for each trait depends positively on the total amount of resource acquired and negatively on the proportion allocated to the other trait. Evolutionary trade-offs result only from the sharing of a limited resource between two traits. When variation among individuals in resource acquisition is high relative to variation in allocation between traits, trade-offs operating at the individual level are likely to be obscured (Van Noordwijk and De Jong 1986; Brown 2003). Indeed, individuals with a higher ability for resource acquisition (Brown 2003; Cam 2009) can invest more into both traits. Consequently, a positive relationship between two traits is observed at the interindividual level, even when a negative relationship exists at the individual level (Cooch et al. 2002).

Future 1+ smolt and future 1+ parr differ greatly in their acquisition of resources during their first winter. Future smolts are aggressive and dominant, allowing them access to the most favorable foraging habitat (Harwood et al. 2003; Finstad et al. 2007). In turn, this aggressiveness gives them high metabolic and growth rates (Nicieza and Metcalfe 1999; Finstad et al. 2007). Individuals staying an extra year in freshwater reduce their activity level in winter and become anorexic (Metcalfe and Thorpe 1992; Thorpe et al. 1992; Metcalfe 1998). Following Van Noordwijk and De Jong (1986) reasoning, we think that the trade-off between smolting and the first winter survival is masked by the large variation in the acquisition of resources during the first winter between future 1+ smolts and future resident 1+ parr. The survival advantage resulting from the higher level of energy acquisition of the future smolts would be larger than the cost of smolting.

Cost of reproduction for survival

Our results suggested a cost of reproduction in survival. Mature male 1+ parr have a lower probability of winter survival (post-reproductive survival) than their immature counterparts. This supported our initial expectation based on previous studies (Baglinière et al. 1993; Whalen and Parrish 1999; Whalen et al. 2000; Jonsson and Jonsson 2005). Noteworthy, our study is the first to provide a quantitative estimate of such a cost of reproduction in wild Atlantic salmon. This quantification was made possible thanks to our state space modeling approach. Indeed, this gave us access to the maturation state of all 1+ parr tagged even though it was only observable for the spermating males captured at 1+ parr stage in autumn 2006.

There is room for improvement to our model. Regarding the demographic process, several simplifying assumptions can be relaxed. Given that by staying an additional year in freshwater, the males can have direct access to reproduction, sex-specific demographic strategies could be introduced even before the first reproductive event occurs. Sex-specific probabilistic reaction norms for the age at smolting could be incorporated. In spring of the second year of life, future maturing males at the 1+ parr stage have been shown to have higher energy reserves or growth rates than nonmaturing individuals (Rowe and Thorpe 1990a,b; Prévost et al. 1992; Duston and Saunders 1997). Instead of a probability of maturation being assumed constant across individuals, introducing a probabilistic reaction norm for the sexual maturation of the males (Morita and Fukuwaka 2006) would be interesting.

These potential improvements are examples picked for the sake of illustration. The important point is that our Bayesian state space modeling approach opens up prospects for these extensions. Overall, we contend the approach offers a generic framework for the study of evolutionary processes. Bayesian state space modeling is well suited for handling the conditioning structure of life-history strategies, which encompasses trade-offs, selective survival, and reaction norms, including when some of the life-history traits at stake are not (or partially) observable.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Choice of prior distributions
Figure S1. Plot of the Beta probability density function for 4 different sets of parameters. Beta(1, 1) is the uniform prior between 0 and 1. Beta(2, 2) is a slightly more informative probability distribution centered on 0.5 and giving a zero probability for values close to 0 and 1. Beta(1, 2) or Beta(2, 1) are triangular distributions giving a zero probability for values close to respectively 0 or 1.
Table S1. List of prior distributions assigned to unknown quantities of our model.

Supporting Information may be found in the online version of this article.

Article 4

Explicit modelling of proximate mechanisms for revealing life-history trade-offs in wild conditions.

Mathieu Buoro, Olivier Gimenez et Etienne Prévost

En préparation pour *Ecology Letters* (Novembre 2011)

Abstract

Evolutionary trade-offs are considered as one of the most critical factors in the evolution of life-history traits and therefore play a key role in the life-history theory. However, empirical studies often show positive (or non-significant) correlations among life-history traits, rather than negative trade-offs as expected. These unexpected results may occurred when variation among individuals in resource acquisition is high relative to variation in allocation between traits. As a consequence, trade-offs operating at the individual level are likely to be masked when their identification is based on inter-individual comparisons. To circumvent the difficulty of identifying trade-offs using empirical data, we argued that their analysis should be based on approaches considering explicitly the proximate mechanisms responsible for trade-off at the individual level. By this way, we looked at trade-offs conditionally on sources of variation that confuse trade-offs identification.

We proposed a statistical modeling approach for analyzing empirical data including a proximate mechanistic model explaining both life history variations and trade-offs. We demonstrate the relevance of our approach for statistical inference by undertaking the estimation of the model unknowns from simulated data. We illustrate our approach with a real case study on stream-dwelling juvenile Atlantic salmon in the Scorff River (Southern Brittany, France). We showed that our approach allowed revealing underlying trade-offs which cannot be highlighted without modeling underlying mechanisms.

Keywords: Bayesian inference, cost of reproduction, life history theory, selective survival.

INTRODUCTION

A life history is a phenotype combining the expression of various life history traits that are closely related to fitness such as age, fertility, or longevity. This combination of life history traits expressions results from a life-history strategy which may allow for optimizing fitness of an individual in its particular environment (Gross 1996). A major topic in evolution of life history deals with relationships between life-history traits. If life-history traits were independent, individuals would simply tend to optimize each trait to maximize individual fitness. Because resources (time, space, energy) are limited, individuals must allocate resources among the various functions essential to survival and reproduction (Van Noordwijk and De Jong 1986). When life-history traits are positively dependent on the same limited resource, they are negatively related to each other. This interdependence is called an evolutionary trade-off (Van Noordwijk and De Jong 1986; Roff 1992; Stearns 1992). Trade-offs are considered one of the most critical factors in the evolution of life-history traits and therefore play a key role in the life-history theory because they constrain the range of adaptive variation open to an animal (Stearns 1992; Clutton-Brock 1998). While evolutionary trade-offs can have genetic and environmental sources (Roff 1992), it is assumed that the differential allocation of resources is a major explanation. For example, energy invested in maturing process can be lacking for survival involving lower survival for maturing individuals, i.e. a cost of reproduction for survival.

However, empirical studies often show positive (or non-significant) correlations among life-history traits, rather than negative trade-offs as expected (Glazier 1999; Brown et al. 2003; King et al. 2010). To explain these unexpected results, Van Noordwijk and De Jong (1986) propose the “Y model” in which two traits (e.g., maturing and survival) compete for the same resource at the individual level, and where individuals differ both in their ability to acquire a resource (e.g., energy) and in the allocation of the latter to the traits at stake. Under this scheme, the amount of resource available for each trait depends positively on the total amount of resource acquired and negatively on the proportion allocated to the other trait. Thus, when variation among individuals in resource acquisition is high relative to variation in allocation between traits, trade-offs operating at the individual level are likely to be masked when their identification is based on inter-individual comparisons (Van Noordwijk and De Jong 1986; Brown 2003). Indeed, individuals with a higher ability for resource acquisition

(Brown 2003; Cam 2009) can invest more into both traits. As a consequence, a real trade-off at the individual level based on limited resource allocation may appear even as a positive correlation between traits based on inter-individual covariation.

Experimental studies may provide direct evidence trade-offs by controlling for the inter-individual variability which could be source of confusion (Svensson et al. 2002; Cox et al. 2010). Such a control is most often not possible in the wild what renders trade-offs investigation much more challenging. Studies attempting to test the Y model in the wild highlighted the difficulties associated with quantifying acquisition and allocation (Glazier, 1999; Christians, 2000; Brown et al., 2003). Trade-offs expression may differ among individuals as a result of variations in their status, the later depending both on resource acquisition and allocation. In line with Hamel et al. (2009), we argue studies of evolutionary life-history trade-offs must account explicitly for individual heterogeneity in their status. However, to circumvent the difficulty of identifying trade-offs, we further argue that their analysis should be based on approaches considering explicitly the proximate mechanisms responsible for trade-off at the individual level. By this way, we could look at trade-offs conditionally on sources of variation that confuse trade-offs identification.

In the present paper we demonstrate a statistical modeling approach following the above principles for analyzing empirical data. It works at the individual level and includes a proximate mechanistic model explaining both life history variations and trade-offs. We use a threshold modeling framework, i.e. the latent environmental threshold modeling (LETM) proposed by Buoro et al. (2011) for modelling life-history decisions. First, we consider two discrete life history traits with alternative tactics (i.e. maturing and migrating decisions) and a survival event. Both traits are involved in a trade-off with survival. We demonstrate the relevance of our approach for statistical inference by undertaking the estimation of the model unknowns from simulated data. We also show that it allows proper identification of the trade-offs while they would have missed by a standard comparative approach between individuals according to the tactic they expressed. Second, we illustrate our approach with a real case study on stream-dwelling juvenile Atlantic salmon in the Scorff River (Southern Brittany, France).

CONCEPTUAL LIFE HISTORY STRATEGY FRAMEWORK

We develop a model of life history strategy involving two common life history tactics (i.e. maturing and migrating decisions) and a survival event. We draw inspiration from a life history of Atlantic salmon in the Scorff River (see section “Case study”). We based our approach on Dynamic Energetic Budget theory (DEB, Sousa et al. 2010) which aims to capture the quantitative aspects of energy metabolism of organisms at the individual level. It assumes that the mechanisms that are responsible for the organization of metabolism are not species-specific. The structure of DEB theory involves splitting energy acquired by individuals into structure and reserve (Kooijman 2004, 2010). This distinction is supported by the idea that reserves mainly of lipids while structure depends primarily on protein resource accumulation (Sousa et al. 2010). We define individual energetic status according to these two body compartments. It is hypothesized that organisms are informed about their level by some proximate cues. Also, we assume that reserves are mainly mobilized to fuel maturing process and maintenance while investment in structure is key for undertaking migration. Following the same line of thought than Buoro et al. (*in press*), we consider the proximate cues cannot be measured directly, but mass of an individual can be used as observable indicator of reserves and size is an observable indicator of structure. Note that maturation and migration do not compete directly with each other and they can therefore occur simultaneously.

Both life history traits and survival (numbered 1 to 3 for maturation, migration and survival respectively), are observe binary variables Y. First, we model life-history decisions for maturing and migrating following the LETM framework (Buoro et al., *in press*). Second, we assume that sexual maturation as well as the preparation for migration requires energy that may be lacking for ensuring survival. As a consequence, evolutionary trade-offs are expected as costs of reproduction and of migration for survival.

MODEL FORMULATION

Modeling life-history decisions

We used the Latent Environmental Threshold Model (LETM; Buoro et al. *in press*) for modeling life history decisions. First, although the proximate cue η_i is not observable, an observable proxy X_i can be measured which is correlated with η_i. The distribution of the unknown proximate cue η_i can be expressed conditionally on the observable proxy X_i with some residual error ε_i:

$$\eta_i = F(X_i) + \varepsilon_i \tag{1}$$

where F is a function, e.g. a linear relationship, summarizing the link between the proximate and the observable cue. The residual error ε_i is assumed normally distributed with mean 0 and standard deviation σ_η:

$$\varepsilon_i \sim N(0, \sigma_\eta) \tag{2}$$

This formulation has the advantage of being assumption free regarding the distribution of the X_i. Consequently, the statistical analysis is made more flexible as it is independent of the procedure used for collecting the X_i observations.

Second, we assumed that life-history decisions resulted from a comparison between individual proximate cue and a threshold to exceed. For an individual *i*, the threshold modeling framework stipulates that if the value of a cue η_i is larger (respectively lower) than a threshold θ_i, then it triggers the expression of a phenotype, say mature (resp. immature). If Y_i is the binary variable indicator of the phenotype (e.g., 1 for mature and 0 for immature), then we have:

$$Y_i = \left\{ \begin{array}{ll} 1 & \text{if} \quad \eta_i \geq \theta_i \\ 0 & \text{if} \quad \eta_i < \theta_i \end{array} \right\} \tag{3}$$

The cue η_i varies among individuals as a function of the environment, while the threshold θ is considered an intrinsic property of the individuals, independent of η_i. See Buoro et al. (*in press*) for more details about the Latent Environmental threshold model (LETM) and its implementation. For identifiability issues and without loss of generality, we assumed here that the threshold is fixed among individuals while the threshold θ_i varies among individuals in the LETM.

Modeling evolutionary trade-offs

First, we assumed that survival depends positively on the amount of reserve R (Thorpe et al. 1998). As, maturing process and survival are interdependent regarding reserve available, a negative trade-off is expected. Second, we assume that large individuals mainly have higher maintenance cost than small individuals, i.e. energy requirements increase with structure. By doing so, we assume that survival depends negatively on the status of structure and migration decision require improving structure and therefore has a negative impact on survival. As a consequence, the status for survival depends on the ratio of reserves and structure, i.e. a condition factor (Thorpe et al. 1998). We introduce underlying potential trade-offs through coefficients affecting condition factor for survival conditionally on previous life-history decisions. We also introduce a coefficient α which impacts the status of reserve if individual previously maturing ($Y_{i,1}$=1) and a coefficient β which affects the status of survival if individual decided to migrate ($Y_{i,2}$=1). Thus, the status for survival is:

$$\eta_{3,i} = (\eta_{1,i} - \eta_{2,i}) + (\log(\alpha) * Y_{1,i}) + (\log(\beta) * Y_{2,i}) \tag{4}$$

where η_1, η_2 and η_3 are proximate cues for maturing, migrating and survival processes respectively; Y_1 and Y_2 are indicators of maturing and migrating decision. Linear transformation can be made (using, e.g., natural logarithm for convenience). Parameters α and β are coefficients indicating the proportion of status remaining conditionally of life history decisions, i.e. the effect of maturing and migrating on survival respectively. If these parameters are not different from 0, there is no trade-off; if coefficients are below 1, there is a negative trade-offs while if above 1, there is a positive trade-off. This formulation implies that if there is no cost for maturing or smolting (α or β are equal to 0), the higher status for maturing, the higher the probability to survive (for a status of structure constant). On the other hand, the higher the status for migrating, the lower probability to survive. Indeed, individuals migrating invest their energy in growth rather than stocking it. The conditional structure of the model can be summarized by a Directed Acyclic Graph (Fig. 1).

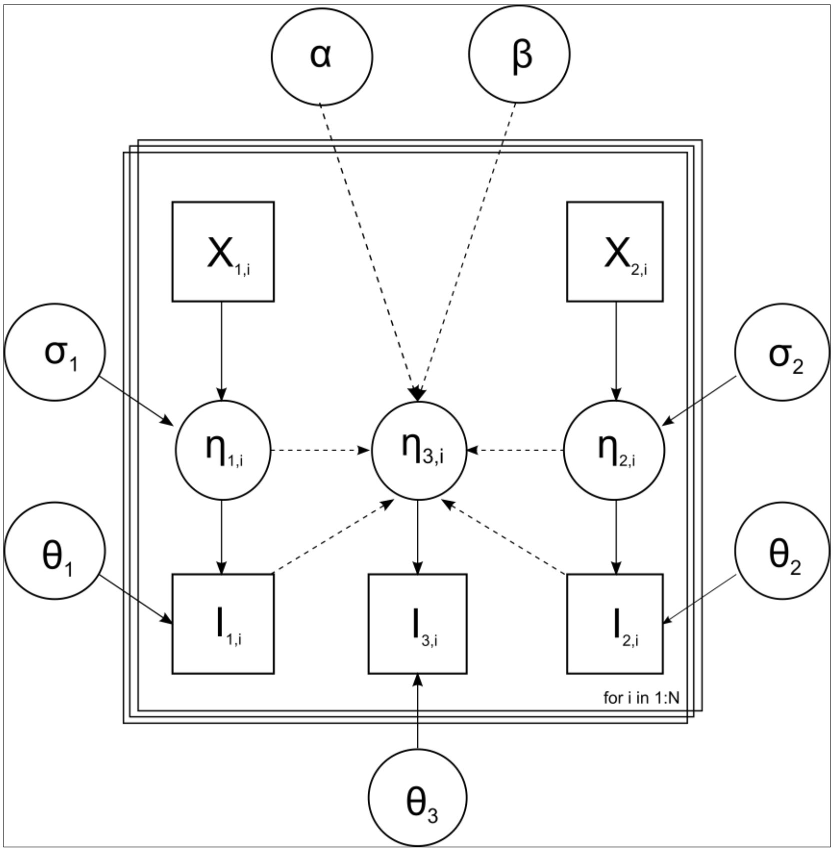

Figure 1: Directed Acyclic Graph of the model. Squares represent observable data and circles represent unknown quantities to be estimated. Solid and broken arrows represent stochastic and logical dependence, respectively. The model is fit to observations of phenotyped individuals, hence the boxes denoting a loop over $i = 1, 2, ..., N$ individuals. For an individual i and for each life history j ($j = 1, 2$ or 3 for maturing decisions, migrating decision and survival respectively), the proximate cue $\eta_{j,i}$ is normally distributed with a mean of the observable cue $X_{j,i}$ and standard deviation σ_j. Finally, $Y_{j,i}$ is a binary indicator variable of the observed phenotype and is modeled as a function of the threshold θ_j and the proximate cue at the individual level, with $Y_{j,i} = 1$ when $\theta_j < \eta_{j,i}$. Here, proximate cue for survival $\eta_{3,i}$ is modeled as a function of the proximate cue for maturing and migrating decisions and their potential costs associated i.e., coefficients α and β respectively.

PARAMETER ESTIMATION

Bayesian approaches using Markov chain Monte Carlo (MCMC) algorithms provide a flexible framework for analyzing latent variables models and their conditional structure (Clark 2004). We therefore adopted this approach to fit the model to data. A Bayesian analysis requires specifying prior probability distributions for the model parameters, i.e. the unknown parameters (α, β, σ_η and θ's; Fig. 1). In our study, all priors were non-informative (see Appendix 2). The joint posterior distributions of all the model unknowns, i.e., the parameters (α, β, σ_η and θ's) were obtained by means of MCMC sampling as implemented in the JAGS software (Plummer, 2003) called from program R using package rjags (Plummer, 2003). The code of the model as well as an example of data are available in appendix 2. Convergence of MCMC sampling was assessed by means of the Brooks-Gelman-Rubin diagnostic (Brooks and Gelman 1998).

SIMULATION STUDY

We evaluated the performance of the model for statistical inference using simulated data. To generate data, we used the model itself with known parameter values (see Appendix 1; fixed values were reported on figure 2) and considered three designs: *(A)* a negative trade-offs (α=0.3 and β=0.8), (B) no trade-offs (α=1 and β=1) and (C) a positive trade-offs for migration decision (α=0.3 and β=1.3). We generated 20 datasets consisting of 500 individuals for each design. Statistical inference was then carried out from the simulated data to check whether the model provided accurate estimates of the parameters (α, β, θ and σ). Note that to ensure that our simulated datasets were biologically realistic, we generated observed phenotypes from parameters of a length-weight relationship (LWR) determined from individuals collected in the Scorff river (see next section; Appendix 1).

CASE STUDY: EVOLUTIONARY TRADE-OFFS IN ATLANTIC SALMON

In this section, we describe a model for the life-history of Atlantic salmon based on the proximate mechanisms that determine an individual's developmental pathway and on the comparison of the physiological status of fish with thresholds. To do so, we illustrate our approach studying evolutionary-trade-offs in Atlantic salmon. Our approach is based on the conceptual life-history framework suggested by Thorpe et al. (1998) and Mangel and Satterwaith (2008) for understanding life-history variations in salmonids.

Atlantic salmon life cycle

The Atlantic salmon is an anadromous species that occupies both freshwater and the ocean during its life cycle (Verspoor et al. 2007). Brittany, the juvenile phase in freshwater lasts one or two years (Baglinière and Maisse 1993). Thereafter, fish migrate to the ocean and return after one or two years to their native stream to breed. Among males, some individuals may breed before undertaking their seaward migration. Atlantic salmon are conditional strategists with state-dependent choice among alternative life history tactics (Hutchings and Myers 1994; Gross 1996; Thorpe et al. 1998; Garant et al. 2003; Hutchings 2004; Hutchings 2011). We focused on young Atlantic salmon during the freshwater phase of the life cycle. During this phase, individuals may adopt different life-history tactics (i.e., maturing or not and migrating or not). These life history tactics depend on, and modify, the way energy is acquired, stored and used by individuals (Thorpe et al. 1998). Evolutionary trade-offs are thus expected in this species.

