De l’envol à la première reproduction : aspects écologiques et évolutifs des traits d’histoire de vie de jeunes oiseaux marins longévifs

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De l'envol à la première reproduction: aspects écologiques et évolutifs des traits d'histoire de vie de jeunes oiseaux marins longévifs

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Réalisée au Centre d'Etudes Biologiques de Chizé, CNRS

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« Les mouvements des plantes vers la lumière et la recherche de la vérité à travers une analyse mathématique ne sont-ils pas des phénomènes du même ordre ? »

Ivan PAVLOV

PREFACE

Ce manuscrit rassemble le travail effectué au cours de mes trois années de thèse. J'ai souhaité à travers celui-ci intégrer mes travaux dans le cadre général des stratégies d'histoire de vie et de l'écologie évolutive. L'introduction présente donc une vue d'ensemble des patrons et mécanismes évolutifs expliquant les variations des traits d'histoire de vie de l'échelle des espèces à celle des individus. Elle introduit les cinq articles que j'ai rédigé durant ce doctorat. La discussion générale qui suit reprend les principaux résultats obtenus durant ces travaux. J'ai voulu cette discussion complémentaire de celles déjà présentées au sein de chaque chapitre. Aussi, les points largement développés dans les articles n'ont pas été répétés. A l'instar de l'introduction, j'ai tenté de mettre mes résultats en perspective des connaissances actuelles dans le contexte le plus large possible.

Liste des publications :

- **Fay R**., Weimerskirch H., Delord K. and Barbraud C. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. **Journal of Animal Ecology**, 84:1423-1433.

- **Fay R**., Barbraud C., Delord K. and and Weimerskirch H. Contrasting effect of climate and population density over time and life-stages in a long-lived seabird. Accepted in **Functional Ecology**.

- **Fay R**., Barbraud C., Delord K. and and Weimerskirch H. 2016. Paternal but not maternal age influences early-life performance of offspring in a long-lived seabird. **Proceedings of the Royal Society B**, 283 (1828), p. 20152318.

- **Fay R**., Barbraud C., Delord K. and and Weimerskirch H. 2016. Variation in the age of first reproduction: different strategies or individual quality? **Ecology**, 97(7), 1842-1851.

- **Fay R**., Barbraud C., Delord K. and and Weimerskirch H. 2016. From early-life to senescence: individual heterogeneity in a ling-lived seabird. Under review in **Ecological Monographs**.

Liste des communications orales :

- Parental effects in a long-lived seabird: evidence for transgenerational effects of aging. **International student conference "Ecology and Behavior"**, Toulouse, May 2015.

- Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. **GDR Ecologie Statistique**, Lyon, Mars 2015.

- From fledging to the first reproduction: Climatic effect on the early-life demography of a long-lived seabird. **International conference "Birds and climate change"**, Paris, October 2015.

- Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. **World Seabird Conference**, Cap Town, November 2015.

- Variation in the age of first reproduction: different strategies or individual quality? **GDR Ecologie Statistique**, Montpellier, Mai 2016.

- From early-life to senescence: individual heterogeneity in a long-lived seabird. **Seabird Group Conference**, Edinburgh, September 2016.

Participation à des workshops:

- **Matrix Population Models**, Olivier Gimenez and Dominique Lebreton, CEFE (Montpellier), Mars 2014.

- **Bayesian integrated population modeling** using BUGS and JAGS, Michael Schaub and Marc Kéry, La Tour du Valat, Mars 2015.

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A ce titre je remercie l’IPEV et les TAFF pour leur appui logistique et financier qui permettent de réaliser ces missions scientifiques sur ces territoires reculés. Les travaux de cette thèse reposent sur le suivi démographique à long terme mené sur une population d’albatros hurleurs sur l’archipel de Crozet. Ce suivi exceptionnel ne serait possible sans le soutien de ces organismes depuis de plus de 50 ans.

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Introduction Générale

1 Les traits d’histoire de vie, des espèces aux individus

L’histoire de vie d’un individu, délimitée par sa naissance et sa mort, est constituée d’évènements clés que l’on appelle composantes biodémographiques ou plus communément, *traits d’histoire de vie*. Parmi les traits d’histoire de vie fondamentaux figurent le patron de croissance, l’âge et la taille à la maturité sexuelle, la fréquence de la reproduction, le nombre, la taille et le sexe des jeunes produits lors de la reproduction ou encore la longévité. Les traits d’histoire de vie sont très variables à l’échelle des espèces, des populations au sein d’une même espèce et des individus au sein d’une même population.

1.1 Variation des traits d’histoire de vie entre espèces

1.1.1 Les stratégies d’histoire de vie : continuum rapide-lent

Les traits d’histoire de vie sont particulièrement variables à l’échelle des espèces. Par exemple, au sein des vertébrés, nous pouvons citer l’antechinus à pattes jaunes *Antechinus flavipes*, petit marsupial d’une trentaine de grammes, mature avant l’âge de 1 an et qui meurt généralement rapidement après s’être reproduit, et le requin du Groenland *Somniosus microcephalus* qui atteint une masse de 1400 kg, se reproduit à partir de 150 ans et peut vivre vraisemblablement plus de 300 ans. A travers les taxons, les traits d’histoires de vie s’organisent selon différentes combinaisons créant ce que l’on appelle des stratégies d’histoire de vie (Stearns 1976). Cependant, toutes les combinaisons possibles ne sont pas observées dans la nature. Par exemple aucun vertébré n’est capable à la fois de se reproduire au bout de quelques mois et de vivre plusieurs centaines d’années. Les ressources accessibles étant finies, la maximisation simultanée de tous les traits d’histoire de vie n’est pas possible (Fisher 1930). L’individu fait ainsi face à des compromis d’allocation d’énergie vers les différents traits d’histoire de vie, on parle de *compromis évolutifs* (Cody 1966, Roff 1992, Stearns 1992). L’exemple ci-dessus implique un compromis évolutif fondamental particulièrement étudié en écologie évolutive, celui entre la survie et la reproduction. Les ressources étant limitées, l’énergie engagée dans la reproduction se fait au détriment de celle allouée à la survie. Toute reproduction à un instant t compromet donc la survie et/ou la reproduction future, c’est le coût de la reproduction (Williams 1966, Bell 1980, Gustafsson and Pärt 1990). Il existe ainsi des compromis entre les traits d’histoire de vie liés à la reproduction et ceux associés à la survie. Les espèces se répartissent le long d’un continuum de stratégies d’histoire de vie (ou stratégies biodémographiques) qui peut être interprété comme une gamme de solutions possibles aux compromis entre reproduction et survie (Sæther 1988, Gaillard et al. 1989, Bennett and Owens 2002). On observe à une extrémité de ce continuum, des espèces à stratégie dite rapide avec une forte fécondité, une maturité précoce, et une durée de vie courte, et à l'autre extrémité, des espèces à stratégie dite lente, avec une faible fécondité, une maturité tardive, et une forte longévité. C'est le continuum rapide-lent qui a été décrit chez de nombreux taxons. Plusieurs métriques temporelles permettent de situer les espèces sur ce continuum, telles que l'âge de première reproduction ou la longévité, ces métriques pouvant être intégrées sous la forme du temps de génération (Gaillard et al. 2005).

1.1.2 Où se situer sur le continuum?

Une fois les contraintes allométriques et la phylogénétique corrigées, l'existence du continuum rapide-lent persiste, ce qui pose la question du rôle des facteurs écologiques dans l'évolution des traits d'histoire de vie des espèces et donc de leur position sur ce continuum. Au cours de l'évolution, la sélection naturelle maximise la survie et le succès reproductif des individus dans un environnement donné. Ce sont donc les forces sélectives qui s'appliquent aux individus et aux espèces qui déterminent leur place sur le continuum rapide-lent (Cole 1954). Ainsi, lorsque les espèces sont soumises à un environnement variable et d'une manière générale à un fort risque de mortalité extrinsèque, la sélection naturelle favorise les stratégies d'histoire de vie rapide (McArthur 1967, Pianka 1970). Dans ces circonstances, les individus qui produisent un maximum de descendants en un minimum de temps ont une *valeur sélective* plus importante. Au contraire, dans un environnement plus stable et plus prévisible avec des risques de mortalité extrinsèque plus faibles, les individus allouant leur effort reproductif sur un nombre réduit de descendants, tout en assurant leur survie, sont favorisés (McArthur 1967, Pianka 1970). En effet, dans ces conditions, la compétition entre les individus est le principal facteur limitant leur performance. Ainsi, produire peu de descendants, mais de bonne qualité et de manière répétée dans le temps, devient la stratégie dominante. Dans le premier type d'environnement, il s'agit de la sélection de type r, en référence au taux d'accroissement intrinsèque d'une population, dans le second cas, on parle d'une sélection de type K, en référence à la capacité maximale d'accueil d'un milieu donné (Stearns 1976).

Des exemples variés illustrent ces types de pression sélective intervenant dans des environnements contrastés. Ainsi, les espèces d'oiseaux de haute latitude, soumises à des conditions climatiques plus variables et moins prévisibles, adoptent des stratégies de vie plus rapides que les espèces vivant sous les tropiques où l'environnement est plus stable (Cody 1966, Wiersma et al. 2007). De même, des données paléontologiques suggèrent que le rythme de vie des espèces de thérapsides a augmenté durant la période suivant l'extinction de masse Permien-Trias, probablement en réponse à l'établissement de nouveaux écosystèmes très perturbés et instables (Botha-Brink et al. 2016). La prédation étant une cause majeure de mortalité chez de nombreuses espèces, l'exposition à la prédation est également un facteur déterminant expliquant la position des espèces sur le continuum rapide-lent. Par exemple, l'aptitude au vol chez les oiseaux et les chauves-souris, de même que le mode de vie arboricole de certains mammifères, diminuent le risque de prédation et sont associés à des stratégies d'histoire de vie plus lentes (Holmes and Austad 1994, Shattuck and Williams 2010). En suivant le même principe, il a été montré chez les oiseaux et à l'échelle du globe, que plus une espèce est exposée à la prédation, plus son rythme de vie est élevé (Valcu et al. 2014). L'absence courante de prédateurs dans les milieux insulaires et souterrains est également fréquemment avancée pour expliquer l'évolution de stratégie d'histoire de vie lente dans ces habitats (Cody 1966, Culver 2005).

1.1.3 Mortalité âge spécifique et stratégie de minimisation des risques

Le risque de mortalité extrinsèque semble être un facteur clé pour comprendre la position d'une espèce sur le continuum rapide-lent. Toutefois, dans le cas où le risque de mortalité extrinsèque varie en fonction de l'âge des individus, la réponse évolutive des populations peut être modifiée (Stearns 1976). Lorsque le risque de mortalité se concentre sur les individus adultes, la sélection naturelle favorise une accélération du rythme de vie conformément à ce qui a été dit précédemment. Cependant, en créant une asymétrie entre les stades immature et adulte, ces circonstances particulières favorisent également l'évolution de la sémelparité, c'est-à-dire le fait d'avoir un seul évènement de reproduction dans son cycle de vie (Charnov and Schaffer 1973). Ce type de sélection s'applique à de nombreuses espèces d'insectes incluant notamment des coléoptères et les cigales, dont les larves, enfuies dans le sol où dans le bois mort, sont relativement peu exposées aux prédateurs et aux intempéries relativement aux adultes qui ont une vie aérienne. Chez ces espèces, les larves peuvent vivre plusieurs années alors que les adultes meurent rapidement, après quelques mois de vie, à la suite de la reproduction. Dans le cas inverse, lorsque ce sont les jeunes individus qui sont spécifiquement soumis à une forte mortalité, une stratégie d'histoire de vie plus lente peut être sélectionnée (Murphy 1968). Ces circonstances peuvent favoriser la répartition de l'effort de reproduction dans le temps. En effet, cette stratégie, qui nécessite une allocation importante à la maintenance somatique pour assurer la survie, augmente la valeur sélective des individus en diminuant le risque de ne laisser aucun descendant qui atteindra l'âge de maturité. Ce processus peut être généralisé à tout paramètre environnemental diminuant spécifiquement la prédictibilité du succès reproducteur et ou de la survie juvénile. Le ralentissement du rythme de vie qui s'en suit est appelé stratégie de minimisation des risques (Schaffer 1974, Partridge and Harvey 1988). Cette stratégie évolutive est l'expression de l'adage « ne pas mettre tous ses œufs dans le même panier ».