In the following, we use the term “0+” for individuals of less than one year of age in freshwater, “1+” for those of more than 1 year of age and “2+” for those of more than 2 years of age. Juveniles are named “parr” if resident in freshwater and “smolts” when they migrate to the sea.

Life-history tactics decisions

First, males parr have to decide to mature or not prior to ocean migration during spring-summer transition of their first and/or second year of life (Thorpe et al. 1998). Maturing process (gonadal development) starts very early in juvenile life (spring) while reproduction occurred in winter. It may depend on lipid reserve and a amount of energy to exceed (i.e., threshold for maturing) triggering maturation (Rowe et al 1991; Hutchings & Jones 1994; Thorpe et al. 1998; Mangel & Satterwaith 2008; Piché et al. 2008).

Second, whatever the maturing decisions, juveniles can either migrate to the ocean the next spring (1+ smolt) or reside in freshwater for an additional year (1+ parr; Thorpe et al. 1998). In the scorff river, we assumed that all survivor juveniles must to migrate in their second year of life (2+ smolt). The choice between the migrant vs. the resident alternative tactics is related to the size of the individuals in their first autumn (Nicieza et al. 1991; Thorpe and Metcalfe 1998; Buoro et al. 2010). Migration to the ocean is accompanied by a smolting process preparing individuals for seawater life (McCormick and Hansen 1998; Thorpe et al.1998).

Observed cues vs. proximate cues

The individual energetic status influences these life-history decisions (Jonsson and Jonsson 2005) because maturing and smolting processes are energetically costly. Although weight and size are observable cues, they are probably best considered as a proxy for energetic status (Thorpe et al. 1998), i.e. likely more proximate cues, which is to be compared to a threshold for triggering maturing and smolting (Thorpe et al.1998; Mangel and Satterthwaite 2008; Satterthwaite et al. 2010). Thus, we assumed that (1) weight is a proxy for reserve status as it is correlated with lipid reserve and gonad mass, and (2) size is a proxy for structure status as it is a revelator of growth conditions and investment in structure (i.e., protein.

Overwinter survival and evolutionary trade-offs

Following maturing and migrating decisions, individuals faced to winter survival events in the first and second year of life. We assumed that winter survival is a critical period energetically demanding especially regarding fat reserves (Thorpe et al. 1998). Thus, we contended that the proximate status for survival is the ratio of the status of reserves (status for maturing) and status of structure (status for smolting). Note that this formulation is equivalent to the common condition factor (Fulton 1902; Ricker 1975). However, we argued that status for survival can be impacted by previous investment in life history tactics. First, sexual maturation and reproduction of resident males in freshwater is energy demanding (Rowe et al. 1991; Fleming 1996; Arndt 2000). Combined with the exposure to the agonistic behaviour of the large anadromous males on the spawning grounds (Hutchings & Myers 1987; Fleming 1996), this should lead to reduced survival (Myers 1984; Fleming & Reynolds 2004). Second, we assumed the decision of smolting modified survival. During the first winter, future migrants adopt a very different behaviour from those intended to reside an additional year in the river as they try to maximize their growth rather than saving their energetic reserve (Metcalfe & Thorpe 1992; McCormick et al. 1998). In addition, we assumed that the higher the juvenile, the higher the maintenance cost (Cutts et al. 2002) involving a potential cost of growth. According to our conceptual approach (see section 2), we modelled these potential trade-offs at the individual level by linking the status for winter survival to the states indicator of the decision of maturation/migration and coefficients α and β respectively (Eq. 4).

Data collection

In autumn 2005, YOY (young of the year) juveniles were sampled by electrofishing at 39 stations along the main course of the Scorff. Every fish captured individually marked with a Passive Integrative Transponder (PIT) tag (11 mm long, 2.2 mm in diameter) inserted into the peritoneal cavity according to the protocol described in Acolas et al. (2007). Maturing males were also identified (if spermating). One-year old seaward migrating juveniles (smolts) previously PIT tagged were identified during their downstream migration in the spring of 2006. They were captured at two successive traps (Leslé Mill and Princes Mill) located at the lower end of the river system below all sites where YOY were marked. At both facilities, their individual PIT tags were identified. PIT tagged resident juveniles, i.e., future two years old smolts, were identified in autumn 2007 using sampling by electrofishing according to same protocol used for the YOY the previous year. Maturing males were identified too. Two-year old smolts were also recaptured the following spring (2008) and identified by their PIT tags. Here, we considered the set of YOY juveniles marked in autumn 2005 and recaptured later on (n=1829). For each of them, we recorded both its phenotype (maturing, migrant or resident) and its observable cue (fork length and weigth in autumn; measuring to the nearest 1mm and weighted at the nearest 0.1 gr respectively).

Modeling

Our analyses combine a demographic process model and an observation model. Both are made up of several components, each corresponding to a life history transition or a source of information. Life history events are binary and modelled as random variables with Bernoulli distribution (Buoro et al. 2010).

Demographic process

For each individual i and for each year of the juvenile phase j, the proximate cue $\eta_{i,j,1}$ (reserve status) was assumed to be normally distributed with the mean of its weight in autumn $W_{i,j}$ (the observable cue) and standard deviation σ_R (Eq. 1-2). The alternative phenotype indicators $Y_{i,j,1}$ (Eq. 3) take value 1 if individual i maturates at age j, and 0 if it remains immature. We used the same approach for assessing proximate cue (structure status) $\eta_{i,j,2}$ for migrating using size in autumn ($L_{i,j}$) as observable cue and standard deviation σ_S. Again, the alternative phenotype indicators $Y_{i,j,2}$ (Eq. 3) take value 1 if individual i migrates at age j, and 0 if it stays an additional year in freshwater. The proximate cue and alternative phenotype indicators $Y_{i,j,3}$ for survival were acquired following eq. 4.

We introduce two additional assumptions in the specification of the model for Atlantic salmon case study. First, we assumed that parameters α, β and thresholds θ's were fixed across individuals and age. Second, we assumed that there is no costs of migrating in the second year of life since all individuals have to migrate.

Note that survival of resident 1+ parr between their initial marking in first autumn and their first recapture in the following autumn is made of two successive survival events: winter survival (from autumn *t* to spring *t+1*) and summer survival (from spring *t+1* to autumn *t+1*). The explicit distinction of these two survival events allows assessing the first winter survival probability of the future 1+ parr, despite the absence of recaptures for 1+ parr in spring *t+1*. Fisrt, we assumed that summer survival of 1+ parr was higher than previous winter survival in the Scorff river (Baglinière et al. 1994). We incorporated this information by specifying summer survival probability $\phi_{2,i}$ conditionally on winter survival $\phi_{1,i}$ as

$$\phi_{2,i} = \phi_{1,i} + \left(1-\phi_{1,i}\right)\times \mathit{\Delta}_{survival} \qquad \text{(eqn 6)}$$

where $\mathit{\Delta}_{survival}$ is an unknown parameter between 0 and 1 which determines the survival difference between first winter and summer.

Observation process

Captures of tagged fish occurred at each stage of the life history of PIT-tagged individuals. First, recapture of the smolts (spring) for each year of life *j* occurred both at the Leslé Mill with probability pL_j and at the Princes Mill with probability pP_j . At the individual level, capture was modelled as a Bernoulli distribution (Appendix 2) with associated probability of capture assumed fixed across individuals.

Second, the 1+ parr remaining in freshwater (autumn *t+1*) were captured by electrofishing with probability pC_j . Sampling by electrofishing was conducted in the same sites each year. There is evidence of site fidelity in Atlantic salmon parr (Stickler et al., 2008). In our study, almost all the 1+ parr recaptured were caught at the same station where they were marked at 0+ stage. We considered that the probability of capture for 1+ parr was higher than the probability of capture for 0+ parr in the previous autumn, and specified the probability of detection of 1+ parr in autumn, pC_2, conditionally on the probability of detection of 0+ parr in first autumn, pC_1:

(eqn 8)

$$pC_2 = pC_1 + (1 - pC_1) \times \Delta_{capture}$$

where $\Delta_{capture}$ is un unknown parameter between 0 and 1 which determines the difference between pC_2 and pC_1.

RESULTS

Simulation study

Whatever the design considered, the comparison of posterior and prior distributions showed that the information contained in the data led to considerable updating of the prior distributions. The model properly estimated residual variances σ*'s* and thresholds θ*'s*; the posterior medians of these parameters were close to their true value (Fig. 2). The posterior distributions of α and β were well estimated too indicating that these parameters were identifiable. Note that theses parameters might be constrained by identifiability issues, given the information available in the data in hand. Indeed, if contrasted life-history decisions among individuals were not observed (e.g. if all individuals mature, migrate and/or survive), we have only censored information through the observation of phenotypes.

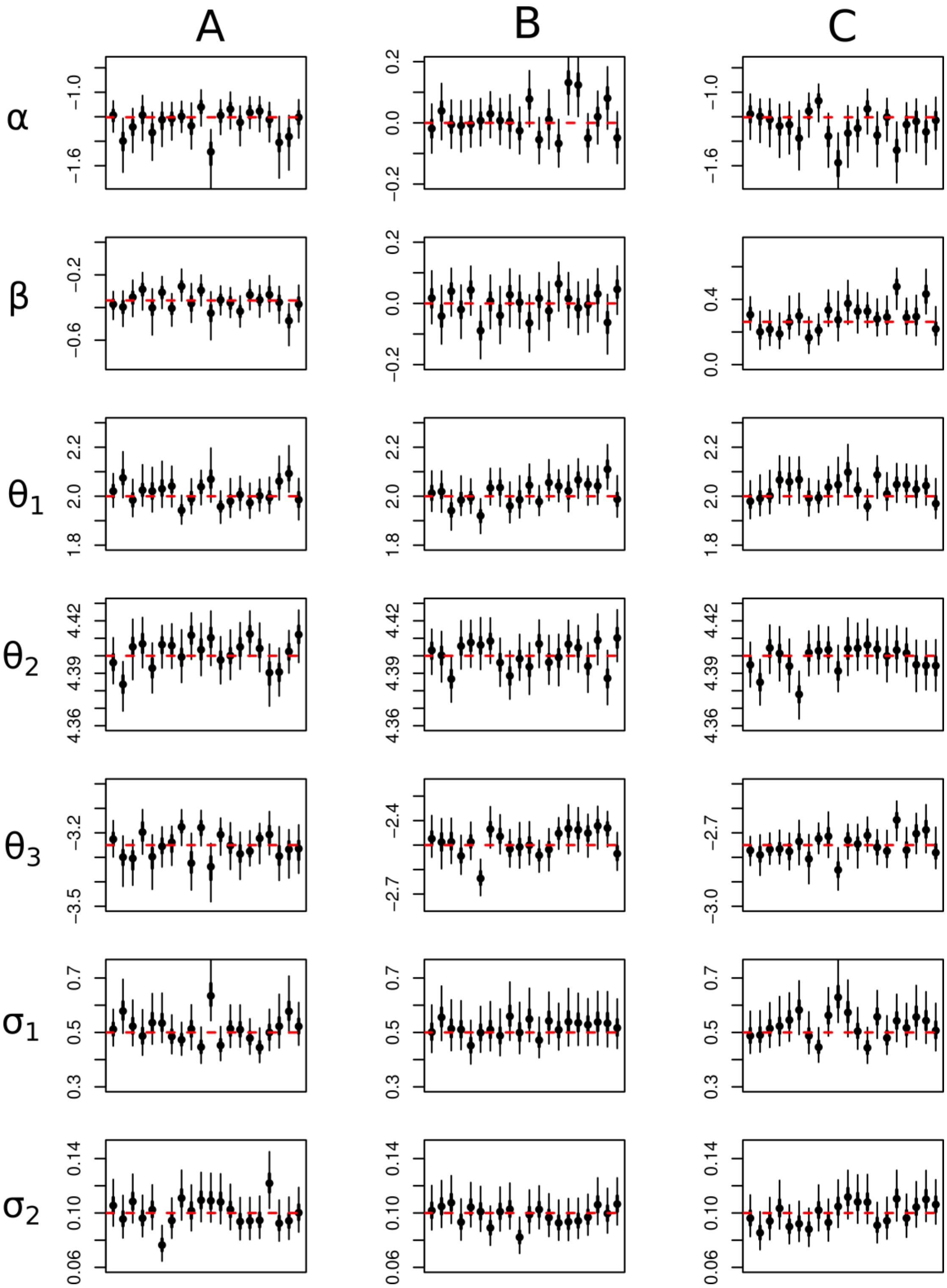

Figure 2: Posterior distributions of the Latent Model parameters (at the logarithmic scale) for each designs: (A) negative trade-offs, (B) no trade-offs and (C) positive trade-offs (for migrating only) and for 20 replicate data sets. The median (black point) and the 95% PPI (Posterior Probability Interval (PPI); solid lines) are displayed based on 25000 MCMC samples. The actual values are also displayed (dashed lines).

Case study

Using our approach, we were able to obtain precise estimates of the latent thresholds and the variance of the proximate cues (Table 1). The posterior distribution of parameters α and β showed the information contained in the data led to substantial updating of the prior distribution, indicating that these parameters could be identified. Posterior distributions for α and β favor low values with a posterior mean of approximately 0.33 and 0.41 respectively.

Parameters	Definition	Posterior distribution	
		Median	95% credible interval
α	Effect of maturing on survival (i.e. proportion of reserve status remaining after maturing)	0.33	[0.26; 0.41]
β	Effect of migrating on survival (i.e. proportion of structure status remaining after smolting)	0.41	[0.35; 0.51]
σ_1	Standard deviation of proximate cue for reserve status	0.42	[0.35; 0.51]
σ_2	Standard deviation of proximate cue for structure status	0.22	[0.16; 0.28]
θ_1	Threshold for maturing decision (at logarithmic scale)	3.28	[3.18; 3.40]
θ_2	Threshold for smolting decision (at logarithmic scale)	4.01	[3.92; 4.15]
θ_3	Threshold for winter survival (at logarithmic scale)	-2.93	[-3.07; -2.72]

Table 1: Summary of posterior distributions (medians and 95% posterior credible intervals) for parameters of interest in Atlantic salmon case study.

The difference of winter survival between future migrants and future residents (Figure 2A) was positive using classical approach (0.35 [0.09; 0.68] considering zero random effect; see Buoro et al. 2010) while negative using our mechanistic approach (-0.36 [-0.46; -0.18]), revealing a cost of smolting in the first winter. The difference in winter survival of mature and immature 1+ parr was negative using classical approach (−0.23 [−0.04;−0.45] considering zero random effect) (Fig. 2B) revealing a cost of reproduction in the second winter. Using our mechanistic approach, we highlighted stronger difference in winter survival (−0.61 [−0.71;−0.50]).

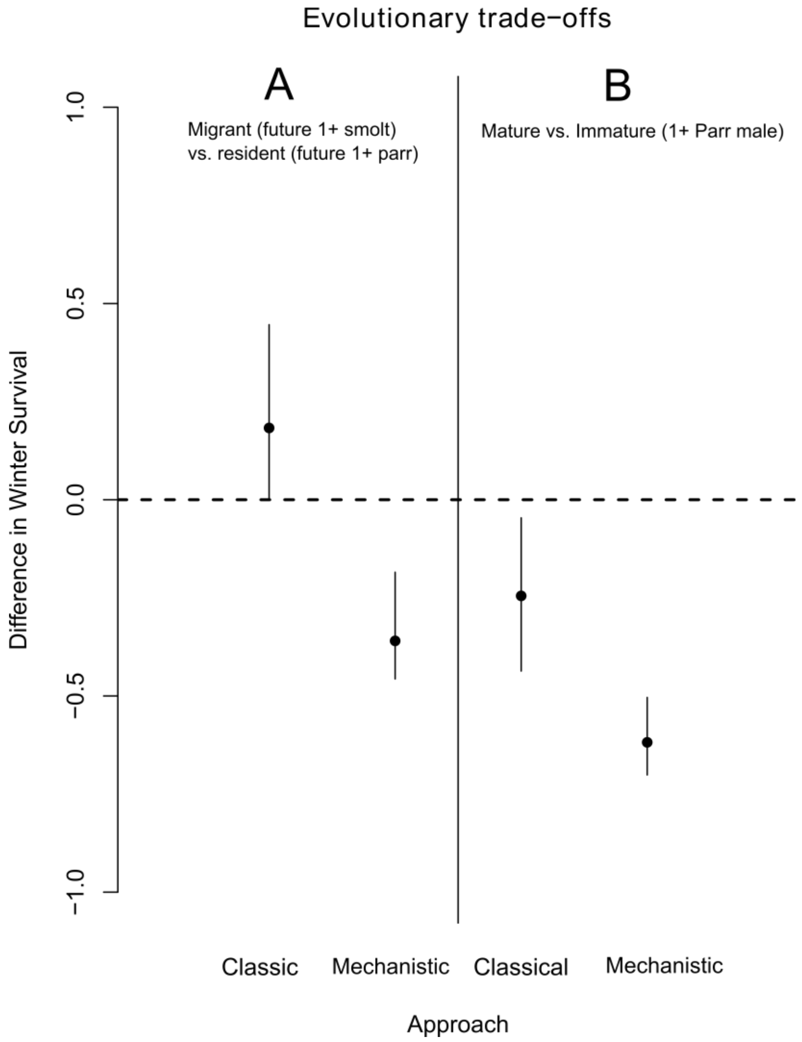

Figure 3: Posterior distributions of the difference in survival probability for (A) migrant (future 1+ smolt) versus residents (future 1+ parr) during the first winter and (B) mature 1+ parr versus immature 1+ male during the second winter (cost of reproduction for survival). We compared a classical approach (using a correlation between life history traits) and mechanistic approach (model proposed). The median (black point) and the 95% PPI (Posterior Probability Interval (PPI); solid lines) are displayed based on 25000 MCMC samples.

DISCUSSION

A great challenge in evolutionary biology is to understand pattern and variation in life histories because variation is the substrate on which natural selection may act. Thus, studying life history variations requires highlighting major patterns such as life history tactic decisions and their interdependence through evolutionary trade-offs. Here, we presented a model combining these patterns at individual level. A key feature of our approach is the use of hierarchical modeling representing proximate mechanisms through latent variables. We explicitly recognize that often little biological knowledge is available regarding the proximate mechanism influencing the expression of the phenotype (Metcalfe 1998; Thorpe 2007). A key feature of Bayesian Hierarchical modeling (BHM) is the ability to use latent (unobserved) variables to represent underlying causes while observed variables serve as indicators of these processes (i.e., are assumed to be a manifestation of these processes). Latent variables allow representing relationships between observations and theoretical knowledge, i.e., underlying mechanisms. Our approach considered explicitly the proximate mechanisms responsible for life history decisions and trade-offs at the individual level. By doing so, our approach allowed revealing underlying trade-offs which cannot be highlighted without modeling underlying mechanisms.

Evolutionary trade-offs

Positive or non significant phenotypic correlation between life history traits are often observed with empirical data while underlying (physiological) negative trade-offs are expected. These unexpected results can be explained at individual level by variation in acquisition and allocation of resources (Van Noordwijk and De Jong 1986). Individuals with higher ability to acquire resources can invest their energy in competitive traits. Observing these groups of individuals can mask underlying trade-offs. Thus, we argue it is essential to define individual state which reflect the ability of individuals to acquire and to allocate resources and working at individual level. A key feature of our study is to present a mechanistic approach with a modeling of successive life history decisions, the individual’s state and explicitly introducing and estimating the effects of life history decisions on these states i.e. underlying trade-offs from empirical data. In other words, we argued that trade-offs should be look conditionally on sources of variation that confuse trade-offs identification. Our simulation study and the Atlantic salmon case study showed that parameters were identifiable and that adopting a mechanistic approach at an individual level (i.e., introducing explicitly trade-offs conditionally on status) allowed highlighting underlying negative trade-offs. Our results confirmed that phenotypic plasticity (i.e. individual heterogeneity) in life history decisions can obscured life history trade-offs. In a previous study, we showed a positive correlation between decision of smolting and winter survival (Buoro et al. 2010). In line with Van Noordwijk and De Jong (1986), we suggested that future smolts continue to acquire resources during winter which favor their survival despite of physiological cost of smolting and higher risk of predation. Thus, variation in acquisition of resources is higher than variation in allocation. In this study, we introduced explicitly a potential effect of maturing and smolting decisions on status for survival. Note that because such life history decisions may have positive effect on survival, we keep the possibility to be higher than 1. Indeed, observed trade-offs can result from others factors such as behavioral or ecological. For example, cost of reproduction for survival can be associated with predation and injures induced by congeners during breeding activities. Our approach allowed taking into account these potential additional effects through coefficients capturing all positive or negative effects associated with life history decisions.

State-dependent life history decision

In our study, we assumed that life history decisions are state-dependent according to Houston and McNamara (1992). Also, we observed alternative phenotype (i.e. maturing or not, migrating or not) and treated them as conditional strategies using the LETM approach. We assumed that life history decisions results from a comparison between a proximate cue (the individual state; e.g. energetic status) and a threshold. While these variables were unobserved, our approach allowed estimating them and associated parameters through the use of observable phenotype as proxy. Representing underlying causes while observed variables serve as indicators of these processes (i.e., are assumed as a manifestation of these processes) are commonly used in the Structural Equation Modeling framework (SEM; Pugesek et al. 2003; Grace and Bollen 2006, 2008). We contended that status is a conceptual variable which is difficult to define and interpret. This state reflects individual quality and is greatly dependent on the field of research where it is applied (Wilson et al. 2010; Lailvaux et al. 2010; Bergeron et al 2001). In this paper, we contended that life history decisions are depending on energetic quantities allocated regarding organism and/or trait considered. According to DEB theory, we chose a simple structure distinguishing the energy allocated into reserve and structure. Sousa et al. (2010) argued that simplifications as well as extensions should be done, but should be consistent with the existing assumptions of DEB theory. While reserve are used for maturing process and maintenance, energy allocated to structure allow growth and/or functions allowing dispersal. The choice of morphological traits as proxy of acquisition/allocation of resources was made in accordance with knowledge available in Atlantic salmon. Previous studies showed a size-dependent reaction norm for smolting in autumn (Buoro et al. 2010) and weight-dependent reaction norm for maturing (Piché et al. 2008 ; Morita et al 2009). We assumed that variation in size and weight in population result from variations in acquisition/allocation of resources between each functions (i.e., structure and reserve respectively). It reflects past events in life history of the individuals i.e. growth trajectory. Finally, we used a simple linear function to make the link between the proximate cue and the observable phenotype (see eq. 3). But more complex relationships can be introduced such as multiple regression or additional information on coefficients of regression (e.g., more efficient estimation on the relationship between weight and lipid reserve).

Perspectives

There is room for improvement to our model. Regarding other potential trade-offs, we did not account for the effect of maturation on growth. Indeed, individuals stocking their energy into reserve cannot invest in growth. However, we did not introduced this assumption in the salmon case study as observed maturing males at 0+ parr stage and non migrants at 2+ stage were lacking. But we evaluated the ability of our model to estimate this additional parameter in an alternative model including an effect (using simulated data) of maturing decisions on the status for structure (unpublished data). Key parameters of life history decisions (threshold) and trade-offs (coefficients α and β) were assumed fixed among individuals. These parameters can vary among individuals but there were unidentifiable regarding our data at hand.

Our model opens up interesting prospects for the study of life history evolution using observational data. It allows including major evolutionary processes such as phenotypic plasticity and evolutionary trade-offs at once. It is a generic tool that could be applied to a wide range of taxa and to different life cycles. By incorporating cues that allow organisms to match their phenotypes to the conditions encountered and associated constraints, it improves our ability to predict how populations will respond to environmental changes (Reed et al. 2010). It also facilitates the quantification of patterns of quantitative genetic variation and heritability of conditional strategies. Despite the introduction of the proximate mechanisms, our model is still a relatively simple model in the version we presented here. It can be extended. While a simple structure for energy allocation was assumed both in our simulated data and in our salmon case study, the model can be applied to any other more complex structure including bioenergetics model, keeping in mind that the power of the analysis depends crucially on data at hand. In the other hand, genetic effects can be introduced through quantitative genetic approach. The threshold can vary among individuals and exhibit additive genetic variance (Tomkins & Hazel 2007). Thus, heritability and genetic correlation of life history tactics may be assessed (Buoro et al. in press).

In the context of rapid and global environmental change, both evolution and plasticity are likely to prove critical for species adaptation (Gienapp et al. 2008). The joint appraisal of both phenomena from observational data is required, for which the use and further developments of our approach should help.

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APPENDIX 1

Weight-length relationship

First, we generated two observed cues X_1 and X_2 (e.g., length and weight). Observable cue X_1 were generated from a normal distribution with mean $\mu_{X1} = 80$ and standard deviation $\sigma_{X1} = 12$. Thus, X_2 (e.g., weight values) were generated from a log-normal distribution with mean $\log(\mu_{X2})$ and standard deviation $\sigma_{X2} = 0.2$. We assumed that it exists a strong relationship between phenotypes X_1 and X_2 such as:

$$\log(\mu_{X2,i}) = \log(a) + b \times \log(X_{1,i}) \qquad (5)$$

Where a=0.00001(exponent describing of the rate of change of weight with length) and b=3 (weight at unit length). Linear transformation was made using natural logarithm at the observed lengths and weights.

Proximate cues and life history decisions

Second, for each individual i, given the value of the observed cue $X_{1,i}$, we generated its latent (proximate) cue $\eta_{1,i}$ from a normal distribution with mean $\log(X_{1,i})$ and standard deviation σ_1=0.4 (Eq. 1-2; Table A1). Given the values of the proximate cue $\eta_{1,i}$ and that of the threshold $\theta_{1,1}$ ($\theta_{1,i}$=2), we assigned the phenotype indicator values $Y_{1,i}$ for maturing decision (Eq. 1). We used the same approach for generating latent (proximate) cue $\eta_{2,i}$ and phenotype indicator values $Y_{2,i}$ for migrating decision but using standard deviation σ_2=0.2 and threshold $\theta_{2,i}$=4.4.

Finally, given proximate cues $\eta_{1,i}$ and $\eta_{2,i}$, coefficients α and β and phenotype indicator values $Y_{1,i}$ and $Y_{2,i}$, the proximate cue for survival $\eta_{3,i}$ was generated according to eq. 4. Given the values of the proximate cue $\eta_{3,i}$ and that of the threshold $\theta_{3,1}$, we assigned the phenotype indicator values $Y_{3,i}$ (Eq. 3). Note that we fixed the threshold for survival $\theta_{3,1}$ to -3.25 for design A, -2.5 for design B and -2.75 for design C to ensure that whatever the life history decision (i.e., maturing and/or migrating), a proportion of individuals died.

Table A1: List of real values assigned to parameters for simulating data.

Parameters	Descriptive	Designs		
		A	B	C
σ_1	Standard deviation of the proximate cue for reserve	0.4	0.4	0.4
σ_2	Standard deviation of the proximate cue for structure	0.2	0.2	0.2
α	Effect of maturing on status for survival	0.3	1	0.3
β	Effect of migrating on status for survival	0.7	1	1.3
θ_1	Threshold for maturing decision (at logarithm scale)	2	2	2
θ_2	Threshold for migrating decision (at logarithm scale)	4.4	4.4	4.4
θ_3	Threshold for survival (at logarithm scale)	3.25	-2.5	-2.75

APPENDIX 2

Table A2: List of prior distributions assigned to unknown quantities of our model.

Parameters	Descriptive	Prior distributions
σ_1	Standard deviation of the proximate cue for reserve	$\sigma_1 \sim \text{Uniforme}(0,100)$
σ_2	Standard deviation of the proximate cue for structure	$\sigma_2 \sim \text{Uniforme}(0,100)$
α	Effect of maturing on status for survival (at logarithm scale)	$\alpha \sim N(0, 0.001)$
β	Effect of migrating on status for survival (at logarithm scale)	$\beta \sim N(0, 0.001)$
θ_1	Threshold for maturing decision (at logarithm scale)	$\theta_1 \sim N(0, 0.001)$
θ_2	Threshold for migrating decision (at logarithm scale)	$\theta_2 \sim N(0, 0.001)$
θ_3	Threshold for survival (at logarithm scale)	$\theta_3 \sim N(0, 0.001)$

Mechanistic model for revealing underlying mechanisms in evolutionary trade-offs using JAGS

```
model {

## LIKELIHOOD
        for (i in 1:N){
        # Reserve status
        eta[i,1]~dnorm(X[i,1], tau[1])
        # Structure status
        eta[i,2]~dnorm(X[i,2], tau[2])
        # Maturing decision
        I[i,1]~dinterval(eta[i,1],theta[1])
        # Migrating decision:
        I[i,2]~dinterval(eta[i,2],theta[2])
        # Survival:
        I[i,3]~dinterval(((eta[i,1]+alpha*I[i,1] + beta*I[i,2]))-eta[i,2],theta[3])
        } # end loop i


## PRIORS
        alpha~dnorm(0, 0.001)
        beta~dnorm(0, 0.001)
        # Thresholds:
        for (j in 1:3){theta[j]~dnorm(0, 0.001)}
        for (j in 1:2){
        tau[j]<-pow(sigma[j],-2)
        sigma[j]~dunif(0,100)
        } # end loop j

}       # End of the model



## DATA
```

```
list(N=7,

    I[,1]    I[,2]    I[,3]

[1,]    0    1    0

[2,]    1    1    1

[3,]    0    1    0

[4,]    1    1    1

[5,]    0    0    0

[6,]    0    1    0

[7,]    0    0    0

         X[,1]  X[,2]

  [1,]  1.5 4.3

  [2,]  1.8 4.5

  [3,]  0.9 4.0

  [4,]  1.9 4.5

  [5,]  2.521 4.478

  [6,]  1.883 4.481

  [7,]  1.950 4.510

)
```

Article 5

Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross.

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Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross

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Keywords:

Bayesian framework;
heritability;
liability to disperse;
local scale;
natal dispersal;
seabird;
threshold model.

Abstract

Natal dispersal is a key life history trait for the evolution and adaptation of wild populations. Although its evolution has repeatedly been related to the social and environmental context faced by individuals, parent–offspring regressions have also highlighted a possible heritable component. In this study, we explore heritability of natal dispersal, at the scale of the sub-Antarctic Possession Island, for a large-scale foraging seabird, the Wandering albatross *Diomedea exulans*, exploiting a pedigree spanning over four decades and a maximum of four generations. The comparison of three different methods shows that heritability on the liability scale can vary drastically depending on the type of model (heritability from 6% to 86%), with a notable underestimation by restricted maximum likelihood animal models (6%) compared to Bayesian animal models (36%). In all cases, however, our results point to significant additive genetic variance in the individual propensity to disperse, after controlling for substantial effects of sex and natal colony. These results reveal promising evolutionary potential for short-scale natal dispersal, which could play a critical role for the long-term persistence of this species on the long run.

Introduction

The movement of individuals between different locations is a major component of gene flow, and thereby a central life history trait for the evolution and adaptation of populations and species. For this reason, considerable interest has been brought to understanding the ultimate and proximate causes of and explaining the variation in traits involved in these movements, i.e. dispersal (Bohonak, 1999; Ronce *et al.*, 2001; Bowler & Benton, 2005). Some key biotic and abiotic factors, such as inbreeding avoidance, competition for food or mates and especially kin competition, condition dependence and environmental heterogeneity, have repeatedly been related to the evolution of dispersal (see e.g. Clobert *et al.*, 2001). However, a prerequisite for these forces of selection to influence the evolution of dispersal in the wild is the presence of additive genetic variance in the factors characterising the movement. Studies on plants and insects have provided evidence for additive genetic variance in dispersal traits (Olivieri & Gouyon, 1997; Roff & Fairbairn, 2001), but results on vertebrates are still scarce and ambiguous (see e.g. Massot & Clobert, 2000; Hansson *et al.*, 2003).

In particular, for the study of natal dispersal, i.e. the movement of individuals between their natal area and their location of first breeding, heritability estimates are still very limited, even for the well-studied avian species (Table 1). In a review discussing parent–offspring comparisons in dispersal behaviours (including both natal and breeding dispersal), Doligez & Part (2008) report five out of 12 studies with statistical evidence for a resemblance in dispersal propensity (natal or breeding) between parents and their offspring. However, these studies often suffer from low statistical power because of restricted sample sizes. Since 2000, four of five avian species with estimates of heritability for natal dispersal showed similarity between parents and offspring in either their propensity to disperse before their first breeding attempt or their natal dispersal distances

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Table 1 A literature review of recent heritability estimates of avian natal dispersal, published since 2000, using parent–offspring regressions or pedigree-based animal models. Doligez & Part (2008) provide an extensive review of parent–offspring resemblance in dispersal behaviour explored in birds and mammals.

Species	Data span	Trait	h^2 (SE)	Method	References
Great reed warbler *Acrocephalus arundinaceus*	1983–2001	Philopatry vs. inter-population dispersal	PS: 0.50 (0.19) FS: 0.60 (0.29) MS: 0.62 (0.33)	Parent–offspring regressions, *n* = 48	Hansson *et al.* (2003)
Red-cockaded Woodpecker *Picoides borealis*	1986–2001	Natal dispersal distance	FS: 0.30 (0.15)–0.88 (0.25) MD: 0.17 (0.10)–0.19 (0.10)	Parent–offspring regressions, *n* = 43–330	Pasinelli *et al.* (2004)
Great tit *Parus major*	1960–1998	Natal dispersal distance	Male: 0.247 (0.063) Female: 0.253 (0.058)	Restricted maximum likelihood animal model, *n* = 1607 males and 1758 females	McCleery *et al.* (2004)
	1994–2002	Natal dispersal distance	FS: −0.12 (0.22) MD: 0.05 (0.20)	Parent–offspring regressions, *n* = 92, 86	Matthysen *et al.* (2005)
Blue tit *Cyanistes caeruleus*	1994–2002	Natal dispersal distance	FS: 0.05 (0.28) MD: −0.06 (0.58)	Parent–offspring regressions, *n* = 46, 31	Matthysen *et al.* (2005)
Collared flycatcher *Ficedula albicollis*	1980–2005	Philopatry vs. inter-plot dispersal	PO: 0.469 (0.098) FO: 0.458 (0.069) MO: 0.330 (0.074)	Parent–offspring regressions, threshold model, *n* = 404, 946, 985	Doligez *et al.* (2009)
	1980–2005	Philopatry vs. inter-plot dispersal	0.39, Credible Interval: [0.31; 0.47]	Bayesian animal model, *n* = 4848	Doligez *et al.* (2011)

For parent–offspring regressions, estimates were based on comparisons of values between mid-parent and offspring (PO), father and offspring (FO), mother and offspring (MO), father and son (FS) or mother and daughter (MD). The use of a threshold model in the last two studies on collared flycatchers implies that heritability of the binary trait (philopatry-dispersal) has been transformed to heritability of liability to disperse (Falconer & Mackay, 1996).

(Table 1). Additionally to these direct estimates of heritability, studies with lower sample sizes have found that siblings dispersed similar distances and/or in similar directions (Sharp *et al.*, 2008), although in several cases it was suggested that the similarity resulted from siblings sharing environmental conditions (Forero *et al.*, 2002; Dale, 2010). Finally, natal dispersal has been shown to correlate with heritable personality traits such as exploratory behaviour (Dingemanse *et al.*, 2003), thereby suggesting that natal dispersal is not only a condition-dependent trait, but it is also explained in part by genetic effects.

The scarcity of heritability estimates for natal dispersal is very likely the result of methodological issues, especially the problem raised and underlined by van Noordwijk (1984) regarding nonrandom spatial distribution of possible dispersing sites when comparing dispersal distances between parents and offspring. A bypass to this obstacle is to collect natal dispersal data between populations at a scale larger than the species' average dispersal distance (Hansson *et al.*, 2003), rather than focusing on one population, and/or to analyse the propensity to disperse between different plots or sub-populations (as a binary 0/1 trait), rather than dispersal distance (Doligez & Part, 2008; Doligez *et al.*, 2009). Another challenge yet to take up is to gather sufficient dispersal distances or statuses on related individuals during long-term studies, in order to conduct powerful quantitative genetic analyses. Table 1 illustrates that in short- and medium-lived passerines, monitoring during one or two decades rarely provides more than 50 parent–offspring pairs with known natal dispersal status or distance. For this reason, combining comparisons between different types of relatives in the same model as allowed by pedigree-based 'animal model' techniques (Kruuk, 2004) may represent a very helpful improvement in exploiting all the available data. Finally, dispersal data add an additional complexity to the analysis because they usually display non-Gaussian distributions, especially in the binary coding of dispersers and nondispersers. In this case, Bayesian approaches might prove more powerful than classic frequentist (maximum likelihood) approaches, because they can properly model non-normal responses and can provide a measure of confidence for heritability estimates (O'Hara *et al.*, 2008). Bayesian animal models have been developed already some time ago to model heritability of economically important traits in animal breeding science (e.g. Sorensen & Gianola, 2002), yet their application to characters measured on wild animals or plants is very recent and limited to a restricted number of case studies (Papaïx *et al.*, 2010; Serbezov *et al.*, 2010; Steinsland & Jensen, 2010), with one application to the study of (natal) dispersal (Doligez *et al.*, 2011).

Seabirds are an interesting case for the study of natal dispersal because they are well known for their wide-ranging capacities and dispersive behaviour at sea, yet most species are highly philopatric, returning close to their land-based natal site to breed. Albatrosses represent an extreme case in this regard, among seabirds. They breed on remote oceanic islands and have slow demographic life histories, with late sexual maturity, low fecundity (one egg clutch, some species breed every second year only) and high longevity (Weimerskirch, 1992). Although they can cover several thousands of kilometres during foraging trips and range over oceanic basins, they show very low natal dispersal from their colony of birth, and even higher fidelity to their breeding colony after they have started breeding. However, short-scale natal dispersal between colonies of the same island does occur regularly (Bried *et al.*, 2007), as well as occasionally long-distance dispersal between islands as far as 900 km apart (Inchausti & Weimerskirch, 2002). The long-term monitoring of wandering albatrosses (*Diomedea exulans*) initiated in 1966 on the sub-Antarctic Possession Island in the Crozet Archipelago (Weimerskirch *et al.*, 1997) offers a unique opportunity to gather pedigree data along with phenotypic data on natal dispersal between colonies of one island, in order to estimate heritability of natal dispersal propensity at a short scale. Here, we investigated whether part of the variation in natal philopatry observed in this species can be attributed to a heritable component by examining the heritability of philopatry versus natal dispersal between the breeding colonies of the entire island, where most of the dispersive movements occur.

Materials and methods

Colonies, population monitoring and pedigree

The entire population of wandering albatrosses on Possession Island, the largest of the Crozet Islands (south western Indian Ocean), has been monitored annually since 1966. The population has presently around 380 pairs breeding annually. It had *c.* 500 breeding pairs in the 1960s, declined steeply in the 1970s to reach 260 pairs and increased progressively to the present numbers (Weimerskirch *et al.*, 1997; Delord *et al.*, 2008). As the species has a biennial breeding cycle, the entire breeding population consists presently of *c.* 600 breeding pairs. The species breeds in loose aggregations, called colonies, that are located on the northern and eastern coasts of the island (Fig. 1). Colonies are divided by geographical barriers (such as a river or ridges) unsuitable as breeding grounds, which allow a clear spatial separation of aggregations. In total, eight colonies can be distinguished, six of them located on the eastern part of the island on northern and southern slopes of rivers (e.g. the Baie du Marin location is split between a northern and southern colony, see Fig. 1).

For every year since 1966, all of the nests have been located after the egg-laying period (around January 15th). For each nest, the incubating bird present is identified using its unique metal band number, or banded if it is its first capture. Two other visits take place 10 and 20 days later to identify the bird's partner. In April, the presence of a hatched chick is recorded, and thereafter its survival is monitored every second month until it fledges, in November. The chick is banded in October. Using this procedure, after 2000 only 4–27 individuals (average 18.6) were captured annually without a band as opposed to *c.* 600 individuals captured with a band (the few unringed birds can be immigrants, chicks missed during the banding operations or adults having lost their bands). This low number of birds without bands is the result of a systematic banding programme for breeding adults and chicks on Possession Island, coupled with very high natal philopatry and recruitment rate (Inchausti & Weimerskirch, 2002). For all birds banded as chicks and that do not disperse outside the island, we can determine their short-scale dispersal from their birth colony: we considered that local natal dispersal occurred when a bird reproduced for the first time in a colony of Possession Island different from its birth colony on the same island.

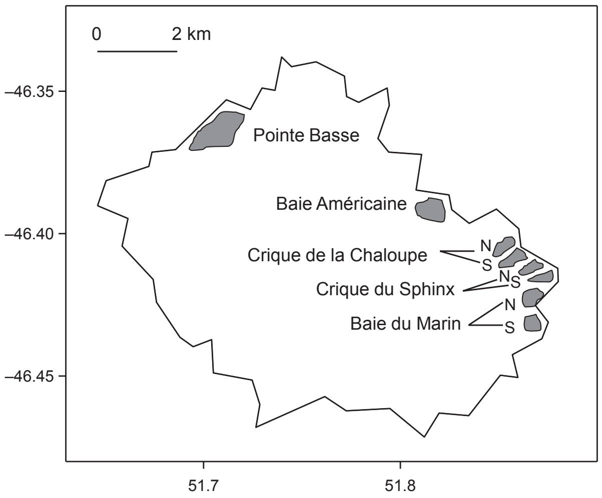

Fig. 1 Map of Possession Island, in the southern Indian Ocean, with eight colonies of wandering albatross (N: North; S: South).