1.1.4 Autres facteurs écologiques

A l'échelle des espèces, des contraintes écologiques, en dehors de celles influençant le taux de mortalité extrinsèque ou la prédictibilité du succès de reproduction et de la survie des jeunes, peuvent affecter l'évolution des traits d'histoire de vie. Chaque espèce vit dans une niche écologique spécifique comprenant des contraintes particulières. Les espèces se spécialisent par exemple sur un type de ressources alimentaires. Chez les oiseaux nidicoles, on remarque qu'à taille égale, une espèce se nourrissant de grandes proies tend à avoir une taille de ponte plus importante que les espèces spécialisées sur des proies plus petites (Saether 1994). La taille des proies consommées contraindrait la fécondité des espèces en affectant l'efficience de l'investissement reproductif lors du nourrissage des poussins. Chez les espèces se nourrissant de petites proies, le ratio entre l'énergie allouée au nourrissage de la progéniture, à travers la recherche alimentaire, et l'énergie effectivement apportée aux jeunes serait inférieur à celui des espèces spécialisées sur des proies de taille plus importante (Saether 1994). Cette spécificité écologique serait donc une contrainte pour l'évolution de la fécondité chez les oiseaux nidicoles. D'une manière générale, la valeur énergétique de la ressource alimentaire exploitée, bien qu'elle doive être pondérée par l'effort effectué pour l'acquérir, peut affecter les traits d'histoire de vie d'une espèce (Van Noordwijk and de Jong 1986). En effet, l'intensité des compromis d'allocation entre traits d'histoire de vie varie en fonction des ressources disponibles pour un individu. Par exemple, le contexte de vie exceptionnel des reines au sein des espèces d'insectes eusociaux, leur permettent d'avoir à la fois une fécondité élevée ainsi qu'une longévité importante. Chez les fourmis et les mites eusociales, les reines ont fréquemment la capacité de pondre des milliers d'œufs et de vivre plus de 10 ans (Keller 1998), le record étant une reine de fourmis noires des jardins *Lasius niger* qui a atteint l'âge de 28 ans et 8 mois (Hölldobler and Wilson 1990).

1.1.5 Contraintes physiques et phylogénétiques

Les stratégies d'histoires de vie font référence à la diversité des traits démographiques mis en place au cours de l'évolution par sélection naturelle en fonction des pressions de sélection qui s'exercent sur les espèces. Cette évolution s'effectue dans le cadre de contraintes qui sont physiques et phylogénétiques (Partridge and Harvey 1988, Stearns 1992). Les espèces ont une histoire évolutive, c'est-à-dire qu'elles ont hérité de caractéristiques qui peuvent contraindre leur réponse adaptative aux variations de l'environnement. Par exemple, les insectes possèdent un squelette externe ce qui contraint fortement la taille maximale qu'ils peuvent atteindre. En effet, lors de la mue, les insectes se retrouvent dépourvus de structure de soutien si bien que sous l'action de la gravité terrestre, un insecte de plusieurs mètres serait incapable de préserver son organisation interne, ses organes s'écraseraient et l'organisme entier ne serait pas viable (Gould 1977). L'exosquelette des insectes (contrainte phylogénétique) et la gravité (contrainte physique) nous protègent donc de l'apparition de moustiques géants tels ceux poursuivant Alan dans Jumanji. De même, seuls les métazoaires disposent d'une mobilité suffisante pour permettre un investissement reproductif post-natal incluant une protection physique directe et le nourrissage actif de leur progéniture. Ainsi, plusieurs espèces de mammifères et d'oiseaux longévifs concentrent leur investissement reproductif sur un unique descendent à chaque évènement de reproduction. La fécondité ne pourrait certainement pas évoluer vers cette valeur minimale si ces organismes n'étaient pas capables d'investir autant d'énergie dans leur progéniture unique via les soins parentaux post-natals. Par exemple, on remarque qu'aucune espèce de plante ne limite sa fécondité à un seul descendant bien que de nombreuses espèces soient également soumises à des pressions de sélection comparables à celles d'espèces animales longévives. L'immobilité des plantes les empêchent d'assurer la pérennité d'un unique descendant. De telles contraintes phylogénétiques sont fondamentales et complexifient la compréhension des stratégies d'histoire de vie entre taxons éloignés (Gould and Lewontin 1979).

La taille corporelle est également régulièrement considérée comme une contrainte majeure pour l'évolution des stratégies d'histoire de vie. Le rythme de vie d'une espèce est étroitement associé à sa taille lorsque l'on compare un ensemble de taxon (Figure 1). La taille implique diverses contraintes qui limitent l'évolution des stratégies d'histoire de vie. Par exemple, le temps de développement connait une relation allométrique, un organisme unicellulaire pourra toujours se développer et se reproduire plus rapidement qu'un organisme multicellulaire. La taille implique également d'autres contraintes notamment pour le métabolisme, lui-même étroitement associé au rythme de vie (Ricklefs and Wikelski 2002). Plusieurs raisons empêchent les organismes de grande taille d'atteindre un métabolisme élevé pourtant indispensable pour développer une stratégie de vie rapide. Tout d'abord, toutes choses étant égales par ailleurs, plus la taille d'un organisme est importante, plus la quantité de nourriture nécessaire pour sa survie est grande. Ainsi, pour qu'un éléphant adopte le métabolisme d'une souris, il devrait assimiler quotidiennement des quantités de nourriture gigantesques. Ainsi le métabolisme des grands organismes est probablement limité par leur capacité à acquérir et/ou assimiler la ressource alimentaire. En outre, dans le cas où un organisme de grande taille développerait un métabolisme élevé, il serait confronté à une difficulté supplémentaire, celle de la régulation de la chaleur produite par son corps. En effet, l'évacuation de la chaleur corporelle est directement associée à la surface de l'organisme. Or le rapport surface/volume n'évolue pas linéairement avec la taille, le volume augmente plus rapidement que la surface. Pour qu'un métabolisme élevé évolue chez une espèce de grande taille, des adaptations permettant la bonne régulation de la température corporelle du corps devraient évoluer en parallèle représentant une contrainte additionnelle.

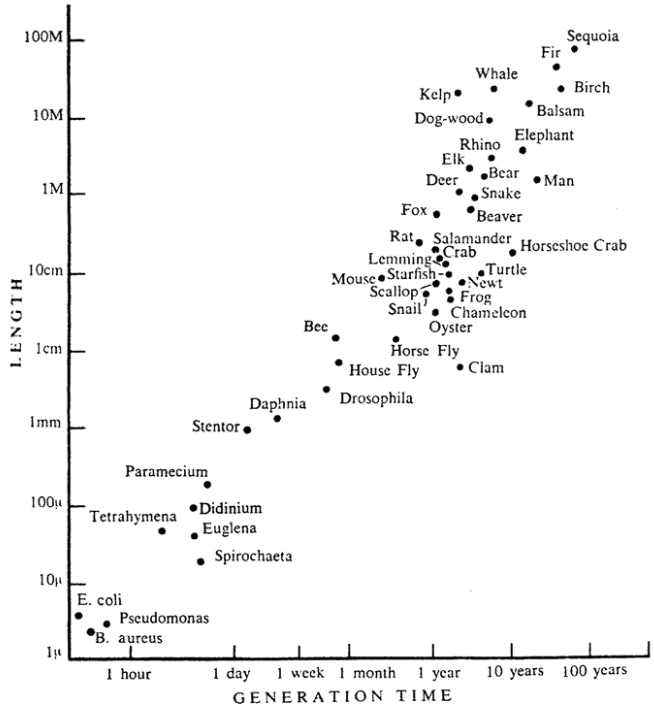

Figure. 1 : Représentation graphique, sur une échelle logarithmique, de la relation entre la taille d'un organisme en état de se reproduire et le temps de génération. Source : Bonner, *Size and* Cycle, 1965.

Bien que les contraintes allométriques apparaissent réelles, il ne faut cependant pas surévaluer leur importance. Par exemple, bien que la taille d'un mammifère soit un bon indice de sa position sur le continuum rapide-lent, il serait une erreur d'interpréter cette position comme l'expression unique de la contrainte allométrique. La taille elle-même évolue en relation à des pressions de sélection. Dans un environnement où les risques de mortalité extrinsèques sont importants, la fécondité est généralement favorisée au détriment de la croissance. Ainsi, la taille d'une espèce est fondamentalement liée aux conditions écologiques dans lesquelles elle évolue. Chez les mammifères, le risque de prédation d'une espèce et fortement corrélé à sa taille. On pourrait donc expliquer la relation entre la taille des mammifères et leur position sur le continuum rapide-lent par les facteurs écologiques liés aux risques de mortalité extrinsèques. Par sélection artificielle, le porc domestique *Sus scrofa* est capable en l'espace de 6 mois d'atteindre sa maturité sexuelle ainsi qu'un poids de plus de 100 kg. Ces performances sont exceptionnelles aux regards des traits d'histoire de vie observés chez les espèces des mammifères sauvages de taille comparable. En effet, le rythme de vie des espèces de taille comparable restent largement en deçà de leurs capacités physiques et biologiques suggérées par celles du porc montrant que leurs stratégies d'histoire de vie ont évolués en fonction de contraintes écologiques fortes. Bien que les contraintes allométriques existent, celles-ci pourraient rester secondaires au sein d'unité taxonomique restreinte. Ainsi on ne trouve pas de relation entre la masse corporelle et la position sur le continuum rapide-lent chez les oiseaux (Bennett and Owens 2002). A titre d'anecdote, l'autruche d'Afrique *Struthio camelus*, le plus grand oiseau actuel, atteint sa maturité sexuelle vers 3-4 ans et montre une longévité de 30 à 40 ans. Ce rythme de vie apparait comparable sinon plus rapide à ceux observés chez les procellariiformes. Ce dernier taxon comprend pourtant de petites espèces, les Hydrobatidae (océanites), de quelques dizaines de grammes, soit une masse 7000 fois inférieure à celle d'une autruche.

1.2 Variation des traits d'histoire de vie entre populations de la même espèce

1.2.1 Continuité espèce-population

Comme le conclut Darwin à la fin du chapitre sur l'hybridation dans son ouvrage *De l'origine des espèces au moyen de la sélection naturelle*, il n'y a aucune différence fondamentale entre deux espèces et deux populations de même espèce dans le sens où ces deux entités constituent des lignées évolutives. Pour cette raison, tous les mécanismes décrits dans la partie précédente peuvent également être avancés pour expliquer les variations de traits d'histoire de vie observées entre différentes populations de la même espèce. Les populations soumises localement à des pressions de sélection différentes peuvent adopter des stratégies d'histoire de vie qui leur sont propres. Par exemple, les populations peuvent diverger sur le continuum lent-rapide lorsqu'elles sont soumises à des risques de mortalité extrinsèques différents. Ce type de mécanisme a été observé empiriquement entre des populations de gupy *Poecilia reticulata* en Amérique du sud, naturellement exposées à des pressions de prédation variables en fonction des localités (Reznick and Endler 1982). En fonction des taux de prédations et des risques de mortalité âge-spécifique, les populations évoluent vers des stratégies de vie plus ou moins rapide comme décrit dans les partie 1.1.2 et 1.1.3. De manière similaire, l'homme peut être à l'origine de l'évolution des traits d'histoires de vie des populations lorsqu'il les exploitent, comme cela a été décrit pour des populations de poissons (Law 2007) ou d'ongulés (Gamelon et al. 2011). Le caractère stochastique de l'environnement pouvant varier dans l'espace, différentes populations de la même espèce peuvent adopter des stratégies de minimisation des risques plus ou moins prononcées. Les populations exposées aux environnements les plus variables devraient montrer des stratégies de vie plus lentes. Un tel mécanisme a été suggéré pour expliquer les différences de traits d'histoire de vie observées entre deux populations d'albatros à sourcils noirs *Thalassarche melanophris*. La population d'albatros à sourcils noirs de Géorgie du Sud, exposée à un environnement beaucoup plus variable que la population de Kerguelen, montre un taux de survie adulte plus fort et un succès de reproduction plus faible, en accord avec un ralentissement de sa stratégie d'histoire de vie (Nevoux et al. 2010a).

1.2.2 Stochasticité environnementale

Nous venons de voir que deux populations de la même espèce peuvent adopter des stratégies d'histoire de vie différentes suite à leur adaptation à un environnement particulier. Les populations étant des entités évolutives, elles sont capables de diverger et donc de se distinguer génétiquement, on parle de microévolution. Cependant, deux populations génétiquement proches peuvent également montrer des traits d'histoire de vie très différents parce que les contraintes environnementales qu'elles subissent à un moment donné ne sont pas les mêmes (McMahon et al. 2003, Devenish-Nelson et al. 2013, Bleu et al. 2015). Dans ce cas, il s'agit simplement de l'expression de la plasticité phénotypique qui peut être similaire entre les populations de la même espèce. Parmi les contraintes environnementales figure en première position la disponibilité alimentaire (White 2008), puis plus ponctuellement la pression de prédation (Horswill et al. 2014) ou encore l'exposition à des pathogènes, parasites inclus (Descamps et al. 2009). Tous ces facteurs étant eux-mêmes influencés par les conditions climatiques, la densité de population ou encore la dynamique de population d'autres espèces (Lack 1954, Newton 1998, White 2008). D'une manière générale, lorsque l'environnement est favorable, les populations peuvent montrer des performances démographiques plus élevées simultanément pour différents traits d'histoire de vie. Une étude expérimentale basée sur une population de Spermophile du Columbia *Spermophilus columbianus* montre qu'une augmentation de la disponibilité alimentaire peut entrainer simultanément une diminution de l'âge de première reproduction, une augmentation du succès de reproduction et un plus fort taux de survie (Dobson and Oli 2001). Au-delà des effets directs des contraintes environnementales sur les performances démographiques, ces facteurs extrinsèques peuvent également modifier les mécanismes de compromis évolutifs entre les traits d'histoire de vie. Les compromis évolutifs reposant sur la limitation des ressources disponibles, les variations de leur abondance impactent l'intensité de ces compromis (Van Noordwijk and de Jong 1986, Descamps et al. 2016). Par exemple, une augmentation des températures permet une acquisition de ressources plus efficace chez le lézard vivipare *Zootoca vivipara*. Ainsi, une diminution de l'intensité du compromis entre la taille de la ponte et la taille des œufs a été observée pour les populations soumises, lors de la gestation, à des températures plus importantes (Rutschmann et al. 2016).

1.3 Variation des traits d'histoire de vie au sein d'une population : l'échelle de l'individu

Au sein d'une espèce, pour une population donnée, tous les individus ne présentent pas les mêmes traits d'histoire de vie. Des facteurs biologiques expliquent cette variabilité parmi lesquels le sexe, l'âge et l'existence de stratégies individuelles. Les performances individuelles sont également étroitement liées à l'état physiologique (condition corporelle, charge parasitaires, état immunitaire), en relation avec l'environnement singulier qu'expérimente chaque individu (McNamara and Houston 1996). On retrouve ici la plasticité décrite dans la partie précédemment 1.2.2. sur la stochasticité environnementale. Pour éviter la répétition cet aspect n'est pas abordé de nouveau dans cette partie au profit des facteurs propres à l'échelle individuelle.

1.3.1 L'effet du sexe

Le sexe est un facteur biologique important expliquant les différences de traits d'histoire de vie observées à l'échelle individuelle. Pour comprendre le rôle fondamental du sexe, il faut remonter à son origine. Le sexe prend racine, d'un point de vue évolutif, à l'apparition de gamètes de tailles différentes c'est-à-dire à l'émergence de l'anisogamie (Parker et al. 1972). Cette asymétrie, première manifestation du sexe, favorise une fécondité variable entre individus. Certains individus produisant des gamètes de petites tailles et peu couteux (les mâles) ont une fécondité potentiellement supérieure relativement aux individus produisant des gamètes plus gros mais en moindre quantité (les femelles) (Dawkins 1976). Une conséquence déterminante de cette inégalité de fécondité est que les stratégies reproductives qui maximisent le succès reproducteur d'un individu ne sont pas les mêmes en fonction de son sexe. Les mâles augmentent leur performance en multipliant les occasions de reproduction alors que les femelles maximisent leur valeur sélective en choisissant les meilleurs mâles. Ainsi, ce dimorphisme gamétique initial a pu entrainer l'apparition de la *sélection sexuelle* et du *conflit entre sexes* avec pour conséquences l'accentuation du dimorphisme sexuel et une divergence des traits d'histoire de vie entre les sexes.

D'une manière générale, la compétition pour accéder à la reproduction tend à être plus importante entre mâles qu'entre femelles. Dans ce contexte, la sélection naturelle favorise des stratégies d'histoire de vie plus rapides chez les mâles (Bonduriansky et al. 2008). De manière concordante, on observe, chez les vertébrés, que la longévité est généralement plus faible chez les mâles. Par ailleurs, plus l'intensité du dimorphisme sexuel, qui reflète le niveau de compétition entre mâles, est important, plus la différence de longévité entre sexes est forte (Clutton-Brock and Isvaran 2007). Les pressions de sélection qui s'exercent sur les individus n'étant pas les mêmes en fonction de leur sexe, l'ensemble des traits d'histoire de vie, sans exception, peuvent diverger entre les mâles et les femelles. La croissance, l'âge de première reproduction ou la taille à l'âge adulte sont des traits d'histoire de vie qui varient couramment en fonction du sexe.

1.3.2 L'âge comme contrainte : l'expérience et le vieillissement

Au cours de sa vie, les performances démographiques d'un individu sont fortement contraintes par son âge. D'une manière générale, les chances de survie et de succès de reproduction tendent à augmenter en début de vie pour atteindre un plateau avant de décroitre plus ou moins rapidement en fin de vie (Clutton-Brock 1988, Newton 1989, Forslund and Pärt 1995, Martin 1995, Gaillard et al. 2000b). En début de vie, les jeunes individus sont particulièrement limités d'un point de vue morphologique par leur petite taille et leur faiblesse physique du fait que leur développement n'est pas terminé. Dans les premiers mois ou années de vie, les individus sont typiquement exposés à un plus grand nombre de prédateurs, et les espèces capables de se reproduire avant d'avoir atteint leur taille définitive présentent une fécondité plus faible. Les jeunes individus sont également limités d'un point de vue comportemental en raison de leur inexpérience. Chez les vertébrés en particulier, un grand nombre de comportements incluant la recherche alimentaire, la fuite face aux prédateurs ou le processus de reproduction sont, en grande partie, acquis par expérience (Curio 1983, Wunderle 1991, Forslund and Pärt 1995). A l'inverse, le vieillissement s'exprime par une diminution des capacités de survie et de reproduction au cours de la vie adulte. Ce processus a pu évoluer du fait de trois mécanismes. Tout d'abord, du fait de l'accumulation de mutations délétères en fin de vie en raison de la diminution des pressions de sélection avec l'âge, puisque les individus qui atteignent un âge avancé sont nécessairement moins nombreux que les jeunes (Medawar 1952, Hamilton 1966). Ensuite, la sélection naturelle peut favoriser des gènes ayant un effet bénéfique en début de vie en dépit de leur caractère néfaste en fin de vie (théorie de la pléiotropie antagoniste, Williams 1957). Enfin, le vieillissement peut également s'expliquer par l'accumulation d'erreurs dans la réplication du soma au cours du cycle de vie en lien étroit avec les compromis entre l'énergie allouée à la survie et la maintenance d'un côté et la reproduction de l'autre (théorie du soma jetable, Kirkwood 1977). Il en résulte un affaiblissement généralisé des fonctions physiologiques qui impacte les capacités physiques et comportementales (recherche alimentaire, fuite face aux prédateurs), lorsqu'il n'entraine pas directement la mort de l'organisme (Nussey et al. 2013).

Ainsi l'âge d'un individu contraint fortement ses facultés de survie et de reproduction. Les capacités physiques et comportementales des individus les plus jeunes et les plus âgés étant moindres que celles des individus dans la force de l'âge, il en résulte qu'ils sont en général plus sensibles à la compétition intra-spécifique, aux variations environnementales ou encore à l'exposition à des pathogènes (Lack 1954, Fowler 1987, Coulson 2001, Oro et al. 2010, Pardo et al. 2013a).

1.3.3 L'âge et la valeur reproductive : la retenue et l'investissement terminal

Au-delà des contraintes qui viennent d'être évoquées, les individus pourraient activement moduler leur allocation d'énergie en fonction de leur âge. Ce mécanisme constitue le cœur de deux théories qui s'intéressent à l'évolution du succès de reproduction avec l'âge. Il s'agit de la théorie de la retenue (Curio 1983) qui explique l'augmentation du succès reproducteur en début de vie, et de la théorie de l'investissement terminal (Clutton-Brock 1984) qui s'intéresse aux variations de succès de reproduction en toute fin de vie. Dans les deux cas, ces théories suggèrent que les individus modulent leur effort reproductif en fonction de leur valeur reproductive, c'est-à-dire en fonction de leur espérance de reproduction actuelle et future (Fisher 1930). Plus cette espérance est grande, plus les individus devraient limiter l'allocation à la reproduction présente pour ne pas négliger leur propre survie et donc leurs reproductions futures. Ainsi, les jeunes individus ayant une valeur reproductive forte, devraient investir peu d'énergie dans la reproduction au risque d'augmenter la probabilité de l'échec. Inversement, des individus en fin de vie, ayant une valeur reproductive très faible, pourraient investir beaucoup d'énergie dans leurs dernières reproductions au dépend de leur survie dans ce qui a été appelé un investissement terminal (Fisher 1930, Charlesworth and Leon 1976, Stearns 1976). Malgré le fait que ces théories soient solidement bâties sur le plan théorique, elles sont difficiles à tester empiriquement (Clutton-Brock 1984). Bien que des études aient clairement suggéré que le compromis d'allocation entre la reproduction et la survie pouvait varier en fonction de la valeur reproductive des individus notamment chez des insectes (Creighton et al. 2009), des poissons (Poizat et al. 1999) et des oiseaux (Velando et al. 2006), la généralisation de ces mécanismes reste très discutée, en particulier pour l'investissement terminal. D'une manière générale, l'importance de ce mécanisme dans la variation des performances démographiques avec l'âge reste largement inconnue.