Monitoring of other wandering albatross colonies outside Possession Island is very heterogeneous. In the Indian Ocean, only Marion Island (1070 km away from Possession) and the eastern part of Kerguelen (1450 km away) have annual banding and recapture programmes comparable with that on Possession Island, but all other breeding sites of the species have been monitored irregularly for banded birds. Using the same data set and a similar span as ours, Milot *et al.* (2008) reported only 28 natal dispersers from Possession (19 of which were birds breeding on Marion Island), representing approximately 0.3% of birds banded as chicks on the island. The heterogeneity of recapture efforts outside Possession Island hampered a global analysis of natal dispersal, but anyway the very limited proportion of long-range dispersal in this species would not allow any statistical powerful analysis. For this reason, and also because colony philopatry is very high, we restrict out interpretation to local natal dispersal.

The long-term monitoring of wandering albatrosses on Possession Island allowed us to use a quantitative genetic approach to investigate additive genetic effects on dispersal behaviour, based on a pedigree of 2797 individuals over four generations (see Appendix S1 for descriptive statistics on the pedigree). Although the wandering albatross is a highly socially faithful monogamous species, paternity analyses on 75 breeding pairs from Possession Island have previously revealed 10.7% of extra-pair offspring (Jouventin *et al.*, 2007), possibly induced by the male-biased adult sex ratio. This implies that the social pedigree we use here for our quantitative genetic analysis includes some errors in the paternity links, which could result in some underestimation of the additive genetic variance and heritability, although simulations have shown that rates of paternity errors around 5–20% induce little bias on heritability estimation (Wilson *et al.*, 2003; Charmantier & Réale, 2005; Morrissey *et al.*, 2007).

Colony- and sex-specific dispersion

We restricted the data set to cohorts of at least 30 individuals ringed at birth and recaptured as breeders (see Fig. S1 for all sample sizes), hence birds born between 1970 and 1999. The last year of breeding included in this analysis was 2007. When restricting the data set to birds with known sexes, and born between 1970 and 1999, natal dispersal status (disperser/non-disperser) was known for 1890 individuals, including 421 father–offspring pairs (with 60 dispersing fathers) and 413 mother–offspring pairs (112 dispersing mothers). Overall, the data set included 21.8% of natal dispersing individuals, yet males dispersed much less than females: 14.0% of males were dispersers versus 30.0% of females. Preliminary logistic regression models exploring individual and environmental fixed effects influencing natal dispersal behaviour showed significant natal colony and sex effects, and insignificant cohort effects. The high significance of natal colony in these preliminary analyses, as well as in all models described below, is in accordance with the recent demonstration that the rate of natal dispersal varies from 0.70 to 0.92 according to the colony of origin on Possession Island (Gauthier *et al.*, 2010).

Classical frequentist estimation of additive genetic variance and heritability for liability to disperse

Dispersal behaviour can be viewed as a threshold character, whereby the trait has an underlying (unobserved) continuous distribution, called liability, with a threshold determining the discontinuous phenotype (Falconer & Mackay, 1996): in our case, individuals above the threshold would disperse, and those below would not disperse. The phenotypic distribution on the liability scale can be assumed normal, and resulting from genetic and environmental differences between individuals, as any quantitative trait. Several approaches can then be used to estimate the heritability of the character on its underlying liability scale h_c^2.

First, we used a simple approach based on similar reasoning as classic parent–offspring regressions, whereby incidences in the parental generation and in their progeny are used to estimate the mean liability of the parents displaying the character (dispersing parents) and their offspring (Lynch & Walsh, 1998). One way to evaluate the validity of such a threshold model is to compare estimates obtained using different types of relatedness; hence, we based our estimations on father/offspring, mother/offspring, father/son and mother/daughter incidences. We used Edwards' equation detailed by Lynch & Walsh (1998, Equation 25.2 page 733) where the exact phenotypic correlation between relatives on the underlying normal scale is approximated, in order to obtain a simple equation whereby the heritability is directly estimated from the incidences. Unfortunately, this method does not allow a good assessment of the uncertainty of the estimation, because no confidence interval or standard error is associated with the estimation of heritability on the underlying scale.

Second, we modelled the natal dispersal behaviour using a generalised linear mixed model (GLMM) with a logit link function relating the binary data to the underlying normal scale and a restricted maximum likelihood (REML) procedure (Knott *et al.*, 1995; Lynch & Walsh, 1998) run with ASReml 2.0 (Gilmour *et al.*, 2006). This GLMM 'Animal Model' partitioned the variance into an additive genetic and an environmental variance component (Kruuk, 2004). For the analysis of binary data, ASReml uses an approximate likelihood technique called penalised quasi-likelihood (PQL, Breslow & Clayton, 1993), which has caused a call for caution in the use of these models (see our Discussion). It is ill-advised to use the quasi-likelihood computed by PQL as a means of statistical inference (Bolker *et al.*, 2009). However, there is presently no formally rigorous test to evaluate whether the additive genetic variance and heritability estimates obtained using a generalised linear mixed animal model are significant. We chose to run similar models using a normal scale and compared the REML models with/without an additive genetic variance using the standard Akaike's information criterion (A Gilmour, pers. com., Burnham & Anderson, 2002). As justified above, individual sex (male/female) and natal colony were included as fixed effects. For each individual i, we denote the dispersal event y_i, which takes values 1 if it has dispersed and 0 otherwise. This binary random variable was assumed to be related to a continuous underlying latent variable l_i such that $y_i = 1$ if $l_i \geq 0$ and 0 otherwise. The random variable l_i is usually referred to as the liability for individual i and was assumed to be normally distributed with mean η_i and some variance (see below for a decomposition of this variance). The natal dispersal probability $\Pr(y_i = 1)$ was related to the mean liability on the scale of a link function g via $g(\Pr(y_i = 1)) = \eta_i$. In turn, the mean liability was modelled as:

$$\eta_i = \mu + \text{sex} + \text{natal colony} + a_i + e_i,$$

where μ is the population mean, a_i is the individual's additive genetic value, and e_i is the random residual value. Hence, the total phenotypic variance in the liability to disperse (V_P) was portioned into a variance attributed to additive genetic effects (V_A) and a residual variance (V_R): $V_P = V_A + V_R$. In various species of plants and animals, the propensity to disperse is under strong maternal influence (e.g. Venable & Burquez, 1989; Mousseau & Dingle, 1991; Massot & Clobert, 1995). Hence, a maternal identity was also fitted as an extra random effect but it explained an insignificant portion of the variance and was removed. Heritability of short-scale natal dispersal behaviour (h_c^2) was calculated using $V_R = \pi^2/3$ if g was the logit link function and $V_R = 1$ if it was the probit (Nakagawa & Schielzeth, 2010). Both link functions gave very similar results (see Results section).

Bayesian animal model

As a third method for estimating heritability of liability to disperse (h_c^2), we ran animal models with Bayesian inference (e.g. Papaïx *et al.*, 2010) incorporating the same random and fixed effects as described above for the REML animal model. We adopted a Bayesian approach using Markov chain Monte Carlo (MCMC) algorithms because it provides a flexible framework in quantitative genetics to analyse non-normal data (Damgaard, 2007; Waldmann, 2009). The Bayesian approach combines the likelihood (i.e. information derived from observed data) and the prior distribution of the unknown quantities (i.e. knowledge available before the data were observed) to produce the joint probability distribution of all models unknowns conditionally on the observed data. The joint posterior distribution of all parameters was obtained by means of MCMC sampling as implemented in the OpenBUGS software (Lunn *et al.*, 2009; code available in Appendix S2). We ran two parallel MCMC chains and retained 45 000 iterations after an initial burning of 5000 iterations with a thinning of each 10th iteration. Convergence of MCMC sampling was assessed by means of the Brooks–Gelman–Rubin diagnostics (Brooks & Gelman, 1998) and visual inspection of the chains (Fig. S2).

A Bayesian analysis requires specifying prior probability distributions for the model parameters. All priors were selected as sufficiently vague in order to induce little prior knowledge (Clark, 2005; McCarthy & Masters, 2005), which ensures that posterior distributions reflect mainly the information from the data. An uninformative (or vague) prior corresponds to a uniform distribution or normal distribution with large variance (see below for specific prior choices). When fitting animal models, the use of noninformative priors on the standard deviations of the random effects is usually used. However, noninformative priors on the additive genetic standard deviations lead to an informative prior on the heritability associated, which can influence posterior results in the case of weakly informative data (Gelman, 2006). We used the probit link function, hence $V_R = 1$ and the heritability h_c^2 was fully dependent on the additive genetic variance ($h_c^2 = V_A/(V_A + 1)$). Thereby, the higher the additive genetic variance (through a noninformative prior) was, the higher the probability for the heritability would be close to 1. To address this issue, we assigned noninformative priors on the heritability h_c^2 (U[0,1]). The one-to-one transformation relating V_A to h_c^2 ($V_A = h_c^2/(1 - h_c^2)$)) thereby induces a relatively noninformative prior on V_A (see Fig. 2). Regarding the regression coefficients of the fixed effects (intercept μ, sex effect α and natal colony β), normal distributions with mean 0 and variance 10 were used. We conducted a prior

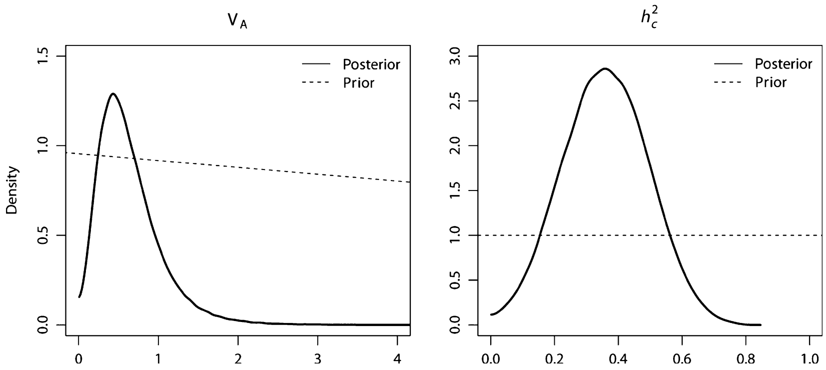

Fig. 2 Posterior density distributions (full lines) for additive genetic variance and heritability in propensity for natal dispersal estimated using a Bayesian animal model. Prior density distributions are also displayed (dotted lines). Notation: V_A is the additive genetic variance and h_c^2 is the heritability estimated on an underlying continuous liability scale.

sensitivity analysis to make sure that information in the data was sufficient to update the prior.

Bayesian animal models with/without an additive genetic variance were compared using the deviance information criterion (DIC, Spiegelhalter *et al.*, 2002). Several other methods exist to compare models in a Bayesian framework (O'Hara *et al.*, 2008); we adopted the DIC following the advice of Hadfield (2010) and as implemented in MCMCglmm.

Results

Overall, 22% of the birds ringed as chicks on Possession Island were captured breeding in a different colony from their birth colony (minimum and maximum dispersal distances within the island were 100 m and 12 km). These natal dispersal rates focus on a small-distance scale compared to the great flight capabilities of wandering albatrosses, yet these rates are close to that found in a previous study investigating dispersal between six islands of the Southern Ocean, with colonies as far as 6050 km (23% of natal dispersal from the birth colony, including within- and between-island groups, the longest natal dispersal distance observed was 1450 km, Inchausti & Weimerskirch, 2002). This suggests that long-distance natal dispersal remains exceptional in this species. Mean natal dispersal distance within the island was 0.67 km overall (SD = 2.21), 0.89 km (SD = 2.46) for females and 0.46 km (SD = 1.92) for males.

The occurrence of local natal dispersal in offspring from dispersing fathers or mothers was notably higher than the mean population occurrence (Table 2), suggesting a clear heritable basis for this character. This translated in heritabilities of liability to disperse locally estimated between 0.31 and 0.86 using parent–offspring occurrences (Table 2). The smaller estimate came from a father–son regression and the largest estimate from a mother–daughter regression, suggesting that maternal effects could partly confound this latter heritability estimate, although this was not confirmed by animal models because none of the models below showed significant maternal effects. Alternatively, the known extra-pair paternities in this species (Jouventin *et al.*, 2007) could partly explain the difference between father–son and mother–daughter regression estimates.

The heritability of the liability to disperse, as estimated using a generalised linear mixed animal model, was $h_c^2 = 0.06 \pm 0.05$ (SE, these estimates are the same using a logit or probit link function), and the additive genetic variance $V_A = 0.20 \pm 0.19$ ($V_A = 0.06 \pm 0.07$ using a probit link). Although standard errors of these estimates were high, AICs were lower for models with additive genetic variance compared to without (−1959.1 vs. −1951.8 for GLMMs on normal scale), supporting the presence of a heritable component in the propensity for natal dispersal, even though the absolute heritability value was small.

Finally, the results from the Bayesian animal models also showed significant heritability for the propensity to disperse, with $h_c^2 = 0.36$ (95% credible interval [0.10; 0.62]): the model incorporating an additive genetic effect was associated with the smallest DIC value (DIC: 1042 vs. 1094 when excluding the additive genetic variance). The posterior distributions are displayed in Fig. 2, and the resulting summary estimates are presented in Table 3. The comparison of posterior to prior distributions suggested that the information contained in the data led to considerable updating of the prior distributions (see Fig. 2).

Discussion

Our analyses based on the long-term monitoring of wandering albatrosses on Possession Island revealed that additive genetic effects contribute to heritable variation for short-scale propensity to disperse between birth and first breeding colonies. All three methods used to estimate heritability pointed to significant heritable effects on short-distance natal dispersal, yet the estimations varied substantially between methods (see Discussion below). The heritability of natal dispersal measured over a few hundred metres is notable considering the great flight capabilities and extreme navigation performance of these birds. Natal dispersal outside the natal island in wandering albatrosses, although rare, can be as far as 6050 km (H. Weimerskirch, unpublished data), and they can travel even longer distances during foraging trips while breeding (e.g. Lecomte *et al.*, 2010) and especially during their sabbatical year when they can circumnavigate Antarctica and pass close to all the

Table 2 Heritability of natal dispersal behaviour in the wandering albatross estimated on the underlying continuous scale (h_c^2) using Edwards' approximation method based on the behavioural occurrences in parents (M = males, F = females) and offspring.

	Occurrence of natal dispersal			
	In population (*n* = 960 M + 930 F)	In offspring of dispersing parents	Number of dispersing parents	h_c^2
Father–offspring	M + F: 0.218	0.383	60	0.586
Mother–offspring	M + F: 0.218	0.393	112	0.618
Father–son	M: 0.140	0.216	37	0.312
Mother–daughter	F: 0.300	0.536	56	0.860

Table 3 Parameter estimates from the Bayesian animal model of propensity for natal dispersal. Posterior means, medians, standard deviations (SD) and 95% credible intervals (CI) are provided: μ is the intercept, α is the sex effect (female), β is the colony of birth effect, V_A is the additive genetic variance and h^2_c is the heritability estimated on an underlying continuous liability scale.

	Mean	SD	Median	CI
μ	−3.07	0.37	−3.05	[−3.86; −2.46]
α	1.03	0.16	1.02	[0.75; 1.39]
β_2	1.58	0.28	1.56	[1.08; 2.19]
β_3	2.02	0.40	2.00	[1.28; 2.88]
β_4	2.72	0.36	2.68	[2.13; 3.57]
β_5	2.72	0.40	2.68	[2.04; 3.59]
β_6	2.26	0.31	2.23	[1.74; 2.95]
β_7	2.14	0.30	2.11	[1.64; 2.81]
β_8	1.80	0.28	1.77	[1.35; 2.44]
V_A	0.64	0.39	0.56	[0.11; 1.63]
h^2_c	0.36	0.13	0.36	[0.10; 0.62]

breeding sites of the species (Weimerskirch, unpublished data). Yet, we have shown here that if we consider only the birds that remain faithful to one island, the local-scale dispersal within one island is heritable. This result suggests that microevolution in natal dispersal behaviour is possible, especially in situations where selection will operate towards higher dispersal, e.g. in disturbed habitats (Bowler & Benton, 2005). Unfortunately, the very long lifespan of wandering albatrosses prevents us from testing how philopatry relates to lifetime fitness in order to measure selection acting on this life history choice in this species.

Since 1966, all breeding wandering albatrosses and their chicks have been banded on Possession Island. This amounts to 8707 ringed chicks, of which, up until 2006, 28 were found breeding in other islands of the Southern Ocean (Kerguelen, Cochons Island, Prince Edward and South Georgia, see Milot *et al.*, 2008). Natal dispersal movements between these islands were asymmetric, at least between Marion Island (Prince Edward Islands) and Possession Island where similar mark–recapture efforts are carried out, with more natal dispersers witnessed coming from Possession. In any case, these recent analyses of capture–mark–recapture data and genetic diversity and structure (Milot *et al.*, 2008) demonstrate ongoing gene flow between the different islands, which is not surprising considering the flight abilities of wandering albatrosses. However, this rate of dispersal remains extremely low, and the few cases available do not allow statistical analysis. Here, we have chosen to use records of natal dispersal within one island comprising eight colonies in order to estimate quantitative genetic parameters by comparing related and unrelated individuals. It is difficult to envisage how the long-distance natal dispersal would affect our estimates if data were available to investigate natal dispersal both on small and on large scales, yet if anything our short-scale restriction should only underestimate natal dispersal heritability by ignoring a few dispersing individuals, in the same way that ignoring extra-pair paternity might reduce the resemblance between fathers and offspring in their dispersal behaviour.

Our results offer support to previous analyses based mostly on parent–offspring regressions, showing within-family resemblance in dispersal liability (e.g. most recently Doligez *et al.*, 2011), and they widen the phylogenetic range of study because previous work focused on short-lived species, mainly passerines (Table 1), yet they also highlight important differences in estimates of heritability depending on the statistical approach used. As animal models control for various fixed and random effects and use information from across the pedigree, they often provide lower estimates of heritability compared to the classic parent–offspring regression (Quinn *et al.*, 2006; Postma & Charmantier, 2007), with a decline of typically 5–30% in heritability estimation (Kruuk *et al.*, 2001; MacColl & Hatchwell, 2003; McCleery *et al.*, 2004). In a recent study that compared heritability of natal dispersal using parent–offspring regression versus Bayesian animal model, a decline of 17% was observed (Doligez *et al.*, 2011; see Table 1). Here, however, the REML animal model provided an estimate of heritability for the liability to disperse (0.06 ± 0.05) 80–90% lower than estimates from parent–offspring regressions (Table 2). Notably, this REML estimate was also smaller than the 95% credible interval estimated with the Bayesian animal model (CI = [0.10; 0.62]). We view this as a worrying result that confirms the doubts over the robustness of using linear mixed models with non-Gaussian data (Bolker *et al.*, 2009). Indeed, it has been suggested that animal models based on generalised linear mixed models using the PQL technique as implemented in ASReml may provide biased estimates (Gilmour *et al.*, 2006), especially so for binary data where PQL would underestimate the variance components, as well as the absolute value of fixed effects (Breslow & Clayton, 1993). These warnings suggest that our results from the Bayesian animal model may be more robust than those with the two other methods, yet it is beyond the scope of this study to evaluate the validity of the GLMMs on binary data. This would necessitate a simulation study in order to draw conclusions on the type of bias induced by this practice, especially whether it will consistently under-estimate heritability on a liability scale. However, we feel our results underline that it is presently useful for evolutionary biologists to compare estimates from the most commonly implemented approaches, while keeping an eye on the ongoing work carried out by biostatisticians to investigate the suitability of the different approaches.