1.3.4 Différentes stratégies individuelles

Indépendamment de leur sexe et de leur âge, les variations de traits d'histoire de vie entre individus peuvent refléter l'existence de différentes stratégies au sein d'une même population (Gross 1996). Dans cette partie je considère uniquement les stratégies adaptatives qui sont susceptibles de se maintenir car elles ont, en moyenne, la même valeur sélective. Une considération plus large des stratégies intégrant les particularités de chaque individu sera abordée dans la discussion. Au sein de la population, ces stratégies sont généralement l'expression d'un polymorphisme génétique associé à un processus épigénétique et sont couramment densité dépendantes, fréquence dépendantes ou condition dépendantes (Taborsky et al. 2008). Chez les poissons par exemple, il est fréquent d'observer deux types de stratégies de reproduction au sein des mâles : la stratégie « combattant » et la stratégie « parasite » (Taborsky et al. 2008). Les mâles suivant la première stratégie ont une croissance lente, atteignent une taille importante et tentent de se reproduire en adoptant les caractéristiques phénotypiques et comportementales nécessaires à la parade nuptiale de leur espèce. A l'inverse, les mâles adoptant la seconde stratégie montrent une croissance plus rapide ainsi qu'une taille adulte plus petite ce qui leur permettent de se reproduire à un âge plus précoce. Cependant n'ayant pas les attributs pour attirer le sexe opposé, ils se reproduisent en parasitant les accouplements des mâles « combattants ». Pour ce faire, ils mettent à profit leur petite taille en s'introduisant près des couples en pleine reproduction afin de féconder les œufs avant les mâles « combattants », au moment même où la femelle relâche sa ponte. Différentes stratégies de reproduction ont également été décrites chez des insectes (Moczek and Emlen 2000), des malacostracés (Shuster and Wade 1991), des reptiles (Sinervo et al. 1996) et des oiseaux (Lank et al. 1995). Ces stratégies alternatives résolvent différemment le problème posé par la compétition entre mâles pour l'accès à la reproduction et s'accompagnent d'adaptations morphologiques et comportementales (Gross 1996). D'autres stratégies concernent directement la résolution des compromis évolutifs entre traits d'histoire de vie. Par exemple, deux solutions alternatives pour résoudre le compromis entre le nombre et la taille des œufs au sein d'une ponte coexistent dans une population de lézards à flancs maculés *Uta stansburiana* sous la forme de deux stratégies de reproduction (Sinervo et al. 2000). Certaines femelles investissent beaucoup d'énergie sur un nombre réduit d'œufs alors que d'autres favorisent de grandes pontes au détriment de la taille des œufs. Ces stratégies sont fixes, c'est-à-dire qu'un même individu emploie toute sa vie la même stratégie. Plus généralement, le compromis entre la quantité et la qualité des descendants produits pouvait être résolu de manière différente en fonction des individus (Cameron et al. 2008, Reid et al. 2010). Ces études suggèrent que différentes stratégies, qui rappellent le continuum lent-rapide décrit à l'échelle interspécifique, pourraient coexister au sein des populations

2. Hétérogénéité individuelle

Dans la partie précédente, nous avons vu que des individus au sein d'une même population pouvaient montrer des traits d'histoire de vie très différents en fonction de leur état physiologique, de leur sexe, de leur âge ou même selon des stratégies différentes. Cependant, lorsque l'on prend en compte ces facteurs observables, il persiste toujours de fortes variations entre les individus. Ces variations résiduelles non observables constituent ce que l'on appelle l'hétérogénéité individuelle ou hétérogénéité cachée.

2.1 Hétérogénéité dynamique ou fixe?

2.1.1 Le hasard et l'hétérogénéité dynamique

Quelle est l'origine de cette variabilité résiduelle qui ne s'explique pas, ni par le sexe, ni par l'âge, ni par d'autres caractéristiques observables ? Une première réponse est de considérer que cette hétérogénéité résulte de la stochasticité des processus démographiques. Bien que l'on puisse attribuer à un individu, dans un environnement particulier, selon une caractéristique observable (sexe, âge…), une chance de survie et de reproduction, la réalisation de ces évènements reste probabiliste. L'observation d'une histoire de vie d'un individu est le résultat de chaînes de causalité qui dépassent largement les caractéristiques de cet individu et les particularités de son environnement. Cette variabilité résiduelle serait donc le résultat du hasard, en lien avec notre incapacité à prévoir avec certitude les évènements démographiques à l'échelle de l'individu. Récemment, le caractère contingent des performances démographiques et des trajectoires d'histoire de vie a été décrit sous le nom d'hétérogénéité dynamique (Tuljapurkar et al. 2009). Ces auteurs suggèrent que les taux vitaux varient en fonction de l'état physiologique des individus, souvent définies par le statut de reproduction (en succès, en échec ou non reproducteur). L'état physiologique d'un individu, incluant sa condition corporelle, est effectivement un facteur déterminant pour les performances d'un individu à un moment donné (McNamara and Houston 1996). Cependant, les variations de condition, ici considérées indépendamment du sexe et de l'âge, sont déterminées de manière ultime par les conditions environnementales rencontrées par l'individu. Prendre en compte l'état de l'individu permet donc de capturer une partie de l'hétérogénéité individuelle causée par l'environnement particulier rencontré par un individu, environnement qui est par ailleurs difficile à mesurer directement. Au sein d'un état physiologique, les taux vitaux sont supposés identiques pour tous les individus. Un point important de cette théorie est que tous les individus ont initialement les mêmes espérances de trajectoire de vie. Seul l'environnement rencontré et la stochasticité démographique créent les divergences observées. Pour ces auteurs, l'hétérogénéité dynamique suffit à elle seule à expliquer l'hétérogénéité individuelle observée au sein des populations (Steiner et al. 2010, Orzack et al. 2011, Steiner and Tuljapurkar 2012). Toute la variabilité résiduelle des histoires de vie des individus, une fois pris en compte les effets du sexe et de l'âge, serait donc due à la stochasticité démographique en lien avec le statut des individus, lui-même déterminé de manière aléatoire par l'environnement.

2.1.2 Hétérogénéité fixe et le concept de qualité

D'une manière alternative mais non exclusive, les variations de traits d'histoire de vie résiduelles au sexe et à l'âge, pourraient également être expliquées par la singularité biologique de chaque individu. Cette théorie de l'hétérogénéité fixe suggère que les individus diffèrent intrinsèquement dans leur capacité à croitre, survivre et se reproduire (Coulson 1968, Cam and Monnat 2000). Pour un état physiologique donné, les individus peuvent montrer des performances démographiques contrastées du fait de leurs différences phénotypiques (Vaupel et al. 1979). Cette hétérogénéité est fixe dans le sens ou les caractéristiques du phénotype qui affectent les performances d'un individu peuvent être considérées comme dues à des différences d'origine génétique et/ou de conditions de développement (voir 2.3.). Cet aspect durable est conforté par l'observation d'individus ayant des performances constamment supérieures à celles d'autres individus tout au long de leur vie (Descamps et al. 2008, McCleery et al. 2008, Zhang et al. 2015). Usuellement, le terme *qualité* a régulièrement été utilisé pour qualifier le phénotype d'un individu. Bien que très souvent cité, le concept de qualité est malheureusement rarement défini, ce qui a conduit à de nombreuses confusions et ambiguïtés (Wilson and Nussey 2010). En écologie des populations, la qualité individuelle, généralement considérée comme fixe, est définie comme une caractéristique du phénotype de chaque individu qui est positivement corrélée à ses performances au cours de sa vie (encadré 1). A travers sa qualité, le phénotype d’un individu pourrait fortement contraindre ses capacités à survivre et se reproduire. Un nombre important d’observations ont été interprétées comme l’expression des variations de qualité individuelle. Par exemple, les différences de taux vitaux observées de manière répétable dans le temps entre des individus partageant le même environnement ont été interprétées quasi systématiquement comme des variations de qualité individuelle. En outre, la totalité des études à long terme basées sur des suivis individuels en milieu naturel ont rapporté des corrélations inattendues entre différents traits d’histoire de vie au regard des compromis évolutifs présentés dans la partie 1.1.1. Par exemple, alors qu’un compromis d’allocation est attendu entre la reproduction et la survie, les individus reproducteurs ont fréquemment une survie supérieure aux individus non reproducteurs (Harvey et al. 1985, Bérubé et al. 1999, Cam et al. 2002, 2012, Barbraud and Weimerskirch 2005, Beauplet et al. 2006, Votier et al. 2008, Hamel et al. 2009b, Zhang et al. 2015). De plus, parmi les individus reproducteurs, ceux en succès présentent souvent un taux de survie plus élevé (Smith 1981, Harvey et al. 1985, Wooller et al. 1990, Weladji et al. 2008, Lescroël et al. 2009). Enfin, la fécondité, parmi les individus en succès, est parfois associée positivement aux chances de survie (Coulson and Porter 1985). Ce paradoxe avec les compromis d’allocation n’est qu’apparent. En effet, ces corrélations peuvent être expliquées si les capacités d’acquisition des ressources, ou l’efficience de leur utilisation, varient en fonction de la qualité des individus. Des études ont pu mettre en lien les variations de performances entre individus avec leur aptitude respective à acquérir des ressources alimentaires (Annett and Pierotti 1999, Lescroël et al. 2010, Gélin et al. 2015), illustrant empiriquement un résultat anticipé théoriquement par Van Noordwijk et de Jong (1986).

2.1.3 Distinguer l’hétérogénéité fixe et l’hétérogénéité dynamique

L’existence de ces deux types d’hétérogénéité ne fait aucun doute. Chaque individu, à son échelle, expérimente un environnement qui lui est propre. Ses performances sont donc soumises de manière dynamique à la stochasticité environnementale. De même, dans le cadre théorique de l’évolution par sélection naturelle, les individus sont, par nécessité, intrinsèquement différents les uns des autres et cette variabilité explique en partie la diversité de leur trajectoire d’histoire de vie

Encadré 1 : Le concept de qualité individuelle et la notion de *fitness*.

La fitness est un concept complexe qui a été utilisé de diverses façons depuis les premières théories évolutives par sélection naturelle (Dawkins 1982). Historiquement le terme fitness réfère directement à l'expression *the survival of the fittest* traduite par *la survie du plus apte*. Par la suite, ce concept a été redéfini dans le cadre de la génétique. La *fitness* génétique, traduit en français par valeur sélective, désigne la capacité d'un génome, ou d'un allèle, à se répliquer à travers les générations. Ce concept décrit une potentialité et se définie plus pertinemment à l'échelle d'un groupe d'individu. En effet, pour estimer sa valeur au sein d'une population, il faut mesurer la performance moyenne d'un génome ou d'un allèle dans un environnement donné. En milieu naturel il n'est généralement pas possible de mesurer la valeur sélective et les écologues ont naturellement utilisé un autre concept dérivé de la valeur sélective. Danchin et al. (2005) utilisent la notion d'aptitude phénotypique (*fitness* ou *individual fitness*) qu'ils définissent comme la capacité moyenne d'un phénotype à produire des descendants matures relativement aux autres phénotypes de la même population. C'est une notion proche du concept de valeur sélective qui s'intéresse indirectement aux caractéristiques génétiques à travers des traits phénotypiques. L'aptitude phénotypique est évaluée à travers les performances démographiques obtenues par un individu, ou groupe d'individus, au cours de leur vie. On peut également définir l'aptitude phénotypique par la contribution d'un individu au taux d'accroissement de la population (Coulson et al. 2006). Une variation de ce concept est l'aptitude inclusive (*inclusive fitness*) qui prend en compte les performances démographiques des congénères apparentés.

Le concept de qualité se distingue des concepts de fitness dans le sens où il ne désigne ni la capacité d'un génome, ou d'un allèle, à se répliquer au fil des générations, ni le résultat d'une trajectoire d'histoire de vie. Deux génomes identiques ont par définition la même valeur sélective mais ne seront pas nécessairement associés à des individus de même qualité. De même, des individus de même qualité n'auront pas nécessairement les mêmes performances démographiques. Bien qu'elle soit également corrélée aux performances des individus, la qualité est une propriété fondamentalement individuelle contrairement à l'aptitude phénotypique généralement associée aux performances démographiques moyennes des individus au regard d'un trait phénotypique particulier.