On the other hand, REML and Bayesian animal models provided similar evaluations for the explored factors affecting the decision to disperse before breeding, including the major effect of individual sex, with twice as many females dispersing as males, and their birth colony. The latter confirms recent multi-state mark–recapture models showing that on Possession Island, philopatry varies from 70% to 92%, depending on the colonies (Gauthier *et al.*, 2010), with lower natal dispersal in larger colonies, and least dense colonies attracting dispersers. Sex-specific liability to disperse is also in line with the mark–recapture analysis and confirms that natal dispersal is partly a condition-dependent trait. Maternal effects did not statistically influence the natal dispersal propensity, as opposed to the only other study, to our knowledge, that investigated maternal effects by partitioning the variance in dispersal behaviour (natal dispersal distance in the great tit *Parus major*, McCleery *et al.*, 2004) into components attributed to additive genetic and environmental effects. The heritable component shows that condition-dependent and environmental traits do not explain all the individual variance displayed in the propensity to disperse. The origin of the heritable variation revealed here is however not necessarily purely additive genetic, and in this type of study it is especially important to consider the possibility of family-specific correlations owing to ecological or cultural inheritance. We have attempted to control for potential influences of maternal care and several environmental factors, yet other common environment effects such as local habitat quality could be involved if they are shared closely by relatives. As females lay one egg every 2 years, sibs are likely to share less local environmental effects than in passerine avian model species with large clutches. Also, it is difficult to envisage how wandering albatross offspring could assess the natal dispersal status of their parents, unless natal dispersal is strongly correlated with other behaviours they can witness. Hence, we believe our estimation of heritability of local natal dispersal is most likely not inflated by nongenetic inheritance. In any case, if one is interested in the potential for evolution of a character, one should estimate the heritable variation displayed by this trait, on which natural selection will operate, regardless of the mode of transmission. Note that removing nongenetic effects from heritability estimation is most optimally carried out by cross-fostering experiments in the field, a prospect difficult to consider in such long-lived species as albatrosses.

In this study, we have attempted to estimate additive genetic variance and heritability of the liability for local natal dispersal, attributing the status of disperser or nondisperser to each wandering albatross born and breeding on Possession Island. After controlling for the fixed effects discussed above, a large portion of the variance between birds in their liability to disperse was not explained by additive genetic effects and remained unexplained in our models. We know from past research that the decision to disperse or not is highly dependent on a suite of environmental factors. Hence, as has been previously suggested (Ronce *et al.*, 2001), an interesting avenue would be to consider dispersal as a plastic response to a set of biotic and abiotic conditions rather than a fixed dispersal status, although obviously such a reaction norm approach cannot be undertaken on the single event of natal dispersal but rather on breeding dispersal. Although breeding dispersal remains very low in wandering albatrosses (rate of breeding fidelity to a nesting colony ranges from 0.957 to 0.977 on Possession Island, Gauthier *et al.*, 2010), another interesting follow-up to this study would be relating natal and breeding dispersal, both on a phenotypic level and also genetically. Obviously, these enterprises would be very challenging as they would require an even greater amount of data on the natal and breeding conditions for related and unrelated individuals than has been gathered until now in long-term bird studies (Table 1). However, the study of how plastic dispersal strategies depend on environmental conditions remains a necessary step for evolutionary biologists interested in the evolution of dispersal (Kokko & Lopez-Sepulcre, 2006). In part, it will contribute to understanding how such high levels of additive genetic variance for a major behavioural character is maintained, and how fast dispersal can evolve. Natal and breeding dispersal are complex life history traits, which interact closely with population demography (Ronce *et al.*, 2001) and population genetic structure and display strong genetic covariance with other major life history characters (Roff & Fairbairn, 2001). Hence, this will add further complexity when estimating the forces of selection acting on dispersal, and predicting its evolution.

The wandering albatross status in the IUCN Red List of Threatened Species (http://www.iucnredlist.org) is presently vulnerable with a global population decline. In the past, this decline has largely been attributed to incidental catch in fisheries (Weimerskirch *et al.*, 1997). Recent studies have shown that wandering albatrosses as well as other albatrosses are also strongly influenced by environmental variation, and thus susceptible to future climate change (Rolland *et al.*, 2009). In the context of environmental change, some islands presently occupied by breeding sites of these central place foragers are likely to become less optimal breeding sites in the near future. Similarly, several present breeding sites were not available for breeding during the last glaciations, suggesting that natal dispersal has, and will in the future, play(ed) a critical role for the long-term persistence of these species. Natal dispersal in this long-lived bird is of major importance for the dynamics and conservation of their global populations. Hence, if areas in the bird distribution are affected negatively by environmental changes, an evolution towards higher natal dispersal or higher plasticity in dispersal can constitute a keystone for the population persistence. In any case, the slow pace of life of this species as illustrated by its generation time of 18.9 years (Weimerskirch, unpublished estimate) suggests that such a microevolutionary process would require several decades before any significant change in dispersal behaviour.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Summary statistics for the wandering albatross pedigree used.

Appendix S2 R script and OpenBUGS code for the Bayesian animal model.

Figure S1 Annual sample sizes of records of natal dispersal for wandering albatrosses on Possession Island.

Figure S2 Mixing of the MCMC algorithm used to fit the Bayesian animal model to the wandering albatross data.

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Article 6

Combining capture–recapture data and pedigree information to assess heritability of demographic parameters in the wild

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Combining capture–recapture data and pedigree information to assess heritability of demographic parameters in the wild

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Keywords:

Binary trait;
Capture–Recapture Animal Model;
Cormack–Jolly–Seber model;
Individual heterogeneity;
State–space model;
Threshold model.

Abstract

Quantitative genetic analyses have been increasingly used to estimate the genetic basis of life-history traits in natural populations. Imperfect detection of individuals is inherent to studies that monitor populations in the wild, yet it is seldom accounted for by quantitative genetic studies, perhaps leading to flawed inference. To facilitate the inclusion of imperfect detection of individuals in such studies, we develop a method to estimate additive genetic variance and assess heritability for binary traits such as survival, using capture–recapture (CR) data. Our approach combines mixed-effects CR models with a threshold model to incorporate discrete data in a standard 'animal model' approach. We employ Markov chain Monte Carlo sampling in a Bayesian framework to estimate model parameters. We illustrate our approach using data from a wild population of blue tits (*Cyanistes caeruleus*) and present the first estimate of heritability of adult survival in the wild. In agreement with the prediction that selection should deplete additive genetic variance in fitness, we found that survival had low heritability. Because the detection process is incorporated, capture–recapture animal models (CRAM) provide unbiased quantitative genetics analyses of longitudinal data collected in the wild.

Introduction

Quantitative genetic models (Falconer & Mackay, 1996; Lynch & Walsh, 1998) allow identification of components of variance observed in a phenotypic trait (either morphological or demographic) by jointly analyzing data on the trait and on genealogical relationships in a pedigree. In particular, the 'animal model' approach allows, through the use of generalized linear mixed models, simultaneous estimation of components of phenotypic variance that can be attributed to genetic factors, environmental factors and other unknown factors (Kruuk, 2004). Heritability of the phenotypic trait can then be estimated from the fraction of the variance that can be attributed to the additive genetic effects.

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Although well developed in animal breeding science, it is only recently that the estimation of heritability using the animal model framework has been advocated for wild animal and plant populations as an alternative to more limited classic regressions between relatives (Kruuk, 2004). The methodological advances of the animal model and the increasing use of quantitative genetics in wild populations has resulted in important applications for identifying management strategies for species of conservation concern (Law & Stokes, 2005), for other conservation biology issues (Coltman *et al.*, 2003; Stockwell *et al.*, 2003) and to address questions of a basic nature in evolutionary biology (Kruuk *et al.*, 2008).

However, there are still problems concerning the estimation of heritability in natural systems (Merilä *et al.*, 2001), which Kruuk (2004) suggests 'can to a certain extent be overcome by resorting to statistical techniques that are more elaborate than the ones adopted in a majority of the investigations in natural settings'. Among other problems, it is well known that estimating demographic parameters in the wild can be biased and inference can be flawed when the detectability of studied individuals is not accounted for (Gimenez *et al.*, 2008). Typically, estimating individual survival, and hence heritability in survival, can be strongly biased when individuals are missed during population monitoring. Methods using traditional models for inferring heritability of demographic parameters have been developed (Cox or parametric model for survival e.g. Ducrocq & Casella, 1996). However, such methods do not deal with detection probabilities less than 1 (Cam, 2009). In contrast, capture–recapture (CR) models allow estimation of demographic parameters when the detection is imperfect (Lebreton *et al.*, 1992). The basic Cormack–Jolly–Seber (CJS) model (Lebreton *et al.*, 1992) considers survival and recapture probabilities as varying over time but homogeneous among individuals, which is of little use for estimating individual variability in demographic parameters. Recently, the CJS model has been extended to account for individual effects in both survival and recapture probabilities. Royle (2008) proposed a state–space model (SSM) formulation of the CJS model, specifically to incorporate random individual effects (see Gimenez & Choquet (2010) for an alternative approach). The SSM framework distinguishes the underlying demographic process from the observation process (detection), therefore providing much flexibility for decomposing the variability in demographic parameters (Gimenez *et al.*, 2007).

Our present purpose is to adapt the SSM framework to combine CR with animal models (hereafter CRAM), thus allowing the decomposition of individual variation in demographic parameters into environmental and genetic components (as first suggested by O'Hara *et al.* (2008) in their Fig. 1). We provide the details of the Bayesian inference and its implementation through Markov chain Monte Carlo (MCMC) simulations using the freely available software package OpenBUGS. We refer to O'Hara *et al.* (2008) for a review of the Bayesian approach for quantitative genetic analyses and to Sorensen & Gianola (2002) for exhaustive details on its

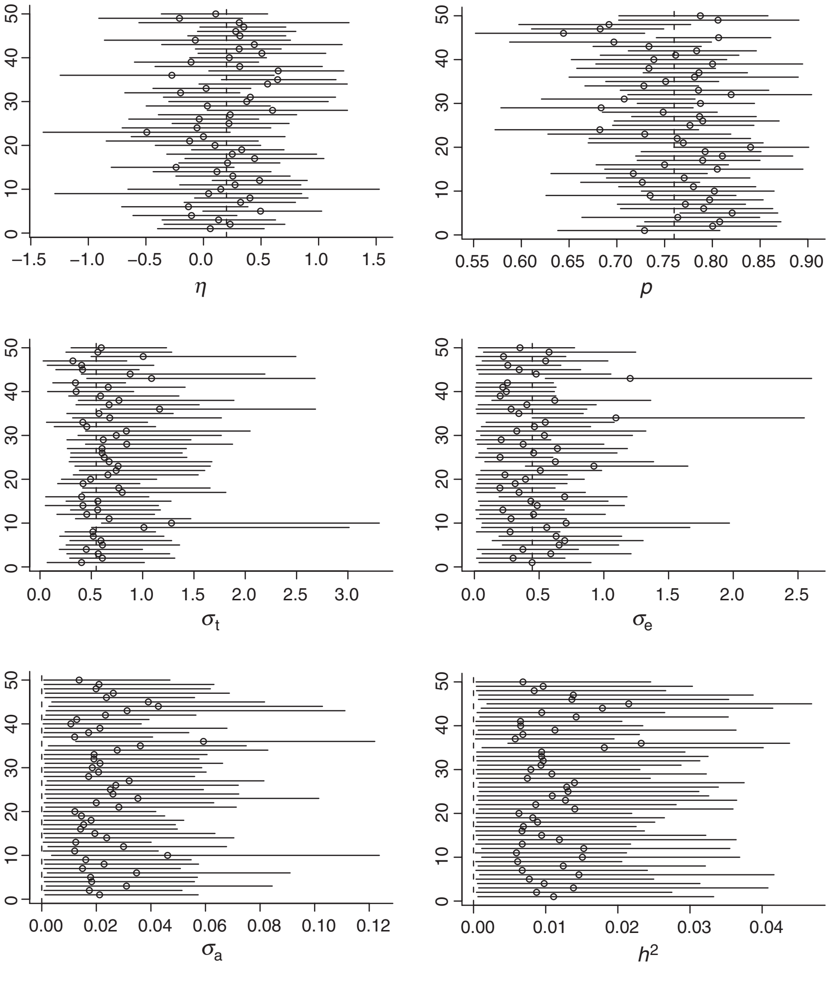

Fig. 1 Performance of the capture–recapture animal model approach – scenario with $\sigma_a^2 = 0$. For each of the 50 simulated data sets, we displayed the median (circle) and the 95% credible interval (horizontal solid line) of the parameter. The actual value of the parameter is given by the vertical dashed line. Notation: η is the mean survival on the probit scale, p is the detection probability, σ_t^2 is the variance of the yearly random effect, σ_e^2 is the variance of the nongenetic individual effect, σ_a^2 is the additive genetic variance and h^2 is the heritability.

implementation. Finally, we illustrate the utility of our method by estimating the heritability of survival using data from a 29-year study of individually marked blue tits (*Cyanistes caeruleus*).

A threshold state–space model for CR–pedigree data

A SSM model can be specified in which there are two layers, one specifying the dynamic process (the state model) and another connecting the demographic process to its observation through the detection of individuals (the observation model). We focused on a binary trait, namely survival, and aimed at calculating its heritability. In standard methods of quantitative genetics, the heritability of a discrete trait is often assessed using so-called threshold models (Gianola, 1982; Falconer & Mackay, 1996; Lynch & Walsh, 1998). This approach assumes that there exists a continuous random variable called a latent variable or liability from which discrete values of the trait are generated.

Under natural conditions, because individual detectability is often less than one, we need to deal with the observation process. To account for this issue in the sampling protocol, we used CR data generally collected under the form of 1's and 0's corresponding to a detection or not of I individuals over T sampling occasions.

The state model

We define X as a binary random variable that represents the demographic process, with $X_{i,t} = 1$ if individual i is alive and available for detection at time t and 0 if it is dead. The state process in the SSM formulation stipulates that if individual i is alive at time $t - 1$, it survives until time t with survival probability $\phi_{i,t-1}$ or dies with a probability $1 - \phi_{i,t-1}$; in other words, $X_{i,t}$ is distributed as a Bernoulli random variable with parameter $\phi_{i,t-1}$ given $X_{i,t-1} = 1$ (Gimenez *et al.*, 2007; Royle, 2008).

The observation model

We define Y as a binary random variable standing for the observation process, with $Y_{i,t} = 1$ if the individual i is detected at time t and 0 otherwise. These observations are generated from the underlying demographic process, which is partially hidden from the observer, because when an individual is not detected, it is not possible to say whether it is alive or not.

If individual i is alive at time t, then it has a probability $p_{i,t}$ of being encountered and a probability $1 - p_{i,t}$ otherwise; in other words, the link between survival and the detection of individuals is made through the observation equation, which states that $Y_{i,t}$ is distributed as a Bernoulli random variable with parameter $p_{i,t}$ given $X_{i,t} = 1$ (Gimenez *et al.*, 2007; Royle, 2008).

Plugging the animal model in CR models: CRAM

We assume that the random survival process is related to a continuous underlying latent variable $l_{i,t}$, which, given $X_{i,t-1} = 1$, is satisfied as:

$$X_{i,t} = \begin{cases} 1 & \text{if} \quad l_{i,t} > \kappa, \\ 0 & \text{if} \quad l_{i,t} \le \kappa. \end{cases}$$

for $t = f_i + 1,\ldots,T$, where f_i is the first time individual i is detected and κ was a threshold value. We assumed that the so-called liability $l_{i,t}$ was normally distributed with mean $\mu_{i,t}$ and variance σ_e. For identifiability issues, and without loss of generality, we fixed σ_e to 1 and κ to 0 (Harville & Mee, 1984; Sorensen *et al.*, 1995).

From this construction, usually referred to as a threshold model (Gianola, 1982), we have $\phi_{i,t-1} = \Pr(X_{i,t} = 1 | X_{i,t-1} = 1) = F(\mu_{i,t})$ where F is the cumulative function of a normal distribution with mean 0 and variance 1. Noting that F^{-1} is the probit function often used to analyse binary data, we specified an animal model on the mean of the liability:

$$\mu_{i,t} = \text{probit}(\phi_{i,t-1}) = \eta + b_t + e_i + a_i$$

where η is a constant term for the mean survival on the probit scale, b_t is a random yearly effect (i.e. year specific), e_i is an individual random effect that has no genetic basis and a_i is the genetic value for individual i. Note that covariates can be incorporated as fixed effects possibly affecting survival, e.g. climate effects (Grosbois *et al.*, 2008) or anthropogenic pressures (Véran *et al.*, 2007). We assumed that the temporal effect b_t is normally distributed with mean zero and variance σ_t^2, e_i normally distributed with mean 0 and variance σ_e^2 whereas the distribution of **a**, the vector of the a_i's, was multivariate normal with mean 0 and variance–covariance matrix $\sigma_a^2\mathbf{A}$, where σ_a^2 is the additive genetic variance and **A** the additive genetic relationship matrix (Sorensen & Gianola, 2002). The additive genetic relationship matrix **A** is built up from the pedigree. For example, for a given individual, $A_{i,i} = 1$, whereas between parents and their offspring, $A_{i,j} = 0.5$. To handle with the complexity of the animal model, we adopted a procedure proposed by Damgaard (2007) (see also Waldmann (2009) for an alternative), which combines a reparametrization (Henderson, 1976) and a recursive algorithm (Quaas, 1989). Heritability was calculated as the ratio of the additive genetic variance to the total variance:

$$h^2 = \frac{\sigma_a^2}{\sigma_t^2 + \sigma_e^2 + \sigma_a^2 + 1}.$$

Implementation

Estimating variance components and heritability

The frequentist approach for fitting our model would require maximizing the likelihood of the data. This is a complex issue because of the high-dimensional integral of the SSM likelihood and the presence of random effects and latent variables. Therefore, we opted for a Bayesian approach through MCMC methods, which provide powerful computer-intensive methods for handling complex models. Bayesian statistical methods are becoming increasingly popular in evolutionary ecology, in particular to analyse CR data (Gimenez *et al.*, 2006), as well as in quantitative genetics, in particular to fit animal models (Damgaard, 2007) and threshold models (Sorensen *et al.*, 1995).

In order to completely specify the Bayesian model, we provided prior distributions for all parameters. All priors were selected as sufficiently vague in order to induce little prior knowledge. Specifically, we chose $p \sim U[0,1]$ and $\eta \sim N(0,100)$. We assigned uniform distributions to the standard deviation of the random effects, $\sigma_t \sim U[0,10]$, $\sigma_e \sim U[0,10]$ and $\sigma_a \sim U[0,10]$ (Gelman, 2006; Royle, 2008).

The simulations were performed using OpenBUGS (Thomas *et al.*, 2006) (which performs block-updating), using the program R (Ihaka & Gentleman, 1996) and package R2WinBUGS (Sturtz *et al.*, 2005); R was particularly useful for manipulating the pedigree and post-processing the MCMC results (see Supporting Information for the R and OpenBUGS codes).

Simulation study

The ability of our model to estimate the genetic basis of individual variation in survival was verified using simulations. We considered two scenarios, without ($\sigma_a^2 = 0$) and with additive genetic variance ($\sigma_a^2 = 0.4$). All other parameters were chosen to mimic the case study on blue tits (see next section). Specifically, we used $p = 0.76$, $\eta = 0.2$ (mean survival ≈ 0.6), $\sigma_t^2 = 0.3$, $\sigma_e^2 = 0.2$ (heritability ≈ 0.2). We simulated 50 pedigrees with 50 individuals (25 dams and 25 sires) over 5 generations (250 individuals in total). In association with the pedigrees, we simulated 50 capture–recapture datasets with 10 sampling occasions. Parent group was assumed to be unobserved. We divided the progeny group into 5 cohorts (every 2 years) of 40 individuals. For five randomly chosen data sets, we first ran two overdispersed parallel MCMC chains to check whether convergence was reached. As a result, we decided to use 60 000 iterations with 20 000 burned iterations for posterior summarization. We then applied our capture–recapture animal model approach on each data set.

The results are shown in Fig. 1 (without additive genetic variance) and Fig. 2 (with additive genetic variance). For each of the two scenarios, our approach was successful in estimating the various parameters. In particular, the value of σ_a was well recovered by our model (see Fig. 2, bottom-left panel), with only one 95% credible interval (out of 50) that did not contain the actual value.

Application to the blue tit data

To illustrate our approach, we used a long-term dataset of individually marked blue tits (*Cyanistes caeruleus*) in a natural population in Pirio, on the island of Corsica (France). The study site is made of evergreen forest, composed essentially of Holm Oaks (*Quercus ilex*). Blue tits are hole-nesting birds that readily breed in artificial nest boxes, which facilitates the individual manipulation required for the marking process (Blondel *et al.*, 2006). We used a total of 614 breeding individuals that were banded, released and recaptured in spring during breeding seasons between 1979 and 2007. We recorded 1366 detection events, from which 41% individuals were captured only once (initial marking) and 25% twice (initial marking and a subsequent recapture). A pedigree was constructed based on nest observations; chicks that were marked in a nest box were considered as the progeny of the male and female captured in the same nest box. Within the 614 observed individuals, 287 individuals have no parents identified, 218 fathers and 215 mothers were recorded. The pedigree counts 327 offspring–parent links, 112 full-sib and 126 half-sib links. The maximal pedigree depth is 11 generations. In addition to the observed individuals, 40 dummy individuals were added to retain sib links when constructing the relationship matrix **A**. We used the R package PEDANTICS to manipulate the pedigree (Morrissey & Wilson, 2010).