(Darwin 1859). Toutefois, la part relative de ces deux sources d'hétérogénéité fait l'objet de vifs débats toujours d'actualité. Un certain nombre de publications ont suggéré que l'hétérogénéité dynamique suffisait à elle seule à expliquer la totalité de la variation des traits d'histoire de vie observée dans la nature au sein des populations (Steiner et al. 2010, Orzack et al. 2011, Steiner and Tuljapurkar 2012). Ainsi, ces auteurs concluent que l'idée de différences individuelles fixes, et donc le concept même de qualité fréquemment utilisé depuis plus de 30 ans en écologie (Smith 1981, Clutton-Brock 1984), est inutile pour expliquer les variations de performances observées entre individus. Ces résultats ont fait l'objet de réponses et critiques (Cam et al. 2012, Plard et al. 2012). La controverse tient notamment aux difficultés méthodologiques à distinguer l'hétérogénéité fixe de l'hétérogénéité dynamique (Cam et al. 2016). Sans entrer dans les détails de modélisation, la méthodologie utilisée pour mettre en évidence l'hétérogénéité dynamique consiste à confronter des données observées en milieu naturel à celles simulées par un modèle considéré neutre incluant exclusivement l'hétérogénéité dynamique (Tuljapurkar et al. 2009). Hors, il s'est avéré que cette méthode d'inférence n'est pas valide dans ce cas précis car elle n'est pas informative à l'échelle de l'individu. Les capacités prédictives d'un modèle ne reflètent pas nécessairement sa capacité à décrire le processus sous-jacent produisant les données considérées dans la nature (Shmueli 2010). Dans le cas de l'hétérogénéité dynamique, les modèles neutres ne sont généralement pas rejetés du fait de leur faible puissance statistique (Bonnet and Postma 2016) en relation avec leur grande flexibilité (Authier et al. in prep). Les études prenant en compte les deux sources d'hétérogénéité suggèrent que l'hétérogénéité fixe n'est pas négligeable (Cam et al. 2012, Plard et al. 2012, Chambert et al. 2013). En démographie humaine, il a été estimé que l'espérance de vie d'une personne de 30 ans est déterminée à moitié par des facteurs individuels fixes, et à moitié par des facteurs dynamiques (Vaupel et al. 1998). Caswell (2014) estime chez des populations captives d'invertébrés, qu'environ 50% à 80% de la variation de longévité et causée par de l'hétérogénéité individuelle fixe. Cependant, à ce jour très peu d'auteurs ont avancé une estimation des parts relatives des deux processus. La question de l'importance relative de l'hétérogénéité fixe ou dynamique reste donc largement non résolue.

D'un point de vue plus empirique, on note que les deux théories sont capables d'expliquer des corrélations inattendues dans le cadre des compromis évolutifs telle qu'une relation positive entre la survie et la reproduction. Les facteurs théoriques proximaux expliquant ce patron étant les différences individuelles d'acquisition et/ou d'utilisation des ressources, la différence entre les deux théories réside dans les facteurs ultimes sous-jacents. L'hétérogénéité dynamique suggère que ces différences nutritionnelles sont uniquement le fruit du hasard en fonction des conditions rencontrées par les individus. Un déclin physiologique peut entrainer en même temps une diminution du succès de la reproduction et une réduction des chances de survie (Rattiste 2004, Robert et al. 2015). Bien qu'une certaine persistance puisse être reconnue du fait de l'inertie de l'état physiologique dans le temps, ces différences individuelles sont par essence labiles. Dans le cas de la qualité, ces différences sont expliquées en partie par des caractéristiques intrinsèques aux individus qui sont considérées comme fixes. Ainsi, un moyen pour soutenir empiriquement la théorie de l'hétérogénéité fixe consiste à identifier les variations phénotypiques qui sont associées aux variations de performance des individus. En d'autres termes, il faut s'intéresser aux origines de la qualité individuelle.

2.2 Les origines de la qualité individuelle

2.2.1 Origine intrinsèque : facteur génétique

L'origine de la qualité individuelle peut tout d'abord être recherchée dans un facteur intrinsèque aux individus, à savoir leur patrimoine génétique. En effet, les facteurs génétiques, typiquement fixes, peuvent fortement affecter le phénotype d'un individu ainsi que l'ensemble de ses traits d'histoire de vie. Il semble donc naturel de supposer qu'il existe une composante génétique à la qualité d'un individu (Hunt et al. 2004). Plusieurs éléments supportent cette hypothèse. Tout d'abord, pour que le processus d'évolution par sélection naturelle puisse avoir lieu, il est nécessaire que les performances des individus soient affectées par leur patrimoine génétique (Huxley 1944). Des études expérimentales ont montré que les taux vitaux tel que la longévité et la fécondité pouvaient évoluer au sein d'une population, démontrant ainsi que des facteurs génétiques affectent les traits d'histoire de vie à l'échelle des individus (Stearns 1992). De plus, on sait aujourd'hui que l'évolution par sélection naturelle peut avoir lieu sur de courtes périodes (quelques générations) au sein des populations sauvages (Pelletier et al. 2009). Cette observation suggère que les facteurs génétiques peuvent être impliqués dans les variations de performances observées entre individus en milieu naturel. L'existence d'une qualité génétique est également mise en évidence lorsque l'on relève que l'aptitude phénotypique d'un individu est fortement associée à son le degré de consanguinité (Keller and Waller 2002).

Une base génétique de la qualité implique qu'il persiste une diversité génétique importante en dépit des pressions de sélection qui l'érodent continuellement. Différents mécanismes peuvent expliquer le maintien de facteurs génétiques ayant un effet néfaste sur les performances individuelles. On peut rassembler ces mécanismes sous deux grandes catégories : l'équilibre mutation-sélection et l'effet de la sélection équilibrante (Charlesworth 2015). Le premier mécanisme suggère que la variabilité génétique se créée continuellement au cours des mutations, et que la sélection naturelle ne pourra, dans le meilleur des cas, éliminer ou fixer l'allèle en question qu'avec un certain délai.

Cependant, la sélection naturelle peut également activement préserver des facteurs génétiques qui pourront, chez certains individus, diminuer leur aptitude phénotypique. Ce sont les mécanismes de sélection équilibrante parmi lesquels on trouve l'avantage hétérozygote, la sélection fréquence-dépendante, la sélection sexuelle antagoniste ou encore l'équilibre sélection-migration. Des études en milieu naturel suggèrent que des mécanismes de sélection équilibrée permettent de maintenir de manière durable des variations génétiques étroitement liées aux performances des individus. Par exemple, on a observé au sein d'une population de Cerfs élaphes *Cervus elaphus* que les mâles faisant preuve de meilleures performances démographiques produisent, en moyenne, des descendants femelles à plus faibles aptitudes phénotypiques. Ces résultats, suggérant que les meilleurs génotypes diffèrent en fonction du sexe, ont été interprétés dans le contexte de la sélection sexuelle antagoniste (Foerster et al. 2007). Johnston et al. (2013) ont montré chez le mouton de Soay *Ovis aries* que le polymorphisme génétique intervenant dans la taille des cornes des mâles, elle-même fortement associée au succès de reproduction, était maintenu par un mécanisme d'avantage hétérozygote (Johnston et al. 2013). Un allèle récessif, représentant un désavantage à l'état homozygote par le développement de cornes atrophiées, représente un avantage sélectif à l'état hétérozygote. En effet, lorsqu'il est associé à l'allèle concurrent dominant qui permet le développement de cornes de plus grandes tailles, il assure une plus grande longévité sans affecter la taille des cornes de son porteur et donc sans compromettre son succès de reproduction (Figure 2).

Figure. 2 : Variations morphologiques des cornes de mouton de Soay *Ovis aries* mâles. a, Mâle adulte de 4 ans homozygote pour l'allèle conférant des cornes de grande taille. b, Mâle adulte de 5 ans hétérozygote. c, Mâle adulte de 5 ans homozygote pour l'allèle conférant des cornes de petites tailles. Source : Johnston et al. 2013.

2.2.2 Origine extrinsèque : environnement du début de vie

Un certain nombre de traits liés à la qualité individuelle ne sont pas innés mais acquis. En effet, un même génotype peut donner différents phénotypes selon l’environnement expérimenté par un individu lors de son développement. Ce processus d’interaction entre un génotype et son environnement est appelé la plasticité phénotypique. L’évolution de cette plasticité, particulièrement importante durant l’ontogénèse, permet aux individus de maximiser leurs performances démographiques dans des conditions environnementales variables. Parmi les contraintes qui peuvent intervenir durant le développement des organismes, on peut citer la restriction nutritive, l’exposition à des pathogènes et des parasites, le stress thermique, l’exposition aux polluants ou encore la présence de prédateurs. Ces facteurs de stress peuvent s’exercer dès la conception des individus (Clark and Galef 1995, Monaghan 2008, Harris and Seckl 2011) et sont expérimentés directement ou indirectement à travers les effets parentaux (Wolf and Wade 2009). Bien qu’elle soit en partie adaptative, la plasticité phénotypique a un coût (DeWitt 1998) qui dans certains cas n’est pas immédiatement visible (Metcalfe and Monaghan 2001). Ainsi, malgré la plasticité, l’environnement expérimenté en début de vie peut avoir des conséquences à long terme sur les performances de survie et de reproduction d’un individu (Lindström 1999, Monaghan 2008, Cam and Aubry 2011, Jonsson and Jonsson 2014).

En milieu naturel, une partie importante des variations de traits d’histoire de vie entre individus pourrait être dûe à l’empreinte de l’environnement natal (Grafen 1988). Des variations de performances démographiques entre individus adultes ont pu être associées aux conditions environnementales natales chez divers taxons couvrant l’ensemble des métazoaires (Lindström 1999, Beckerman et al. 2002, Pechenik 2006). Ces conséquences peuvent s’exprimer via une modification durable de la morphologie, de la physiologie ou du comportement des organismes (Schoech et al. 2011). Chez les vertébrés, les conditions environnementales durant l’ontogénèse peuvent altérer le développement cognitif en affectant les capacités futures d’apprentissage et de mémorisation (Salvanes et al. 2013). Ces déficiences pourraient contraindre les performances des individus à long terme en affectant leur comportement de recherche alimentaire ou les comportements associés à la reproduction (Pravosudov et al. 2005, Spencer et al. 2005, Kitaysky et al. 2006, Salvanes et al. 2013). Sur un plan physiologique, les effets à long terme de l’environnement sur le phénotype des individus pourraient être liés au stress oxydatif (Metcalfe and Alonso-Alvarez 2010, Costantini et al. 2011) et aux dommages irréversibles que celui-ci occasionne à la fois sur le soma et le germen (Selman et al. 2012, Monaghan 2014).

2.2.3 Interaction des facteurs intrinsèques et extrinsèques : les normes de réaction

Pour des raisons de clarté, les origines intrinsèques et extrinsèques de la qualité d’un individu ont été présentées indépendamment dans les parties précédentes.

Cependant, ces deux sources sont en réalité étroitement associées et interagissent fortement. En effet, le développement d'un organisme résulte de l'interaction étroite entre un génome et son environnement en suivant ce que l'on appelle une norme de réaction (Dobzhansky 1970, Lewontin 2001). Une norme de réaction décrit pour un génotype donné, l'ensemble des phénotypes exprimés en fonction des conditions environnementales auxquelles il peut être exposé (Figure 3).

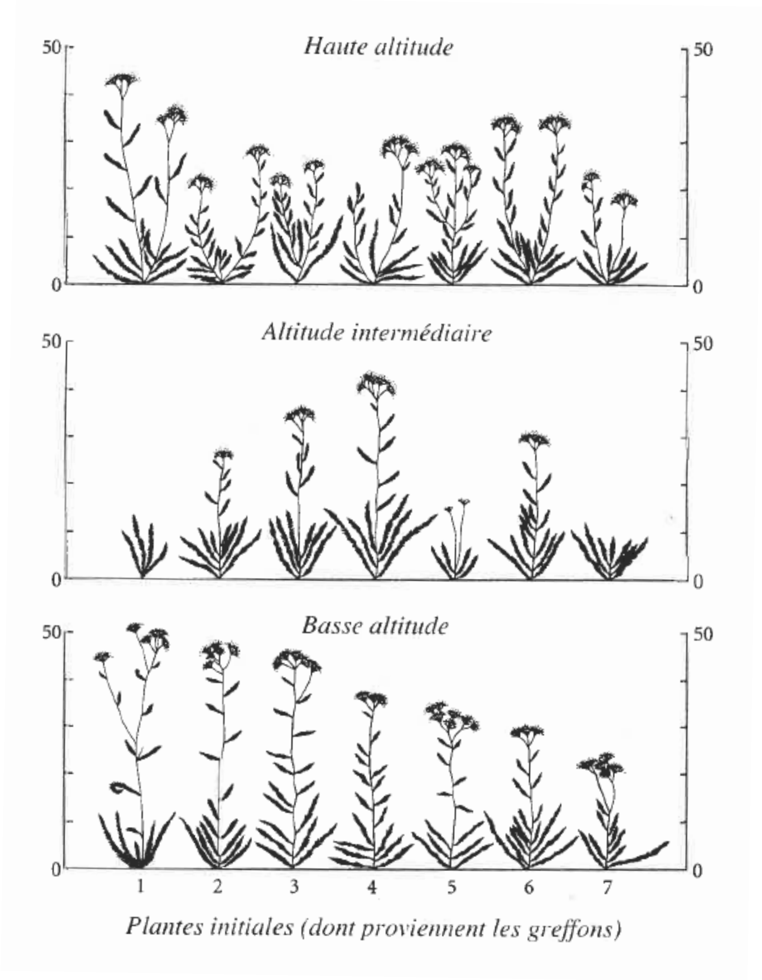

Figure 3 : Exemple de norme de réaction. Croissance de clones de sept plants d'*Achillea sp* génétiquement différents à trois altitudes. Source : *La triple hélice* (Lewontin 2001)

Ainsi l'effet de l'environnement natal sur le phénotype d'un individu dépend en partie de son génotype. Les normes de réactions peuvent elles-mêmes évoluer et donc constituer une composante de la qualité génétique d'un individu. Ainsi la qualité phénotypique d'un individu est déterminée simultanément par son patrimoine génétique et l'environnement dans lequel il s'exprime. L'environnement est considéré ici dans son sens le plus large en incluant par exemple l'environnement sociale. La figure 4 ci-contre synthétise cette conceptualisation de la qualité individuelle.

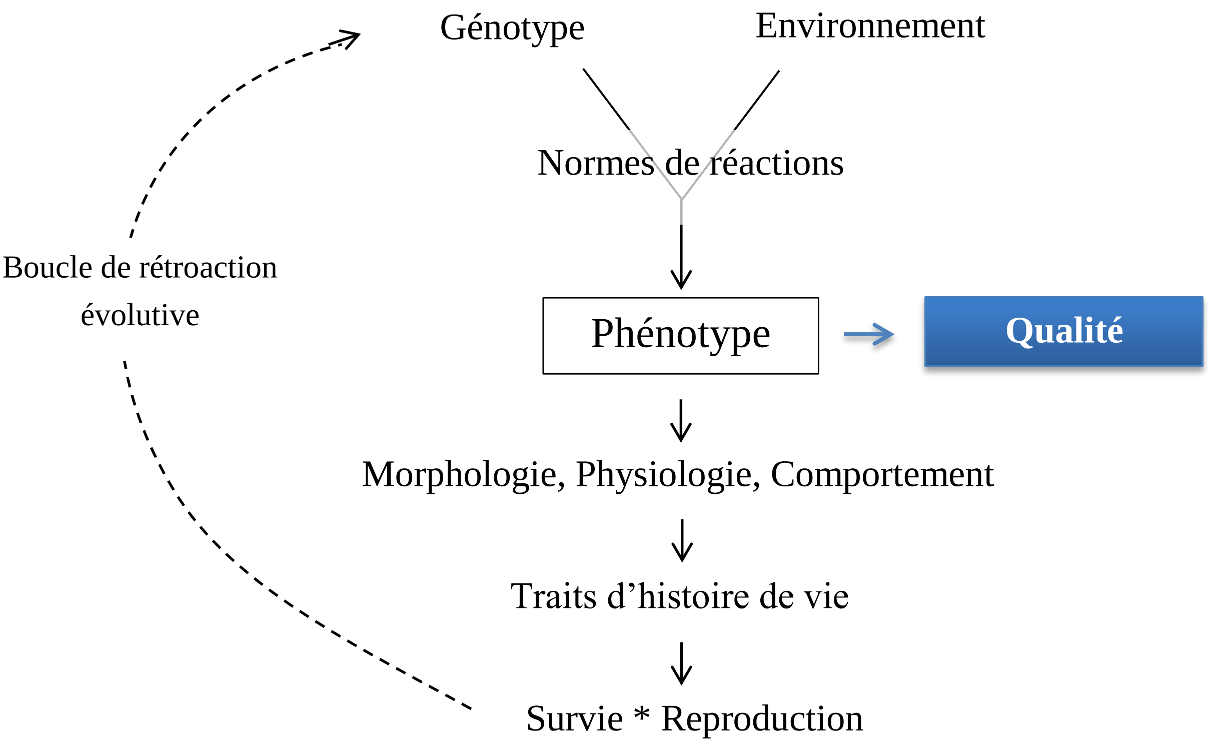

Figure. 4 : Schéma conceptuel de l'origine de la qualité individuelle.

2.3 Les difficultés du concept de qualité

Bien qu'un certain nombre d'ambiguïtés aient pu être levées par une définition approfondie de la notion de qualité dans la partie précédente, il persiste des difficultés dans la définition et la généralisation de l'utilisation de ce concept.

2.3.1 Le caractère fixe de la qualité

Les nombreuses discussions dont a fait l'objet la qualité individuelle, témoignent des difficultés rencontrées par ce concept (Wilson and Nussey 2010, Bergeron et al. 2011). Une des difficultés majeures concerne le caractère fixe de la qualité. Un certain nombre d'études considèrent que la qualité d'un individu n'est pas fixe mais variable. Pour les études portant sur la sélection sexuelle, la condition d'un individu représente typiquement sa qualité (Widemo and Sæther 1999). Comme la condition d'un individu varie dans le temps, ces études considèrent que la qualité d'un individu varie également dans le temps. Cette vision de la qualité individuelle ne pose pas réellement de problème dans notre cas car elle ne correspond simplement pas à la définition que nous en avons donnée (2.1.2). Si la qualité individuelle était condition dépendante, elle serait étroitement liée à l'âge des individus puisque le début de vie comme la sénescence sont généralement associés à des variations de condition corporelle. Or ici, nous définissons la qualité dans le cadre de l'hétérogénéité individuelle, c'est-à-dire indépendamment de l'âge et du sexe des individus. La qualité s'interprète comme une potentialité, non comme le résultat d'une trajectoire de vie. Ainsi on considère que la qualité d'un individu affecte sa condition comme elle affecte d'une manière générale ses performances démographiques, et non l'inverse. Dans le cas où la condition d'un individu ou ses performances définissent sa qualité, le concept de qualité devient tautologique (Bergeron et al. 2011). Il devient redondant vis-à-vis des concepts déjà existants comme la condition corporelle ou la valeur sélective. On retrouve ici la distinction de l'hétérogénéité fixe (qualité) et de l'hétérogénéité dynamique (état physiologique) fait dans la partie 2.1.3. Les variations de la condition d'un organisme seraient d'abord une conséquence de l'âge et de l'hétérogénéité dynamique auxquels est soumis tout individu, et non comme une conséquence de l'hétérogénéité fixe.

Théoriquement, le phénotype d'un individu peut évoluer au cours de sa vie, ce qui suggère que la qualité associée à un individu peut également varier dans le temps. Cette difficulté est réduite chez les organismes où le développement s'effectue sur une période limitée de la vie comme c'est le cas chez les oiseaux, les mammifères ou les insectes. Chez ces taxons, le phénotype peut être considéré comme fixe à la fin de la période de croissance. En comparaison, le caractère fixe de la qualité pour les espèces à croissance continue comme les poissons et les reptiles pourrait être relativisé. Toutefois, même chez ces espèces, les conditions du début de vie sont déterminantes pour les caractéristiques du phénotype futur (Madsen and Shine 2000, Jonsson and Jonsson 2014). En dépit de ce qui pourrait être perçu comme une plasticité naturellement plus importante, la qualité d'un phénotype semble avoir une inertie suffisante chez ces taxons pour justifier l'utilisation de ce concept.

Le caractère fixe de la qualité a également été remis en question par son aspect relatif. En effet la qualité d'un individu se définie par rapport aux autres individus dans un environnement donné. Si les conditions environnementales changent radicalement, on peut envisager que l'appréciation de la qualité d'un individu change également. En d'autres termes, la qualité d'un phénotype dépend de l'environnement dans lequel elle est évaluée, en relation avec les pressions sélectives actuelles et futures (Lailvaux and Kasumovic 2010). Cependant, la définition de la qualité comme une notion fondamentalement dynamique semble exagérée. En effet, dans un contexte environnemental donné, comprenant une gamme de variations importantes, il apparait que la qualité individuelle peut être décrite de manière fixe. Les suivis individuels menés sur le long-terme en milieu naturel semblent révéler que les individus les plus aptes dans un environnement donné reste généralement plus performants lorsque les conditions environnementales changent (Chambert et al. 2013, Jenouvrier et al. 2015). Ainsi, bien que non absolu, le caractère fixe de la qualité semble être une hypothèse de travail valide dans une grande majorité de cas.

2.3.2 Un trait difficile à mesurer

Une seconde difficulté du concept de qualité tient à un aspect méthodologique : comment peut-on mesurer la qualité d'un individu ? La qualité d'un individu étant un résultat multifactoriel, l'ensemble de ses caractéristiques phénotypiques, de l'échelle moléculaire à l'échelle de l'organisme, peuvent être impliquées. Une mesure directe de la qualité d'un individu n'est donc pas possible et l'on utilise généralement des estimations basées sur des critères phénotypiques facilement quantifiables. Le critère le plus simple est la masse de l'individu. Cette métrique est fréquemment utilisée pour les mammifères, particulièrement chez les ongulés où elle fournit généralement une bonne approximation des performances démographiques d'un individu (Bérubé et al. 1999, Gaillard et al. 2000a). En effet, les différences de masses permettent d'anticiper les inégalités futures de performances en termes de survie et de reproduction et ce dès le début de vie (Plard et al. 2015, Vetter et al. 2016). Si la masse peut être utile, elle ne permet cependant pas de capturer toute l'hétérogénéité phénotypique existante entre des individus. Des études expérimentales ont montré que des conditions environnementales stressantes durant le développement pouvaient affecter sur le long terme les capacités intrinsèques de reproduction et de survie d'un individu sans nécessairement modifier sa masse (Metcalfe and Monaghan 2001). La croissance compensatrice est un mécanisme qui permet à un individu de ralentir sa croissance en cas de stress, par exemple alimentaire, puis de l'accélérer lorsque les conditions sont plus favorables. Cette plasticité, bien que plus ou moins développé, est retrouvée chez divers taxons tel que les insectes, les poissons, les oiseaux et les mammifères (Hector and Nakagawa 2012). Cependant, la neutralité du processus n'est qu'apparente. Cette plasticité a en réalité un coût important qui affecte subtilement le phénotype des individus (Dmitriew 2011). Ainsi, la croissance compensatrice peut être associée à une réduction des capacités cognitives adultes, à une longévité plus faible ainsi qu'à des performances de reproduction amoindris (Dmitriew 2011, Lee et al. 2012a, 2012b). Ces effets à long terme pourraient être liés à une allocation plus faible vers la maintenance du corps lorsque la croissance s'accélère, s'exprimant physiologiquement par une plus grande exposition au stress oxydatif (Alonso-Alvarez et al. 2007) et par le raccourcissement des télomères (Geiger et al. 2012).