We assessed the fit of the CJS model to the data using standard goodness of fit techniques (Lebreton *et al.*, 1992) implemented in program U-CARE (Choquet *et al.*, 2009). Overall, the model with both time-dependent survival and recapture probabilities provided a satisfactory fit to the data ($\chi^2_{82} = 65.32$, $P = 0.91$). A preliminary analysis using program M-SURGE (Choquet *et al.*, 2005) suggested that the recapture probability could be simplified by considering it constant over time. Because this test was only valid for the CJS model, we also used a posterior predictive assessment to specifically judge the fit of our CRAM to the observed data (Gelman *et al.*, 1996). The results showed that our model fitted the data adequately well (see Supporting Information).

Two MCMC–chains of 15 000 iterations took around 50 min on a PC (1.8 GHz) with 2 GB of RAM. Convergence was assessed using the Gelman and Rubin statistic which compares the within to the between variability of chains started at different and dispersed initial values (Gelman, 1996). Burn-in was set to 5000, and thinning of each 10th iteration resulted in acceptable mixing and convergence (Fig. 3).

The posterior distributions are displayed in Fig. 4, and the resulting summary estimates are presented in Table 1. Detection probability p was high. Survival probability was in agreement with what we were expecting for a small passerine. The additive genetic

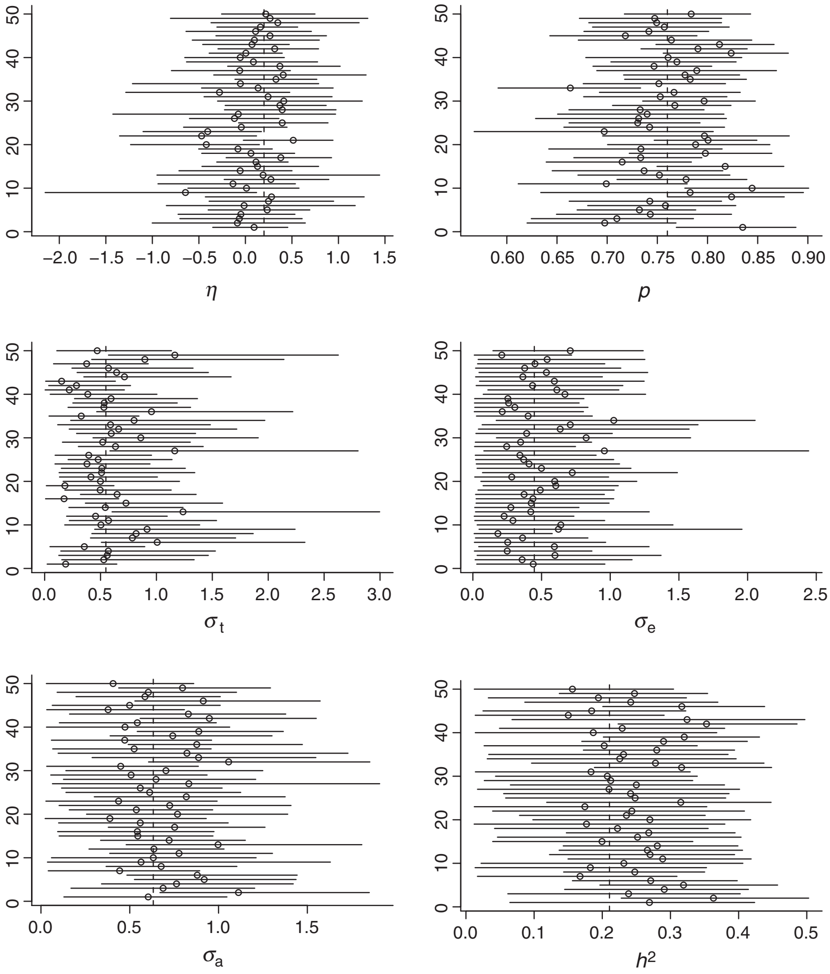

Fig. 2 Performance of the capture–recapture animal model approach – scenario with $\sigma_a^2 = 0.4$. For each of the 50 simulated data sets, we displayed the median (circle) and the 95% credible interval (horizontal solid line) of the parameter. The actual value of the parameter is given by the vertical dashed line. Notation: η is the mean survival on the probit scale, p is the detection probability, σ_t^2 is the variance of the yearly random effect, σ_e^2 is the variance of the nongenetic individual effect, σ_a^2 is the additive genetic variance and h^2 is the heritability.

variance σ_a^2 was low, resulting in a low heritability h^2. The environmental variance σ_t^2 was moderate, suggesting temporal variation in survival should not be neglected.

Finally, we compared the results of this CR study with a naive analysis in which we considered all individuals as being detected with certainty. In practice, we assumed that time to death was obtained as the occasion following that when an individual was last captured. As expected, the naive analysis led to a downward–biased survival estimate (posterior mean $\text{probit}^{-1}(\eta) = 0.530$, $\text{SD} = 0.034$), because tits that were observed for the last time before the end of the study were wrongly assumed as dead by the naive approach, whereas they might actually have been alive but undetected. While the additive genetic variance was greater in the naive analysis (posterior mean $\sigma_a^2 = 0.187$, $\text{SD} = 0.107$) and the estimate of heritability twice as large as in the CRAM analysis (posterior mean $h^2 = 0.040$, $\text{SD} = 0.037$), the inference remained unchanged as heritability was negligible.

Discussion

We developed a model to estimate and make statistical inference about the genetic basis of survival, an important component of fitness. We combined CR data and pedigree information using up-to-date CR and animal models within a Bayesian framework using MCMC techniques. In particular, because survival is a binary trait, we introduced a threshold model that is frequently used in assessing the heritability of qualitative traits. Our approach relies on the SSM methodology, which has the appealing advantage of disentangling the demographic process under investigation from its observation through the detection process.

The analysis of the blue tit data showed that heritability of survival was low. Following the classical interpretation of Fisher's fundamental theorem of natural selection, this is an expected result because traits strongly associated with fitness should be weakly heritable (Fisher, 1958). Yet, estimates of the heritability of longevity in the wild are scarce and, with regard to the

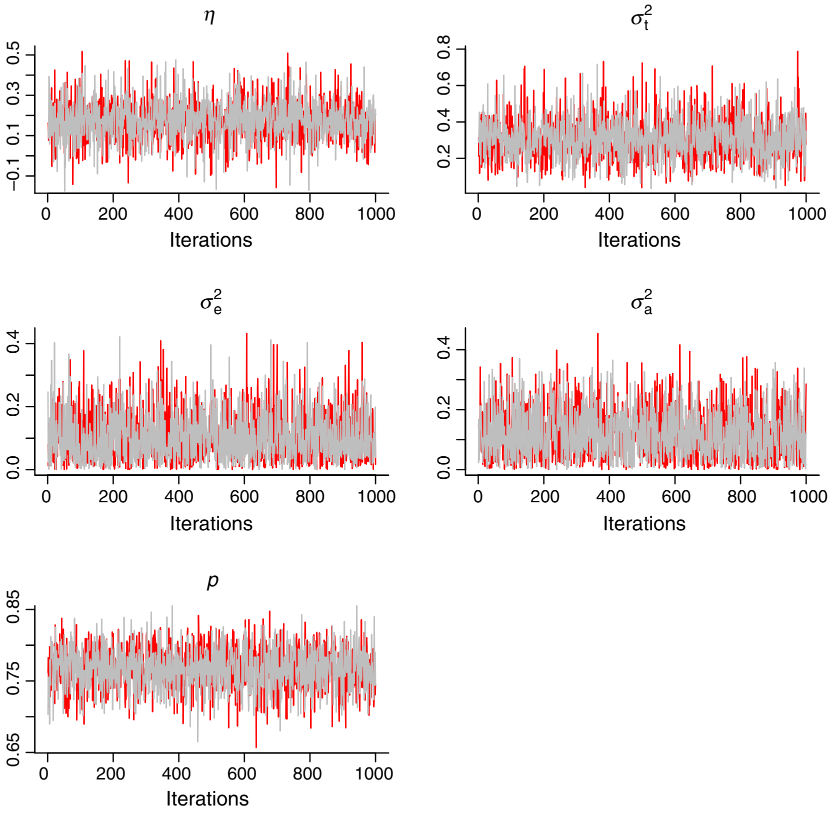

Fig. 3 Mixing of the MCMC algorithm used to fit the capture–recapture animal model (CRAM) to the blue tit data. Two chains of 15 000 iterations were used, with a thinning of each 10th iteration, and 5000 iterations as a burn–in, resulting in 1000 iterations for each chain (one in red/dark grey, the other in light grey) used to summarize the posterior results. Notation: η is the mean survival on the probit scale, σ_t^2 is the variance of the yearly random effect, σ_e^2 is the variance of the nongenetic individual effect, σ_a^2 is the additive genetic variance and p is the detection probability.

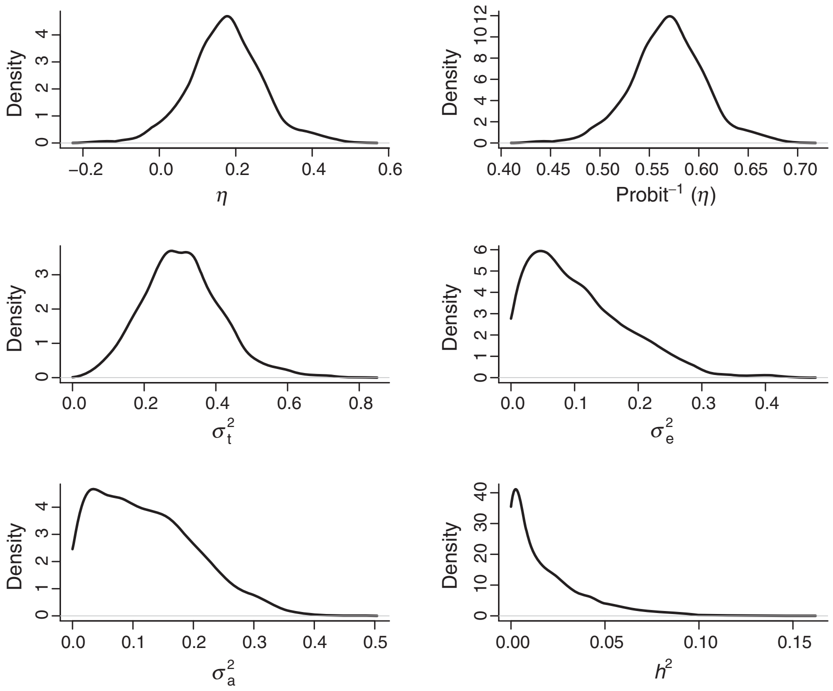

Fig. 4 Posterior density distributions for parameters of the capture–recapture animal model (CRAM) used for the blue tit data. Notation: η is the mean survival on the probit scale, $probit^{-1}(\eta)$ is the mean survival after back-transformation, σ_t^2 is the variance of the yearly random effect, σ_e^2 is the variance of the nongenetic individual effect, σ_a^2 is the additive genetic variance and h^2 is the heritability.

depletion of genetic variation for fitness traits, are inconsistent (e.g. Kruuk *et al.*, 2000; Coltman *et al.*, 2005). Besides, heritability of adult survival in the wild has simply not been estimated until now, to our knowledge. Hence, we present here the first estimate of heritability of survival between breeding seasons in a

Table 1 Parameter estimates for the capture–recapture animal model (CRAM) applied to the blue tits. Posterior means, medians, standard deviations (SD) and 95% credible intervals (CI) are provided: η is the mean survival on the probit scale, $probit^{-1}(\eta)$ is the mean survival after back-transformation, σ_t^2 is the variance of the yearly random effect, σ_e^2 is the variance of the nongenetic individual effect, σ_a^2 is the additive genetic variance, h^2 is the heritability and p is the detection probability.

Parameter	Mean	Median	SD	CI
η	0.175	0.175	0.096	[−0.018, 0.385]
$\text{probit}^{-1}(\eta)$	0.569	0.569	0.035	[0.493, 0.650]
σ_t^2	0.307	0.301	0.112	[0.105, 0.558]
σ_e^2	0.105	0.089	0.078	[0.005, 0.284]
σ_a^2	0.122	0.110	0.083	[0.006, 0.308]
h^2	0.018	0.011	0.021	[0.000, 0.077]
p	0.767	0.769	0.030	[0.707, 0.822]

wild vertebrate using a model accounting for the detection process. Although using a naive analysis assuming perfect detection did not change the inference, this was probably because of a relatively high detection probability, constant through time. This will not be always the case, and, because it is difficult to give guidelines about when the issue of detectability less than one could be ignored and a naive analysis could be conducted, we recommend that joint analysis of CR and pedigree data be undertaken using our new CRAM methodology.

To formally assess the relevance of including an additive genetic variance term, an individual nongenetic effect or both in the model, a model selection procedure could be undertaken. Adapting a method developed by Kuo & Mallick (1998), Royle (2008) recently implemented a way to compute the posterior model probability of a model. In our context, this requires introducing two indicator variables, say w_e and w_a, both having Bernoulli (0.5) prior distributions, and premultiplying the random effects e_i and a_i, respectively, in the expression $\text{probit}(\phi_{i,t-1})$ (see Plugging the animal model in CR models: CRAM). For example, if $w_a = 1$, then the genetic additive effect is present in the model, whereas if $w_a = 0$, it is not. Therefore, a model with $w_e = 1$ and $w_a = 1$ corresponds to $\text{probit}(\phi_{i,t-1}) = \eta + b_t + e_i + a_i$ (both effects). The posterior model probability is calculated from the MCMC histories, using the ratio between the number of iterations giving a particular model over the total number of iterations. In the blue tit data analysis, the simplest model was by far the most visited by the MCMC chains (posterior probability = 96%), indicating that neither individual random effect was needed as suggested by the estimates of variance components. The Bayesian framework offers several alternative approaches that are reviewed in O'Hara & Sillanpää (2009).

For the sake of illustration, we focused on a relatively simple model, although our approach can be fruitfully adapted to address questions involving more complex analyses. We see at least two promising extensions that are the object of our ongoing research. First, our present focus was on survival, but the CRAM framework could easily handle other parameters such as dispersal or age at first reproduction. It would require extending the SSM to multinomial data (Gimenez *et al.*, 2007) and the liability approach to several thresholds (Sorensen *et al.*, 1995). Second, additive genetic variance and heritability are known to vary in natural populations. In particular, changes with age make quantitative genetics tools particularly relevant for investigating senescence in natural populations. CRAM can be extended to incorporate a relationship between the additive genetic contribution and age using a 'random regression' model (Meyer, 1998; Averill *et al.*, 2006).

With the accumulation of longitudinal data on natural populations of most taxa and the constant improvement of methods for assignment of genetic relationships among individuals, an important goal of evolutionary ecology is to predict evolutionary change in the face of natural or anthropogenic influences in wild populations. Our new approach, combining up-to-date quantitative genetic tools and recent methods for the analysis of longitudinal data with imperfect detection, provides reliable quantitative genetic estimates for both applied and basic research.

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Supporting information

Additional supporting information may be found in the online version of this article:

Data S1 R script and BUGS code to implement the 5 capture–recapture animal model.

Data S2 Posterior predictive checking.

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Article 7

Heritability of hibernation emergence date in a wild population of Columbian ground squirrels

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A quantitative genetic analysis of hibernation emergence date in a wild population of Columbian ground squirrels

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Keywords:

additive genetic variation;
animal model;
body mass;
heritability;
hibernation;
mammal;
oestrus;
phenology;
Urocitellus columbianus.

Abstract

The life history schedules of wild organisms have long attracted scientific interest, and, in light of ongoing climate change, an understanding of their genetic and environmental underpinnings is increasingly becoming of applied concern. We used a multi-generation pedigree and detailed phenotypic records, spanning 18 years, to estimate the quantitative genetic influences on the timing of hibernation emergence in a wild population of Columbian ground squirrels (*Urocitellus columbianus*). Emergence date was significantly heritable [$h^2 = 0.22 \pm 0.05$ (in females) and 0.34 ± 0.14 (in males)], and there was a positive genetic correlation ($r_G = 0.76 \pm 0.22$) between male and female emergence dates. In adult females, the heritabilities of body mass at emergence and oestrous date were $h^2 = 0.23 \pm 0.09$ and $h^2 = 0.18 \pm 0.12$, respectively. The date of hibernation emergence has been hypothesized to have evolved so as to synchronize subsequent reproduction with upcoming peaks in vegetation abundance. In support of this hypothesis, although levels of phenotypic variance in emergence date were higher than oestrous date, there was a highly significant genetic correlation between the two ($r_G = 0.98 \pm 0.01$). Hibernation is a prominent feature in the annual cycle of many small mammals, but our understanding of its influences lags behind that for phenological traits in many other taxa. Our results provide the first insight into its quantitative genetic influences and thus help contribute to a more general understanding of its evolutionary significance.

Introduction

Hibernation is a seasonal period of depressed behavioural and metabolic activity, widely assumed to be an adaptation to long-term energy deficits (Wang, 1989; Humphries *et al.*, 2003; but see Lovegrove, 2000; Liow *et al.*, 2009 for alternative hypotheses). It involves an interval of prehibernal energy storage, followed by an extended bout of metabolic depression (torpor), punctuated by periodic arousals to euthermic body temperature (Geiser & Ruf, 1995). During torpor, body temperature is maintained at a drastically reduced set point (e.g. as low as −2.9 °C in arctic ground squirrels, *Urocitellus parryii*; Barnes, 1989), resulting in pronounced metabolic savings (torpid metabolic rate is, on average, 5% of euthermic basal metabolic rate; Geiser & Ruf, 1995). Hibernation lasts several weeks to months (Geiser & Ruf, 1995), with animals in temperate regions typically entering (immerging) in the autumn and emerging in the following spring.

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Hibernating mammals potentially face important energy-mediated trade-offs between the timing of hibernation emergence and reproduction. Emergence from hibernation must be early enough to allow for sufficient time to complete reproduction in the subsequent year and for both mothers and offspring to subsequently allocate the necessary energetic resources prior to immergence for the following winter. Synchronizing the periods of highest energetic need (i.e. lactation and juvenile weaning) with peaks in resource abundance has thus been hypothesized as an ultimate influence on emergence dates (Michener, 1983). However, the energetic costs of reproduction (Speakman, 2008; Lane *et al.*, 2010) may not be supported early in the season, and early emergence may thus negatively influence survival probabilities (Michener, 1979). The ecological significance of the date of emergence from hibernation has recently been shown in yellow-bellied marmots (*Marmota flaviventris*). In years of early snowmelt, marmots emerge from hibernation earlier. This, in turn, yields a longer growing season (for the marmots) and allows individuals to achieve a larger body mass prior to immergence. Over-winter survival is consequently greater and population size has increased in recent years (Ozgul *et al.*, 2010).

In general, the date of emergence should be an important life history trait in hibernating mammals. Relatively few attempts, however, have been made at explaining individual variation in hibernation timing and, to our knowledge, no studies to date have estimated its heritability or genetic associations with other life history traits. For example, a positive genetic correlation between emergence date and reproductive timing is an intrinsic, but yet untested, assumption of the hypothesis that the former has evolved so as to synchronize the latter with the temporal distribution of resource availability. In addition, we would predict a negative covariance between emergence date and energy stores, as the individuals with the greatest stores should be more able to fuel the metabolic costs of early emergence whereas those with diminished stores should remain in hibernation until environmental resources become more plentiful. Under this scenario, understanding the causes of variation in energy stores is necessary for predicting variation in emergence date. To date, however, the associations between energy stores and hibernation and reproductive phenology have only been addressed at a phenotypic, and not genetic, level (Dobson, 1988; Neuhaus, 2000; Humphries *et al.*, 2003).