Une autre méthode pour évaluer la qualité d'un individu consiste à déterminer ses capacités intrinsèques a posteriori au regard de sa trajectoire d'histoire de vie. Les traits alors considérés peuvent être très variables en fonction de l'espèce. On peut citer par exemple l'âge de première reproduction, la date de ponte ou de mise bas ou encore la longévité (Moyes et al. 2009). Plus souhaitable, une approche multivariée permet d'intégrer plusieurs traits simultanément au sein d'un indice de qualité (Hamel et al. 2009a, Wilson and Nussey 2010). Bien que ces approches a posteriori soient très fréquentes, elles s'exposent à un risque de raisonnement circulaire (Bergeron et al. 2011). En effet on définit ici les capacités des individus au regard de leurs performances. La bonne démarche consiste donc à étudier des traits démographiques indépendants des traits utilisés pour établir l'indice de qualité. Cependant, il faut garder à l'esprit que les choix effectués pour les traits retenus sont souvent arbitraires et que différentes métriques peuvent conduire à des évaluations divergentes de la qualité d'un individu (Moyes et al. 2009).

Une alternative pour pallier cette difficulté est d'estimer la qualité individuelle grâce à des modèles statistiques comprenant des distributions discrètes ou continues de qualité individuelle (Cam et al. 2016). La qualité individuelle est alors une variable latente estimée statistiquement. Un point important ici est que ces modèles doivent considérer simultanément l'hétérogénéité dynamique et l'hétérogénéité fixe pour permettre une estimation fiable de la qualité (Cam et al. 2016). Dans certains cas, cette estimation se base sur la structuration des traits d'histoire de vie les uns par rapport aux autres et non directement sur le bilan des performances d'un individu à la fin de sa vie. L'évaluation peut alors conclure à une qualité élevée en dépit par exemple d'un nombre de descendants limité. Dans ce contexte, la qualité individuelle est bien considérée comme une propriété intrinsèque à l'individu qui existe à priori, en accord avec la définition qui a été donnée précédemment (2.1.2).

2.3.3 Effets confondants

L'estimation de la qualité individuelle en milieu naturel réalisée à posteriori de la trajectoire de vie se confronte à des effets confondants. Une étude mettant en évidence la présence d'hétérogénéité fixe au sein d'une population est tentée d'interpréter ce résultat comme l'expression de facteurs intrinsèques aux individus, c'est-à-dire comme l'expression d'une qualité individuelle. Cette conclusion semble d'autant plus naturelle que la qualité individuelle est difficile à quantifier, on parle parfois d'hétérogénéité non observable car les traits phénotypiques la déterminant restent souvent inconnus (Cam et al. 2016). Cependant des facteurs extérieurs aux individus peuvent également être à l'origine de cette hétérogénéité fixe. L'hétérogénéité spatiale de l'habitat peut par exemple être un effet confondant. Au sein d'une population tous les individus ne partagent pas exactement le même environnement. Même chez les espèces grégaires, l'accessibilité aux ressources est modulée par la hiérarchie établie entre les individus. Dans ce contexte, des individus de qualité similaire pourraient montrer des performances divergentes durablement, du simple fait de leur ségrégation spatiale dans un habitat hétérogène (Hogstedt 1981, McLoughlin et al. 2007, Griffen and Norelli 2015). Cependant, cette assertion suggère que la répartition des individus dans l'espace est indépendante de leur qualité. Or de nombreux éléments vont à l'encontre de cette hypothèse. En effet, la répartition spatiale des individus est affectée par leur capacité de compétition, comme il est souvent suggéré pour expliquer la ségrégation âge et sexe spécifique chez de nombreuses espèces (Lack 1954, Newton 1998, Pärt 2001, Phillips et al. 2004). De plus, au sein d'une population, la répartition des individus dans l'espace peut être étroitement liée à des caractéristiques phénotypiques telle que la taille (Camacho et al. 2013). Les habitats les moins favorables pourraient être occupés par des individus ayant intrinsèquement des compétences plus faibles (Coulson 1968, Oro 2008). Ainsi il existe très probablement une relation entre la qualité des individus et leur répartition dans l'espace. Ce résultat complexifie l'étude de la qualité individuelle en milieu naturel mais ne remet en cause ni son existence ni la possibilité de son observation. Par contre, cela rajoute une difficulté considérable à la quantification de la qualité individuelle au sein des populations sauvages. Cette difficulté est plus ou moins importante en fonction de l'espèce considérée et peut donc être en grande partie levée par le choix du modèle d'étude. Notamment, les espèces non territoriales et/ou grégaires sont moins exposées à cet effet confondant et sont pour cette raison de bons modèles biologiques pour étudier la qualité individuelle en milieu naturel.

3 Spécificité du début de vie

3.1 Les traits d'histoire de vie

Les traits d'histoire de vie concernant la période du début de vie sont nombreux et incluent des traits associés à l'investissement parental tels que la taille à la naissance, la durée de gestation ou d'incubation et l'âge à l'indépendance. D'autres traits, moins dépendants des traits de reproduction adultes, peuvent être rassemblés autour de trois évènements principaux: la croissance, la survie et la première reproduction. Les travaux menés au cours de cette thèse se concentrent autour de deux traits d'histoire de vie, la survie et la première reproduction.

3.1.1 La survie

Relativement à la survie des adultes, la survie en début de vie a été peu étudiée au sein des populations sauvages (Pike et al. 2008, Levitis 2011, Cox et al. 2014, Newton et al. 2016). Les jeunes individus sont fréquemment plus petits et surtout plus mobiles que les adultes (Clobert et al. 2001) ce qui complexifie leur étude en milieu naturel. Bien que ces contraintes s'appliquent à une large gamme de taxons, elles semblent avoir particulièrement limitées nos connaissances chez les reptiles et les oiseaux (Pike et al. 2008, Maness and Anderson 2013, Cox et al. 2014, Newton et al. 2016). Pourtant, la survie en début de vie est un paramètre clé pour les performances d'un individu au cours de sa vie. Tout individu doit survivre à sa période de début de vie pour espérer un jour se reproduire. La survie en début de vie est également un paramètre important pour la dynamique des populations en particulier chez les espèces longévives. En effet, les jeunes individus peuvent constituer chez ces espèces jusqu'à 50% de la population (Rivalan et al. 2010). Ainsi, les variations de taille de population sont généralement fortement liées aux variations de survie des plus jeunes individus (Sæther and Bakke 2000, Sæther et al. 2013).

Généralement, la survie en début de vie est plus faible et plus variable que la survie adulte (Gaillard et al. 1998, Levitis 2011). Ce trait évolue avec l'âge en montrant une augmentation progressive jusqu'à la maturité (Clutton-Brock 1988, Newton 1989). Si cette tendance est observée chez de nombreuses espèces, la forme exacte de ce patron varie fortement en fonction des taxons. Alors que la survie est susceptible d'augmenter progressivement en début de vie chez les reptiles, en lien avec leur croissance continue, elle augmente très rapidement chez les oiseaux, où les plus fortes mortalités interviennent durant les premières semaines suivant l'envol (Martín et al. 2007, Cox et al. 2014). Après la première année, la survie des individus encore immatures est généralement proche de celle des adultes, y compris chez les espèces longévives (Hénaux et al. 2007, Millon et al. 2010, Horswill et al. 2014, Chantepie et al. 2016, Payo-Payo et al. 2016). Le patron général d'augmentation des chances de survie en début de vie peut être mis en relation avec les diverses contraintes évoquées dans la partie 1.3.2. liées au jeune âge de ces individus. Du fait de leurs aptitudes plus faibles relativement aux adultes, la survie des jeunes individus est plus sensible à la densité dépendance (Fowler 1987, Coulson 2001, Forchhammer et al. 2001, McAdam and Boutin 2003) et plus généralement aux variations environnementales (Lack 1954, Oro et al. 2010, Pardo et al. 2013a, Horswill et al. 2014). Les contraintes nutritionnelles et la prédation étant les deux principaux facteurs limitant fortement la survie des plus jeunes individus dans la nature (Lack 1954, Sullivan 1989, Anders et al. 1997, Gaillard et al. 2000b).

Ce trait d'histoire de vie est également susceptible d'être impacté par des effets parentaux (Fox et al. 2006). En effet, le devenir des jeunes individus est fortement influencé par leurs parents notamment via le site de ponte ou de mise bas (Van De Pol et al. 2006), la date de ponte ou de naissance (Rodríguez et al. 2016), le rang social (Jones et al. 2010) ou encore la transmission d'éléments immunitaires et microbiologiques. La survie en début de vie est également fortement dépendante de l'investissement parental qui déterminera les ressources nutritionnelles disponibles aux individus en tout début de vie. Que ce soit directement à travers un apport actif de nourriture, ou indirectement via les ressources accumulées dans l'œuf, l'investissement parental influence la condition corporelle des jeunes individus qui est un facteur déterminant pour leur survie à leur indépendance (Albon et al. 1987, Magrath 1991, Clutton-Brock et al. 1992, McMahon et al. 2000, Maness and Anderson 2013). Les variations de l'investissement parental sont particulièrement importantes chez les espèces longévives. En effet, chez ces espèces, l'allocation à la reproduction est particulièrement variable afin de privilégier l'investissement dans les ressources allouées à la survie. Selon la théorie évolutive de la canalisation des traits d'histoire de vie, les paramètres démographiques auxquels le taux d'accroissement de la population est le plus sensible sont protégés contre les variations tant génétiques (Stearns and Kawecki 1994) qu'environnementales (Gaillard and Yoccoz 2003). Chez les espèces adoptant une stratégie d'histoire de vie lente, la survie adulte est fortement canalisée en raison de la forte sensibilité du taux d'accroissement des populations à ce paramètre (Heppell et al. 2000, Sæther and Bakke 2000). Ainsi, chez ces espèces, un individu reproducteur faisant face à des conditions contraignantes sera plus enclin à reporter le coût associé à sa descendance afin de ne pas compromettre sa propre survie. Lorsque l'environnement est moins favorable, les individus reproducteurs vont typiquement assurer leur propre survie en diminuant leur investissement parental (Mauck and Grubb 1995, Navarro and González-Solís 2007, Martin and Festa-Bianchet 2012, Thomson et al. 2014, Jenouvrier et al. 2015).

3.1.2 La première reproduction

La première reproduction est une étape charnière dans l'histoire de vie d'un organisme entre le stade immature ou pré-reproducteur et le stade d'adulte reproducteur. Deux paramètres clés permettent de décrire cet évènement : l'âge à la primiparité et la probabilité qu'elle s'effectue avec succès, c'est-à-dire qu'elle conduise à la production de descendants. L'âge de la première reproduction est plus ou moins variable en fonction de la stratégie d'histoire de vie. Chez les espèces à stratégie dite rapide, l'âge de la première reproduction est généralement très peu variable. Tous les individus se reproduisent lorsque la maturité sexuelle est atteinte. A l'inverse, lorsque que le rythme de vie d'une espèce ralentit, l'âge de la première reproduction est retardé, parfois au-delà de l'âge de maturité sexuelle. Pour les espèces les plus longévives, il est soumis à une grande variabilité interindividuelle (Weimerskirch 1992, Reid et al. 2003a). Ces variations s'expliquent généralement par des contraintes environnementales liées aux ressources alimentaires. Comme il a été dit précédemment, les espèces aux stratégies d'histoire de vie lentes privilégient l'allocation d'énergie vers la maintenance somatique (Gaillard and Yoccoz 2003). Ainsi, lorsque les ressources nutritives sont limitantes, la reproduction est repoussée afin d'assurer la survie de l'individu (Becker and Bradley 2007). Ce processus est mis en évidence lorsque l'on s'intéresse aux variations de l'âge de première reproduction au sein d'une population au cours du temps (Tavecchia et al. 2007, Nevoux et al. 2010b, Szostek and Becker 2015) ou lorsque l'on compare différentes populations de la même espèce exposées à des contraintes environnementales différentes (Sand 1996, Gaillard et al. 2000b, McMahon et al. 2003, Hadley et al. 2006). L'âge de la première reproduction est étroitement lié à la croissance des individus (Fowler 1987, Becker and Bradley 2007). Les individus qui se reproduisent pour la première fois sont généralement en très bonne condition pour leur âge (Massot et al. 2011, Martin and Festa-Bianchet 2012, Lee et al. 2013). Ce mécanisme se traduit également par l'observation d'un seuil de condition corporelle à partir duquel la première reproduction a lieu chez certaines espèces de mammifères et d'oiseaux (Weimerskirch 1992, Gaillard et al. 2000b). Plus ponctuellement, la disponibilité de site de reproduction peut également être un facteur limitant l'âge de la première reproduction pour certaines espèces (Ens et al. 1995, Pradel et al. 1997).