The aim of this study was to examine the quantitative genetic influences on hibernation phenological traits in a wild population of Columbian ground squirrels (*Urocitellus columbianus*). Columbian ground squirrels are herbivorous (Ritchie & Belovsky, 1990; Elliott & Flinders, 1991), and the short growing seasons of plants in the alpine and subalpine regions that they inhabit require that they spend the majority of the year hibernating (8–9 months, depending on sex and age-class; Dobson *et al.*, 1992). The timing of emergence should thus be especially important in this species as reproduction and preparation for hibernation must all be completed during the short 3–4 months of activity. We estimated the heritabilities of emergence date from hibernation for both sexes separately, as well as genetic correlations between the sexes; to our knowledge, this is the first test for heritable genetic variation underlying hibernation phenology in a wild mammal. We also estimated the sex-specific heritabilities and between-sex genetic correlation of body mass at emergence. Individuals in this population are thought to rely entirely on accumulated fat stores to supply the energetic resources during hibernation (Young, 1990), and total body mass has been shown to correlate strongly with total fat content in the congeneric Belding's ground squirrel (*Urocitellus beldingi*; Morton & Tung, 1971). We thus used body mass as a noninvasive proxy for total fat content. For females, we also estimated the heritability of oestrous date and its genetic correlation with the date of emergence. Finally, we estimated the phenotypic and genetic correlations among all of the traits within each sex.

Methods

Study area and population

Columbian ground squirrels are small (< 1 kg), ground-dwelling mammals resident in the Rocky Mountains of North America (Elliott & Flinders, 1991). We studied a free-ranging population in Sheep River Provincial Park, Alberta (50° N, 114° W and 1500 m a.s.l.), from 1992–2009. Details of the study area and population have been provided previously (Skibiel *et al.*, 2009; Viblanc *et al.*, 2010). Briefly, the population inhabits a 1.5-ha mixed-species grassy meadow [common species: tufted hair grass (*Deschampsia caespitosa*), old man's whiskers (*Geum triflorum*) and dandelion (*Taraxacum* spp.)] on the banks of the Sheep River, surrounded by a forest of white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*).

Beginning in the early spring (prior to emergence of the first individual), we conducted daily observations from 3-m-high observation towers that permitted full coverage of the study site to survey for emergent squirrels. Upon emergence from hibernation, squirrels were caught in live traps (Tomahawk Live Trap, Tomahawk, WI, USA) that were baited with peanut butter and placed in the immediate vicinity of the exit tunnel from the hibernaculum. Columbian ground squirrels hibernate individually (Shaw, 1925; Young, 1990) and are relatively sedentary until females enter oestrus in the week following emergence. This allowed us to be certain that we captured the focal animal for which we observed emergence date. Upon capture, individuals were weighed (to the nearest 5 g, using a Pesola spring scale) and received unique dye marks on their dorsal pelage (Clairol commercial hair dye) to facilitate subsequent observation from a distance. Most individuals ($N = 1127$) were originally handled as juveniles and at that time received unique alphanumeric eartags. Adults in the first year of the study (1992; $N = 32$) and any immigrating animals ($N = 51$), similarly, received eartags on first capture. All animals were subsequently followed until either natural death or emigration from the study population. Therefore, any resident animals surviving for two or more years provided repeated measurements of traits (Table 1).

Oestrous dates of females were determined through regular trapping and behavioural observation. Females in oestrus enter burrows with males for periods of up to 2 h, after which most are aggressively mate-guarded by the males (Manno *et al.*, 2007). These events occur for only a few hours on a single day each year, and backdating from known parturition dates (gestation length = 24 days; Shaw, 1925; Murie & Harris, 1982) confirms that this is when mating occurs (F.S. Dobson and J.O. Murie, unpublished).

Nest burrows were located towards the end of the gestation period by following the protocols of Murie *et al.* (1998). From 2001 to 2009, females were removed from the field 22 days after mating (ca. 2 days preparturition) and transported to a nearby (< 1 km) laboratory facility. Females were housed in polycarbonate cages (48 × 27 × 20 cm; Allentown Caging Equipment Company, Allentown, NJ, USA) and provided with wood chip bedding and newspaper or paper towel nest material. To obscure vision from neighbouring females and to simulate the burrow environment, cages were covered with vented black plastic bags. Females were fed lettuce and apple twice daily and a high-protein horse feed (oats, barley, wheat and compressed vegetable material in a molasses mix; 13% crude protein) *ad libitum*. Within 12 h following parturition, neonates were marked individually by removing a small tissue biopsy from an outer hind digit or the tail with sterile scissors. Tissues were subsequently individually preserved in 95% ethanol. Following litter processing, the female and her litter were transported back to the field and released into the nest burrow following protocols of Murie *et al.* (1998). Juveniles emerged from the nest burrow ca. 27 days post-parturition. Individuals of neither sex disperse as juveniles (Boag & Murie, 1981); therefore, all animals surviving their first winter were captured as yearlings the following year. Subsequently, yearling males are more likely to disperse than yearling females (Neuahus, 2006), and our adult data set is consequently female-biased (Table 1). All protocols were approved by the Life and Environmental Sciences Animal Care Committee at the University of Calgary as well as the Animal Care and Use Committee at the University of Alberta (1992–1999) or the Institutional Animal Care and Use Committee at Auburn University (1999–2009).

Molecular analyses, paternity assignment and pedigree reconstruction

DNA was extracted from preserved tissue using DNeasy tissue extraction kits (Qiagen, Venlo, The Netherlands), and polymerase chain reaction amplification was performed for a panel of 13 microsatellite loci. Prior to 2001, maternity was determined through behavioural observation at the nest burrow. Confidence of maternity assignment is assured through individual females occupying separate nest burrows and targeted behavioural observations and trapping effort on and around estimated dates of offspring emergence. For laboratory births, maternity assignment was guaranteed because females were housed in separate cages. Paternity was assigned at 95% to 99% tri-confidence (assumed dam–sire–offspring relationship) using CERVUS 3.0 (Marshall *et al.*, 1998; Kalinowski *et al.*, 2007). Analyses were conducted for each year (2001–2009) separately. Further details of microsatellite loci isolation and paternity assignment are provided elsewhere (Raveh *et al.*, 2010).

Maternities have been determined since the inception of the project (first litters documented in 1992), whereas paternities have been determined since 2001. Consequently, our pedigree consists of a greater number of maternal than paternal links. In total, our pedigree

Table 1 Sample sizes and parental information for the quantitative genetic analysis of three phenotypic traits (emergence date from hibernation, body mass at emergence and oestrous date) for Columbian ground squirrels.

Trait	Sex	Age-class	Number of animals with both parents known	Number of individuals with known maternity only	Base individuals	Average (and range) number of measurements per individual	Total number of measurements
Emergence date	Female	Adult	30	93	16	3.4 (1–9)	472
		Yearling*	68	120	11	1 (1–1)	199
	Male	Adult	12	27	39	2.5 (1–8)	195
		Yearling*	59	144	9	1 (1–1)	212
Body mass at emergence	Female	Adult	30	93	16	3.3 (1–9)	464
		Yearling*	68	115	10	1 (1–1)	193
	Male	Adult	12	27	39	2.5 (1–8)	195
		Yearling*	59	140	9	1 (1–1)	208
Oestrous date	Female	Adult	30	88	15	3.3 (1–9)	444

*Any yearlings surviving to an age of at least two years will be counted in both the yearling and adult data sets.

consists of 1210 individuals (416 with both parents known, 711 with known maternity but not paternity and 83 base individuals). Of these individuals, 732 did not survive their first winter and consequently did not provide any relevant phenotypic data. Sample sizes and parental information for each of the phenotypic traits are provided in Table 1.

Statistical analyses

As a first step, we evaluated the influence of age-class (yearling and adult) and year as, respectively, two- and 18-level factors on emergence dates and body masses of each sex separately by fitting them as fixed effects, with individual as a random effect, in a linear mixed-effects model in the 'NLME' package (ver. 3.1-96; Pinheiro *et al.*, 2009) in R (ver. 2.9.2; R Core Development Team). We did not include yearling data in the analyses of oestrous date because only 15 yearlings entered oestrus over the duration of the study. Consequently, these analyses only include year as a fixed effect. Variance components, heritabilities and trait correlations for hibernation emergence date, body mass and oestrous date were subsequently estimated using restricted maximum likelihood 'animal models' in ASREML 2.0 (Gilmour *et al.*, 2006). The phenotypes of each individual were split into the relevant fixed and random effects using a linear mixed animal model of the form:

$$y = Xb + Z_1a + Z_2m + Z_3\mathrm{pe} + e$$

where y is the vector of observed phenotypic values, b is the vector of fixed effects, a, m and pe are the vectors of additive genetic, maternal and permanent environment effects, respectively, and X and Z_{1-3} are the corresponding design matrices (Lynch & Walsh, 1998; Kruuk, 2004).

The total phenotypic variance (V_P) in each trait was thus partitioned as:

$$V_P = V_A + V_M + V_{PE} + V_R$$

where V_P is the total phenotypic variance, comprising the additive genetic variance (V_A), the maternal effect variance (V_M), the permanent environment effect variance (V_{PE}) and the residual variance (V_R). The maternal effect variance arises due to maternal effects shared by offspring of the same mother. The permanent environment effect arises due to differences between individuals other than those due to additive genetic or maternal effects and can be estimated from repeated measures of a trait on the same individual (Kruuk & Hadfield, 2007). Both were fitted to prevent the variance associated with them being mistaken for additive genetic variance (Lynch & Walsh, 1998; Kruuk & Hadfield, 2007).

Narrow-sense heritabilities (h^2), maternal effects (m) and permanent environment effects (pe) were calculated as $h^2 = V_A/V_P$, $m = V_M/V_P$ and pe = V_{PE}/V_P, respectively. Phenotypic (r_P) and genetic (r_G) correlations were calculated from bivariate animal models. Due to problems with model convergence and because maternal effects were small and nonsignificant in all univariate analyses (see below), we did not include maternal effects in the bivariate analyses. The multivariate phenotypic variances for traits x and y were partitioned first into individual and residual variance components with the added covariance components (individual [$\mathrm{cov}_{ID}(xy)$] and residual [$\mathrm{cov}_R(xy)$]). In those cases, where the individual covariance component was significantly different from zero, we then attempted to partition this component into the constituent genetic [$\mathrm{cov}_G(xy)$] and permanent environment covariances [$\mathrm{cov}_{PE}(xy)$]. Between-sex genetic correlations were calculated by estimating the covariances between the sex-specific traits. Because these traits are measured in different individuals, we cannot evaluate the phenotypic correlations. Fixed effects included in the univariate models [age-class (where appropriate) and year] were likewise included in the bivariate models.

We used likelihood ratio tests (−2× difference in log-likelihood between hierarchical models) to test for the significance of variance and covariance components. Models were reduced either by omitting random effects sequentially or by fitting the covariances to 0. However, to avoid pseudoreplication, the permanent environment variance component was retained in all models. The likelihood ratio was tested against a chi-square distribution with the number of d.f. that corresponded to the difference in the number of variance or covariance components estimated. For univariate analyses, we follow Self & Liang (1987) and provide the P-values from one-tailed tests (because we are testing the hypothesis that the variance component is greater than 0). For bivariate analyses, we provide the P-values from two-tailed tests (because we are testing the hypothesis that the covariance component is either significantly less or more than 0).

Females cannot breed before they emerge from hibernation; some degree of positive correlation between these two traits is thus the null expectation. To evaluate whether the phenotypic and genetic correlations between emergence and oestrous dates that we estimated were significantly different from the null expectation, therefore, in addition to the likelihood ratio tests, we also ran a more conservative permutation analysis (sensu Charmantier *et al.*, 2006). Specifically, for each emergence date, we randomly selected (with replacement and within each year) an oestrous date from the data set. To accommodate the biological constraint that females must emerge from hibernation before mating, we set a rule in the re-sampling procedure that oestrous date must be greater than emergence date. We permuted the data set 500 times to create the re-sampled data sets and estimated the phenotypic and genetic correlations for each with ASREML-R (Butler *et al.*, 2007). The R code for this analysis is available, upon request, from J.E.L, A.C. or M.B. Means, variance components, heritabilities and phenotypic and genetic correlations are presented as ± 1 standard error (SE) throughout, with SEs for the variance components, heritabilities, covariances and correlation estimates being provided by ASREML.

Results

Emergence date

The mean Julian date of emergence from hibernation of adult females and males, respectively, was 116.9 ± 0.3 (ca. 27 April; $N = 472$ records) and 112.7 ± 0.6 (ca. 23 April; $N = 195$ records). By comparison, the mean Julian date of emergence from hibernation of yearling females and males, respectively, was 123.1 ± 0.6 (ca. 3 May; $N = 199$ records) and 122.4 ± 0.7 (ca. 2 May; $N = 212$ records). Yearlings of both sexes emerged significantly later than their adult counterparts [$F_{1,441} = 113.77$, $P < 0.0001$(female); $F_{1,137} = 116.88$, $P < 0.0001$ (male)] (Fig. 1). Emergence dates also differed significantly across the 18 years of the study in both females ($F_{17,441} = 20.03$, $P < 0.0001$) and males ($F_{17,137} = 5.42$, $P < 0.0001$).

Within a year, there was an average 19.1 ± 2.1 (female) and 18.4 ± 2.4 (male) day interval between the emergences of the first and last adults [$N = 18$ years; range, 5–37 days (female) and 5–35 days (male)]. There was also a 17.2 ± 2.2 (female) and 22.0 ± 2.7 (male) day interval between the emergences of the first and last yearlings [$N = 18$ years (female) and 17 years (male; no yearling males emerged in 2003); range, 5–34 days (female) and 2–41 days (male)]. The phenotypic variance in emergence date was comprised of a significant additive genetic variance component in both sexes (Table 2), resulting in heritabilities of 0.22 ± 0.05 (female) and 0.34 ± 0.14 (male). Between sexes, there was a positive genetic correlation in emergence date ($r_G = 0.76 \pm 0.22$; $COV_A = 10.45 \pm 3.77$; $\chi^2_1 = 3.73$, $P = 0.05$).

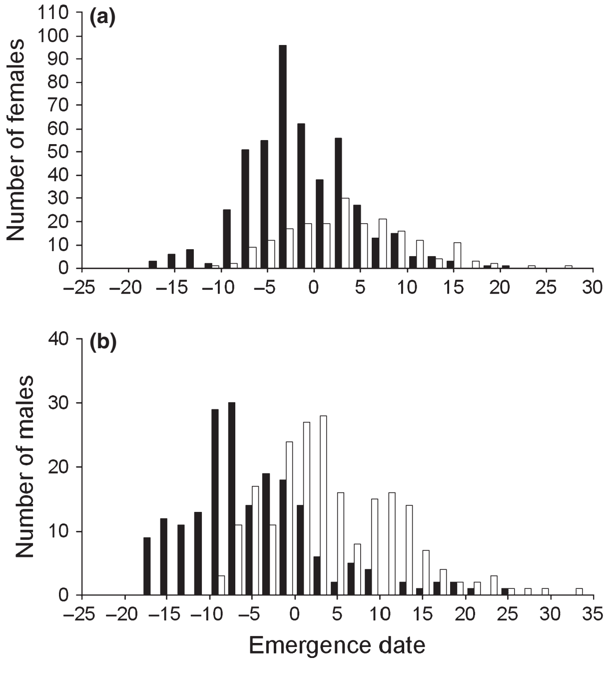

Fig. 1 Individual variation in hibernation emergence date of female (a) adult ($N = 472$ records; black bars) and yearling ($N = 199$ records; white bars) and male (b) adult ($N = 195$ records; black bars) and yearling ($N = 212$ records; white bars) Columbian ground squirrels. Individual emergence dates are represented as the deviation of the individual's Julian emergence date from the sex-specific annual mean Julian emergence date.

Body mass

The mean body mass at emergence of adult females and males, respectively, was 426.17 ± 2.32 g ($N = 464$ records) and 530.80 ± 6.58 g ($N = 195$ records). By comparison, the mean body mass at emergence of yearling females and males, respectively, was 253.73 ± 2.37 g ($N = 193$ records) and 270.34 ± 3.04 ($N = 208$ records). Yearlings of both sexes emerged at a significantly lower mass than their adult counterparts [$F_{1,428} = 2374.09$, $P < 0.0001$ (female); $F_{1,135} = 1130.29$, $P < 0.0001$ (male)]. Body masses at emergence also differed significantly across the 18 years of the study in both females ($F_{17,428} = 22.25$, $P < 0.0001$) and males ($F_{17,135} = 9.04$, $P < 0.0001$).

Within a year, there was an average difference of 182.50 ± 10.69 g (female) and 255.56 ± 16.26 g (male) in body mass between the lightest and heaviest emerging adults [$N = 18$ years; range, 70.00–275.00 g (female); 125.00–410.00 g (male)]. There was also a 83.89 ± 10.15 g (female) and 119.42 ± 12.88 g (male) difference between the body masses of the lightest and heaviest emerging yearlings [$N = 18$ years (female) and 17 years (male; no yearling males emerged in 2003); range, 5.00–155.00 g (female) and 45.00–225.00 g (male)]. The phenotypic variance in body mass was comprised of a significant additive genetic variance component in females ($h^2 = 0.23 \pm 0.09$) but not in males ($h^2 = 0.02 \pm 0.15$; Table 2). Between sexes, there was a positive genetic correlation in body mass ($r_G = 0.74 \pm 0.22$; $COV_A = 866.66 \pm 288.41$; $\chi^2_1 = 5.32$, $P = 0.02$), but this must be interpreted with caution due to the lack of significant heritability for body mass in males.

Oestrous date

Adult females entered oestrus, on average, 3.6 ± 0.1 ($N = 444$ records) days after emerging from hibernation [mean oestrous date = 120.2 ± 0.3 (ca. 30 April)]. Patterns in oestrous date thus correspond closely to those of emergence dates (Fig. 2a). However, as the later-emerging females were less likely to breed, there was less phenotypic variance in oestrous, relative to emergence,

Table 2 Variance components, heritabilities and maternal and permanent environment effects (±SEs) of hibernation emergence date, body mass at emergence and oestrous date in Columbian grounds squirrels. Estimates from both the full models (including all variance components) and the reduced models (including only those retained as significant at the $P < 0.05$ level) are provided.

Trait	Model	V_P	V_A	V_M	V_{PE}	V_R	h^2	m	pe
Female hibernation emergence date	Full	36.99 ± 2.39	8.04 ± 2.24	0.97 ± 1.30	0.00 ± 0.00	27.97 ± 1.80	0.22 ± 0.05	0.03 ± 0.04	0.00 ± 0.00
	Reduced	36.85 ± 2.37	8.67 ± 2.14***	n.f.	0.00 ± 0.00	28.17 ± 1.80	0.24 ± 0.05***	n.f.	0.00 ± 0.00
Male hibernation emergence date	Full	65.11 ± 5.51	14.25 ± 10.64	4.74 ± 4.93	2.86 ± 9.15	43.27 ± 5.10	0.22 ± 0.16	0.07 ± 0.07	0.04 ± 0.14
	Reduced	64.79 ± 5.31	22.04 ± 9.59*	n.f.	0.58 ± 8.69	42.17 ± 4.94	0.34 ± 0.14*	n.f.	0.01 ± 0.13
Female body mass at emergence	Full	1847.93 ± 134.96	428.32 ± 177.56	34.77 ± 81.20	284.34 ± 156.64	1100.50 ± 73.77	0.23 ± 0.09	0.02 ± 0.04	0.15 ± 0.09
	Reduced	1841.90 ± 132.89	430.33 ± 172.83***	n.f.	310.97 ± 144.42**	310.97 ± 144.42	0.23 ± 0.09***	n.f.	0.17 ± 0.08**
Male body mass at emergence	Full	4229.15 ± 329.40	67.05 ± 617.81	0.00 ± 0.00	1631.10 ± 704.10	2531.00 ± 266.31	0.02 ± 0.15	0.00 ± 0.00	0.60 ± 0.06
	Reduced	4229.50 ± 329.29	n.f.	n.f.	1700.60 ± 339.75****	2528.90 ± 265.83	n.f.	n.f.	0.40 ± 0.06****
Oestrous date	Full	24.05 ± 1.95	4.44 ± 2.98	0.00 ± 0.00	1.84 ± 2.53	17.77 ± 1.46	0.18 ± 0.12	0.00 ± 0.00	0.08 ± 0.11
	Reduced	23.78 ± 1.82	n.f.	n.f.	6.09 ± 1.67****	17.69 ± 1.45	n.f.	n.f.	0.26 ± 0.06****

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$ and n.f. indicates 'not fitted'.

date (Table 2). Oestrous dates differed significantly across the 18 years ($F_{17,294} = 14.76$, $P < 0.0001$). Within a year, there was an average of 15.8 ± 1.8 days ($N = 18$ years; range, 1–32 days) interval between the oestrous dates of the first and last adult females. The estimate of additive genetic variance in oestrous date was not significantly different from zero (Table 2), but the heritability of oestrous date ($h2 = 0.18 \pm 0.12$) was very similar to that of emergence date.

Within-sex correlations between traits

There was significant phenotypic covariance between female emergence date and oestrous date ($\mathrm{COV_P} = 25.68 \pm 2.24$; $\chi^2_1 = 412.42$, $P < 0.0001$; Fig. 2a) that was comprised of significant underlying additive genetic covariance ($\mathrm{COV_A} = 7.70 \pm 2.17$; $\chi^2_1 = 15.8$, $P < 0.0001$) (Table 3). We then compared these values with the distribution of covariances expected under a null hypothesis of no association between dates (but with the proviso that emergence date should precede oestrous date). The mean phenotypic and genetic covariances estimated from the simulated data sets were, respectively, $\mathrm{COV_P} = 18.49 \pm 0.08$ and $\mathrm{COV_A} = 6.09 \pm 0.05$ ($N = 424$ data sets; 76 models did not converge). The phenotypic and genetic covariances estimated from the real data are equal to or larger than all (424 of 424) of the $\mathrm{COV_P}$ estimates and 93% (393 of 424) of the $\mathrm{COV_A}$ estimates.

In contrast, neither the phenotypic ($\mathrm{COV_P} = -18.17 \pm 11.71$; $\chi^2_1 = 2.28$, $P = 0.13$; Fig. 2b) nor the individual ($\mathrm{COV_{ID}} = -4.45 \pm 10.89$; $\chi^2_1 = 0.16$, $P = 0.69$) covariances between emergence date and body mass at emergence was significantly different from zero (Table 3). Because the individual correlation was not significantly different from zero, we did not attempt to partition into its constituent genetic and permanent environment covariances. Although there was a significant negative phenotypic covariance ($\mathrm{COV_P} = -41.31 \pm 14.57$; $\chi^2_1 = 10.76$, $P = 0.001$; Fig. 2c) between oestrous date and body mass, only the residual covariance ($\mathrm{COV_R} = -20.10 \pm 7.94$; $\chi^2_1 = 9.42$, $P = 0.002$) was significantly different from zero, whereas the individual ($\mathrm{COV_{ID}} = -21.22 \pm 14.31$; $\chi^2_1 = 2.12$, $P = 0.15$) covariance was not (Table 3). We therefore also did not attempt to partition the individual correlation.

In males, there was a significant negative phenotypic covariance between emergence date and body mass at emergence ($r_P = -0.13 \pm 0.06$; $\mathrm{COV_P} = -70.97 \pm 29.92$; $\chi^2_1 = 11.16$, $P < 0.001$). This covariance was largely due to a significant residual covariance ($r_R = -0.36 \pm 0.07$; $\mathrm{COV_R} = -112.08 \pm 24.59$; $\chi^2_1 = 21.70$, $P < 0.0001$) as the individual covariance ($r_{ID} = 0.18 \pm 0.15$; $\mathrm{COV_{ID}} = 41.11 \pm 32.00$; $\chi^2_1 = 1.66$, $P = 0.20$) was not significantly different from zero. We did not attempt to partition the genetic and permanent environment correlations.

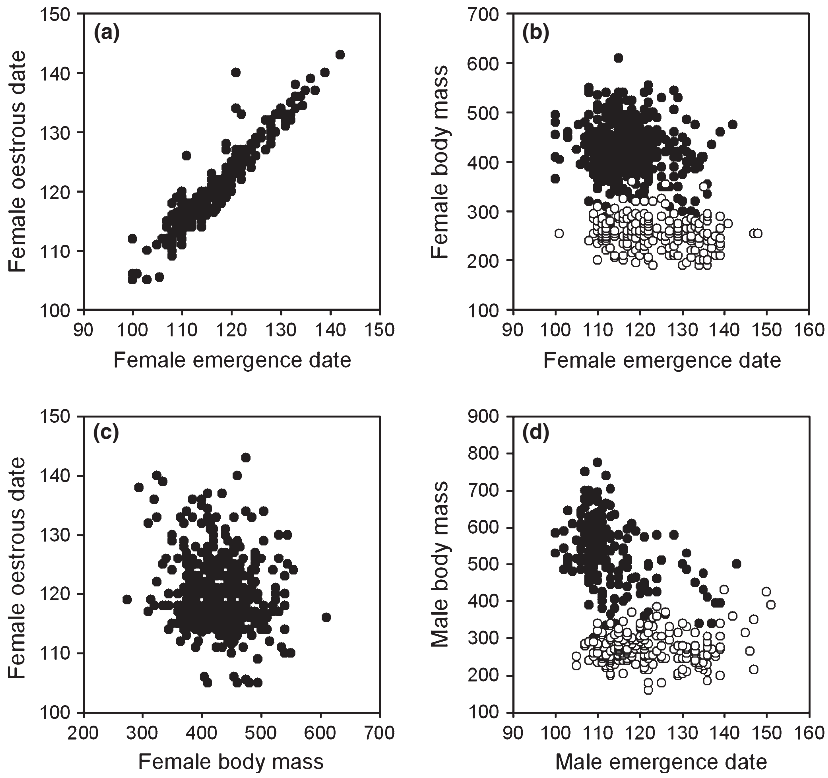

Fig. 2 The phenotypic associations between the Julian date of hibernation emergence and Julian oestrous date (a; $N = 444$ records), the Julian date of hibernation emergence and body mass (g) at emergence [b; $N = 463$ adult (closed circles) and 193 yearling (open circles) records] and the Julian oestrous date and body mass (g) at emergence (c; $N = 438$ records) in female, as well as the phenotypic association between the Julian date of hibernation emergence and body mass (g) at emergence [d; $N = 195$ adult (closed circles) and 208 yearling (open circles) records] in male Columbian ground squirrels.

Discussion

Predictable energy shortfalls are a regular feature of the life cycles of most organisms and have selected for a diversity of physiological and behavioural coping adaptations. Many birds migrate to more favourable climates, perennial plants become dormant and many invertebrates, amphibians and mammals hibernate during temperate zone winters. Although the quantitative genetic influences on avian migration and plant phenological traits have been estimated for a number of species (e.g. Rathcke & Lacey, 1985; Pulido *et al.*, 2001), we are unaware of any similar attempts with hibernation phenological traits. We found that in Columbian ground squirrels the date of emergence from hibernation was heritable in both males and females and that there was a positive genetic correlation between the two sexes in emergence date. Oestrous date displayed a similar (albeit, not statistically significant) heritability as emergence date and the two traits were strongly phenotypically and genetically correlated. Body mass at emergence was also significantly heritable in females. Although it must be interpreted with caution, due to a lack of heritability for body mass in males, there was a positive genetic correlation in body mass between the sexes. There were, however, no significant genetic correlations between body mass and emergence date in either sex or body mass and oestrous date in females.

There was considerable phenotypic variation in emergence dates in our population. For example, the last adult female to emerge in a given year did so, on average, almost three weeks after the first. The compressed growing season at our Rocky Mountain field site, and correspondingly short active season, renders this variation (equal to almost 20% of the, on average, 99-day active season; Neuhaus, 2000) even more striking. Approximately 20% of this phenotypic variation was explained by an additive genetic variance component in females. In addition to our results, to our knowledge, the heritabilities of phenological traits in free-ranging mammals have been estimated in populations of three, nonhibernating species: North American red squirrels (*Tamiasciurus hudsonicus*) in the southwest Yukon Territory of Canada, red deer (*Cervus elaphus*) on the Isle of Rum, UK, and Soay sheep (*Ovis aries*) on the Island of Hirta, UK. Parturition date in both red squirrels ($h^2 = 0.16$; Réale *et al.*, 2003) and Soay sheep ($h^2 = 0.19$; Kruuk & Hadfield, 2007) exhibited significant heritable genetic variation, and heritabilities across eight phenological traits in red deer ranged from 0.05 (female oestrous date) to 0.26 (both female coat change date and male rut start date) (Clements *et al.*, 2010). Although the number of mammalian studies is still limited and an appropriate taxonomic comparison is thus premature at this point, available evidence suggests that many mammalian phenological traits are heritable and that

Table 3 Individual, permanent environment, genetic, residual and phenotypic (maternal effects were not included) covariances (above the diagonal) and correlations (below the diagonal) between hibernation emergence date, body mass at emergence and oestrous date for adult female Columbian ground squirrels. Estimates are provided for two models. In Model 1, we combined the permanent environment and additive genetic components into one variable (individual). If the individual covariance was significantly different from zero, we then attempted to partition it into its constituent additive genetic and permanent environment parts in Model 2. The phenotypic covariance represents the sum of the covariance components from Model 1 or, if the individual covariance was significantly different from zero, Model 2. Values are reported as ±1 SE.

	Hibernation emergence date	Oestrous date	Body mass
Model 1: individual			
Hibernation emergence date	–	7.31 ± 1.88****	−4.45 ± 10.89
Oestrous date	0.99 ± 0.01****	–	−21.22 ± 14.31
Body mass	−0.06 ± 0.14	−0.23 ± 0.14	–
Model 2: permanent environment			
Hibernation emergence date	–	0.00 ± 0.00	n.f.
Oestrous date	0.00 ± 0.00	–	n.f.
Body mass	n.f.	n.f.	–
Model 2: additive genetic			
Hibernation emergence date	–	7.70 ± 2.17****	n.f.
Oestrous date	0.98 ± 0.01****	–	n.f.
Body mass	n.f.	n.f.	–
Model 2: residual			
Hibernation emergence date	–	17.98 ± 1.53***	−13.71 ± 8.51
Oestrous date	0.91 ± 0.01***	–	−20.10 ± 7.94
Body mass	−0.08 ± 0.05	−0.15 ± 0.06	–
Phenotypic			
Hibernation emergence date	–	25.68 ± 2.24***	−18.17 ± 11.71
Oestrous date	0.93 ± 0.01***	–	−41.31 ± 14.57
Body mass	−0.07 ± 0.04	−0.17 ± 0.06	–

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$ and n.f. indicates 'not fitted'.

estimates often overlap with those obtained from, the more often studied, bird populations [range, 0.16–0.45 (Sheldon *et al.*, 2003 and references therein)].

All of the traits that we analysed exhibited pronounced annual variation. Including year as a fixed effect in our analyses does not markedly influence levels of additive genetic variance (e.g. V_A in female emergence date with year as a fixed vs. random effect is respectively 8.04 vs. 8.65). However, because controlling for annual variation influences levels of explained phenotypic variation (e.g. V_P in female emergence date with year as a fixed vs. random effect is respectively 36.85 vs. 56.20), heritability estimates are influenced (e.g. h^2 in female emergence date with year as a fixed vs. random effect is respectively 0.22 vs. 0.15). Consequently, our heritability estimates need to be interpreted as the proportion of phenotypic variation explained by an additive genetic component, after controlling for the influence of annual variation (*sensu* Wilson, 2008). Annual phenological variation likely results from annual variation in climatic conditions, and previous studies have identified the influence of soil temperature and snow depth (Murie & Harris, 1982; Michener, 1992). We believe it is unlikely, however, that a single environmental variable will explain the majority of the variation in hibernation traits. Hibernacula are typically 60 cm below the soil surface (Young, 1990), meaning that ambient temperature, snow depth and thermal inertia of the soil may all interact to influence the conditions experienced by hibernating squirrels.

Microevolutionary trajectories are predicted not only by the heritability of the focal trait but also by any genetic correlations between it and other traits, as well as the adaptive landscape associated with the multivariate phenotype (Lande, 1982; Kruuk *et al.*, 2008). For hibernating species, the associations between hibernation and reproductive timing and energy stores should be important vectors of life history variation. Specifically, the date of emergence from hibernation in ground squirrels has been hypothesized to have evolved so as to synchronize the subsequent reproduction with the peak in vegetation resources (Michener, 1983). In addition to the heritability of emergence date, this hypothesis relies on the assumption of a genetic correlation between it and reproductive timing. We have shown here that oestrous dates, indeed, exhibited strong phenotypic and genetic correlations with female emergence date. Some degree of caution needs to be exercised in this case because, although the estimated heritabilities of emergence date and oestrous date were of similar magnitude, we are not able to conclude definitively that the heritability of oestrous date was statistically significant. We believe, however, that this limitation is due to the reduced statistical power resulting from a smaller sample size (arising from the fact that the oestrous date analyses did not include yearling data) and slightly smaller levels of additive genetic variation (Table 3). On the whole, therefore, we believe that the genetic evidence supports the synchrony hypothesis. Indeed, the strength of the genetic correlation ($r_G = 0.98$) indicates that the two phenological traits are likely influenced by the same set of genes and that the ability of females to adaptively adjust the timing of reproduction is fundamentally linked to their ability to adjust the timing of hibernation emergence. Undoubtedly, there are numerous assumptions underlying the synchrony hypothesis that remain to be tested in this, and other, species (e.g. the correspondence between the ground squirrel and plant phenologies, and the strength and shape of selection on variation in synchrony). Our results, however, provide a necessary first step that can be built upon with subsequent investigations that test these assumptions.

We found no evidence that body mass was genetically correlated with emergence dates (in either sex) or oestrous dates in females. The pronounced metabolic savings achieved through hibernation should be expected to create a covariance between the energetic resources of individuals at emergence and their dates of emergence. Specifically, early emergences should coincide with greater energetic stores (necessary to fuel the elevated metabolic costs whilst active), leading to a negative covariance. There was a negative phenotypic covariance between male emergence date and body mass, as well as female oestrous date and body mass, but this resulted primarily from a negative residual (or 'within-individual') correlation. This suggests that the environmental conditions associated with early emergences or oestruses (e.g. favourable climatic conditions during the hibernation period) are also associated with emergences at higher mass. We chose to analyse body mass as a noninvasive proxy for total body fat (sensu Morton & Tung, 1971). Admittedly, the former represents a somewhat coarse-grained measure of the latter as it also incorporates variation in lean body mass (Peig & Green, 2010). In Belding's ground squirrels, however, body mass correlated strongly with total body fat ($r = 0.87$; Morton & Tung, 1971), and in our population, the rank scores of body mass at emergence correlate strongly with the rank scores of body condition [estimated from the sex-specific regression of body mass on zygomatic arch breadth; statistics not shown (see also Dobson, 1992)]. We did not analyse body condition as our sample size of zygomatic arch breadths ($N = 89$ females and $N = 43$ males) is currently unsuitable for a quantitative genetic analysis. This analysis could be performed in future, however, and may provide improved detail into the relationship between energetic stores and hibernation phenology for this species.

If the level of energetic stores at emergence truly is genetically uncorrelated with emergence and oestrous dates, however, it does suggest that the latter two traits could evolve independently of the former (Lande, 1982). Mothers that emerge from hibernation in better condition tend to give birth to more offspring and, overall, heavier litters (Dobson *et al.*, 1999; Broussard *et al.*, 2003, 2005), suggesting that condition is likely subjected to positive directional selection. By comparison, previous work on Columbian ground squirrels has shown a reproductive advantage to early reproduction (Neuhaus, 2000). Unlike migratory birds, therefore, in which a reproductive/somatic investment trade-off is imposed by the energetic challenges of completing migration (Schmidt-Wellenburg *et al.*, 2008), it is feasible that earlier emergences (and therefore reproduction) could evolve in parallel with higher body masses in this species.

To what extent phenological traits can evolve along sex-specific trajectories will also depend on the magnitude of the between-sex genetic correlation in the traits. In Columbian ground squirrels, a strong between-sex genetic correlation in emergence date implies that such sex-specific evolution will be constrained. In red deer, by contrast, although female oestrous date exhibits a significant genetic correlation with male rut start date, in general there is little evidence for significant genetic correlations between different phenological traits either within or across the sexes (Clements *et al.*, 2010). Recent studies have suggested that elevated levels of protandry (i.e. the earlier arrival of males relative to females to the breeding population; Morbey & Ydenberg, 2001) may arise in response to climate change (Møller, 2004). However, this result has not been observed in other studies (Rainio *et al.*, 2007). The presence of, and interpopulation variation in, between-sex genetic correlations in phenological traits may provide one causal explanation for these divergent results (Lane *et al.*, 2011).

The earth is in the midst of a pronounced warming trend (IPCC, 2007), and there is growing concern as to how natural populations will respond to these rapidly changing conditions (Berteaux *et al.*, 2004). Because an evolutionary response to climate change is assumed to be necessary for the long-term viability of natural populations (Visser, 2008), disentangling the genetic and environmental influences on life history traits is taking on increased applied relevance (Gienapp *et al.*, 2008). Adjustments of phenological traits are the most commonly reported response to climate change (Parmesan, 2006), and the ability to adaptively respond to a changing climate has been shown to influence population dynamics in multiple species (Both *et al.*, 2006; Møller *et al.*, 2008), including hibernating mammals (Ozgul *et al.*, 2010), making them especially pertinent. We have provided evidence for a necessary prerequisite to microevolution, heritable genetic variation, for hibernation phenological traits in Columbian ground squirrels (Falconer & Mackay, 1996). To what extent hibernation phenology may evolve in response to ongoing climate change is currently unknown but, quite independent of these issues, an improved understanding of this phenological trait should provide important insight into a fundamental component of the ecology of natural populations: the temporal linkages between organisms and their environment.

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Conditionnement des stratégies d'histoire de vie et mécanismes adaptatifs à court terme : approche intégrée par capture-marquage-recapture et application au saumon atlantique (Salmo salar) en conditions naturelles.

Résumé

Pour comprendre l'origine des variations d'histoire de vie des organismes, il faut étudier et mettre en évidence les stratégies d'histoire de vie et les processus évolutifs qui les gouvernent. Ce travail de thèse a pour objectif d'étudier les stratégies d'histoire de vie et leur conditionnement par les caractéristiques individuelles en conditions naturelles. Les stratégies d'histoire de vie sont vues comme un agencement de normes de réactions et de compromis évolutifs. Cependant, l'étude des processus évolutifs en milieu naturel se heurte à des problèmes d'ordre méthodologique. En effet, le suivi exhaustif au cours du temps d'individus d'une population est difficilement réalisable, voire impossible en conditions naturelles. Les méthodes de capture-marquage-recapture permettent une observation partielle des histoires de vie et des traits d'histoire de vie. Ce travail se base sur l'idée que nos observations ne sont que la partie visible de processus sous-jacents qu'il est nécessaire de prendre en compte pour ne pas biaiser nos inférences statistiques. J'utilise la modélisation à structure cachée pour *1)* séparer le processus d'observation du processus dynamique d'intérêt, *2)* modéliser les histoires de vie complètes des individus, *3)* intégrer dans un cadre unique et cohérent les décisions d'histoire de vie et les compromis évolutifs et *4)* représenter explicitement les mécanismes sous-jacents qui génèrent nos observations. Dans ce cadre, on peut alors intégrer les théories et concepts de la biologie évolutive dans l'analyse statistique des données d'observations. J'illustre ce travail par l'étude du conditionnement des stratégies d'histoire de vie dans une population naturelle de saumon Atlantique sur le Scorff (Morbihan) à partir de données de CMR. Mes résultats mettent en évidence des décisions d'histoire de vie statut-dépendantes et des compromis évolutifs qui n'auraient pas pu être mis en évidence hors du cadre de modélisation proposé.

Discipline : Biologie des populations et Ecologie Evolutive.
Mots-clés : Stratégie d'histoire de vie, Plasticité phénotypique, Compromis évolutifs, Capture-marquage-recapture, Modélisation hiérarchique, saumon atlantique.

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Conditional life-history strategies and short-term adaptive mechanisms: an integrated approach using mark-recapture data with application to wild Atlantic salmon (Salmo salar).

Abstract

Understanding the origin of life history variations of organisms requires studying life history strategies and evolutionary processes that drive them. This thesis aims at studying life history strategies under natural conditions and how they are conditioned by individual characteristics. Life history strategies are seen as a combination of reaction norms and evolutionary trade-offs. The study of evolutionary processes in the wild faces to methodological issues. Indeed, the exhaustive monitoring of individuals over time is often impossible in the wild. Capture-mark-recapture methods allow a partial observation of life histories and life history traits. This work was based on the idea that our observations are only the visible part of underlying processes that need to be accounted for to limit the risk of flawed statistical inferences. I resort to hidden structure modeling to *1)* separate the observation process from the dynamic process of interest, *2)* model the full life histories of individuals, *3)* integrate within a single and coherent framework life history decisions and evolutionary trade-offs and *4)* explicitly represent the underlying mechanisms that generate our observations. Within this framework, one can confront theories and concepts in evolutionary biology with observational data through appropriate statistical tools. Finally, I illustrate this work by studying the conditioning of life-history strategies in a natural population of Atlantic salmon on the Scorff river (Morbihan) using CMR data. My results highlight status-dependent life history decisions and evolutionary trade-offs that could not be identified without our proposed modeling framework.

Key-words: Life history strategies, Phenotypic plasticity, Evolutionary trade-offs, Capture-recapture, Hierarchical modeling, Atlantic salmon