Les chances de se reproduire avec succès lors de la première occasion de reproduction sont à la fois plus faibles (Curio 1983, Forslund and Pärt 1995, Fowler 1995) et plus variables (Barbraud and Weimerskirch 2005, Tavecchia et al. 2005) relativement aux occasions suivantes. Bien qu'il soit difficile de distinguer les mécanismes de retenue de ceux de la contrainte, on estime souvent que le succès de reproduction en début de vie est fortement contraint par les faibles aptitudes des jeunes individus (Forslund and Pärt 1995). On note par exemple que la probabilité de succès tend à augmenter lorsque la première reproduction intervient à un âge plus avancé (Newton et al. 1981, Krüger 2005). Les contraintes limitant les performances des jeunes individus se cristallisent autour des compétences liées à la recherche alimentaire et la compétition. Une étude semi-expérimentale menée sur une population de merles noirs *Turdus merula* en milieu naturel, a montré que le succès de reproduction des jeunes individus égale celui des adultes lorsque l'on met à leur disposition de la nourriture supplémentaire (Desrochers 1992). De même, le plus faible succès de reproduction des jeunes traquets motteux *Oenanthe oenanthe* est en grande partie expliqué par leur incapacité à acquérir des territoires de bonne qualité (Pärt 2001). L'inexpérience dans la reproduction est elle-même une contrainte qui ne peut pas être évitée. L'effet du manque d'expérience est généralement mis en évidence par l'augmentation des chances de succès lors de reproductions consécutives, indépendamment de l'âge des individus (Harvey et al. 1985, Desprez et al. 2011).

3.2 Variation des traits en début de vie et qualité individuelle

3.2.1 Le processus de sélection

Les patrons démographiques du début de vie observés à l'échelle de la population peuvent être affectés par les différences de qualité phénotypique entre les individus (Vaupel and Yashin 1985). En effet, lorsque les aptitudes à survivre et à se reproduire sont positivement associés, la disparition précoce des individus de moindre qualité peut entrainer, à l'échelle de la population, une augmentation des taux vitaux avec l'âge indépendamment de l'amélioration des capacités des individus (Curio 1983). Bien que les variations âge-spécifiques des paramètres de survie et de reproduction aient été très étudiées, l'importance du processus de sélection sur la forme de ces patrons est peu connue. Concernant la survie, des études montrent qu'une hétérogénéité de survie existe au sein des populations suggérant que des processus de sélection pourraient participer à l'augmentation des probabilités de survie observées en début de vie. Par exemple, en comparant des groupes d'individus, il a été montré que la survie en début de vie était positivement associée à la survie adulte (Reid et al. 2006). De même, alors que la mortalité s'accroit en fin de vie du fait du vieillissement, on observe parfois une décélération de ce taux de mortalité pour les toutes dernières classes d'âges (Vaupel et al. 1998). Cette décélération suggère que les individus qui persistent aux âges les plus avancés ont intrinsèquement une capacité de survie supérieure. Pour ce qui concerne les premières reproductions, le processus de sélection est plus étudié et mieux documenté. Par exemple, l'augmentation du volume des œufs pondus en relation avec l'âge des individus est entièrement expliquée par la disparition progressive d'individus de qualité inferieure chez une population d'huitriers pies (van de Pol and Verhulst 2006). D'une manière générale, il est admis que le processus de sélection participe à l'augmentation du succès de reproduction en fonction de l'âge observé à l'échelle de la population (Curio 1983, Forslund and Pärt 1995, Reid et al. 2003b). Cependant, l'importance de ce processus relativement à l'amélioration des aptitudes individuelles varie en fonction des espèces étudiées. Par exemple, le processus de sélection a été jugé prépondérant pour expliquer l'augmentation du succès reproducteur avec l'âge observée chez une population de mouettes tridactyles *Rissa tridactyla* (Aubry et al. 2009b) et de goélands d'Audubon *Larus occidentalis* (Annett and Pierotti 1999), alors que ce processus est considéré mineur pour une population de goélands cendrés *Larus canus* (Rattiste 2004) et de sternes pierregarins *Sterna hirundo* (Rebke et al. 2010). Chez cette dernière, il est estimé que seulement 15% des variations de performance de reproduction en début de vie sont dues à la disparition progressive des individus de plus faible capacité. A ce jour, ce type d'estimation reste très rare et il est difficile d'apporter une réponse générale sur l'importance du processus de sélection en dehors de cas d'études particuliers. On ignore par exemple l'importance de la stratégie d'histoire de vie de l'espèce étudiée ou encore le contexte écologique dans lequel se situe la population.

3.2.2 Les contraintes liées à la qualité

La qualité intervient également dans les patrons des traits d'histoire de vie à travers les contraintes qu'elle impose aux individus. Les individus de plus faible qualité ont un accès plus restreint à la ressource qu'elle soit alimentaire ou territoriale (van de Pol et al. 2007, Camacho et al. 2013). Ces contraintes peuvent affecter directement les traits démographiques. Par exemple, un individu sexuellement moins attractif trouvera plus difficilement un partenaire sexuel et sera potentiellement contraint de se reproduire pour la première fois à un âge plus tardif, ou encore de s'apparier à un partenaire de faible qualité ce qui diminuera ses chances de succès lors de la reproduction. Les contraintes induites par la qualité peuvent également affecter indirectement les patrons du début de vie à travers les compromis d'allocation des ressources. En effet, les allocations d'énergie dépendent des capacités des individus à acquérir et utiliser des ressources (Van Noordwijk and de Jong 1986) et sont donc fonction de leur qualité. Par exemple, un individu limité par ses capacités intrinsèques d'allocation pourra être amené à repousser son âge de première reproduction afin d'assurer sa propre survie. Ce mécanisme adaptatif peut également expliquer que les individus de plus faible qualité accèdent à la reproduction à un âge plus avancé (Nussey et al. 2006, Aubry et al. 2011, Kim et al. 2011). Ce processus peut fortement affecter les patrons âge-spécifiques liés à la première reproduction. Contrairement à ce qui est attendu selon l'accumulation d'expérience ou le principe de sélection, la probabilité de se reproduire en début de vie n'augmente pas avec l'âge des individus de manière monotone. Chez certaines espèces longévives, la chance d'accéder à la reproduction diminue chez les classes d'âges pré-reproductrices les plus avancées (Hadley et al. 2006, Aubry et al. 2009a, Desprez et al. 2014). Cette décroissance est également rapportée pour la variation du succès de la première reproduction en fonction de l'âge des individus (Aubry et al. 2009a, Blas et al. 2009). Ainsi, plutôt que des relations âge spécifiques monotones, les patrons de début de vie observés chez les espèces longévives suivent régulièrement une forme en cloche.

4 Les oiseaux marins et enjeux de la thèse

4.1 Connaissances sur la démographie des jeunes oiseaux marins

Les oiseaux marins sont des modèles d'études historiques en écologie des populations et notre connaissance des processus démographiques en milieu naturel reposent de manière substantielle sur ces espèces (Lack 1966, Wooller et al. 1992). Les oiseaux marins forment de grandes colonies ce qui permet de suivre un nombre important d'individus, années après années, en raison de leur grande fidélité au site de reproduction (Furness and Monaghan 1987, Gaston 2004). Ce sont en outre des espèces longévives permettant ainsi l'étude des patrons démographiques à travers un gradient d'âge important. Cette dernière caractéristique constitue paradoxalement un inconvénient pour étudier les traits démographiques du début de vie. En effet, ce rythme de vie ralenti est associé à une longue période d'immaturité, qui varie de 2 à 10 ans en fonction des espèces, durant laquelle les individus restent continuellement en mer. La plupart des oiseaux marins ne reviennent à terre que pour se reproduire. Ainsi, après leur envol des colonies, les individus juvéniles ne sont généralement plus observables depuis la terre durant plusieurs années. Cette particularité explique que les traits d'histoire de vie des jeunes classes d'âges soient très peu connus chez ses oiseaux.

Les paramètres démographiques des jeunes oiseaux marins sont restés relativement peu connus jusqu'à la fin des années 1990. Les première études sur la survie en début de vie se sont concentrées sur les conditions natales affectant les performances des jeunes après leur envol comme la date d'éclosion, le nombre d'individus dans la nichée, la croissance au nid et la masse à l'envol (Perrins 1966, Jarvis 1974, Parsons et al. 1976, Coulson and Porter 1985, Harris and Rothery 1985, Spear and Nur 1994). Cependant, ces études pionnières ne reportent pas d'estimation de survie juvénile ou immature parce que les recaptures des jeunes oiseaux sont à la fois rares et espacées dans le temps. Dans bien des cas, l'appréciation de la survie est limitée à un taux de retour des cohortes x années après leur envol. Le processus d'accès à la reproduction est quant à lui un trait naturellement plus accessible et son étude a permis d'identifier l'âge auquel il intervient pour la première fois, ainsi que l'effet du sexe sur ce patron et le succès moyen de reproduction lors que cette première tentative (Wooller and Coulson 1977, Croxall and Prince 1990, Weimerskirch 1992). Toutefois, ce n'est qu'à partir des années 2000, avec l'accumulation des données des suivis démographiques à long-terme et la généralisation de l'utilisation des analyses de type Capture-Marquage-Recapture (Lebreton et al. 1992), que l'étude des traits d'histoire de vie juvénile des oiseaux marins prend réellement son essor. Les premières estimations de survie juvénile prenant en compte le processus de détection des individus, inhérent au suivi d'organismes en milieu naturel, font leur apparition (Schreiber et al. 2004, Crespin et al. 2006, Wanless et al. 2006, Harris et al. 2007, Hénaux et al. 2007, Frederiksen et al. 2008). L'effet de l'environnement sur les processus de survie et de reproduction en début de vie fait également l'objet d'un nombre croissant d'études (Barbraud and Weimerskirch 2005, Nevoux et al. 2007, Tavecchia et al. 2007, Votier et al. 2008, Oro et al. 2010). Malgré cette amélioration des connaissances, notre compréhension des processus démographiques associés aux classes d'âge les plus jeunes restent limitées relativement aux adultes (Barbraud et al. 2012). Dans un article de synthèse et de perspectives publié en 2012, les premiers stades de vie sont toujours désignés comme une priorité pour l'étude et la conservation des oiseaux marins (Lewison et al. 2012).

4.2 Objectifs et structure de la thèse

4.2.1 Objectifs généraux

En se basant sur le suivi à long-terme d'une population d'albatros hurleur *Diomedea exulans*, cette thèse vise en premier lieu à améliorer nos connaissances sur les traits démographiques du début de vie chez une espèce d'oiseau marin. D'autre part, des questions plus fondamentales liées à l'hétérogénéité individuelle ont également pu être abordées. Cet axe s'inscrit dans l'intérêt croissant de la prise en compte de l'hétérogénéité fixe dans l'étude des processus démographiques en milieu naturel. Les objectifs de cette thèse peuvent être déclinés en trois points principaux.

- **Décrire les variations des paramètres de survie et de première reproduction.**

Il s'agit ici de fournir des estimations de survie qui sont encore rares pour la période du début de vie, en particulier chez les procellariiformes. Les patrons liés à l'âge de première reproduction et au succès lors de cet évènement sont également détaillés en fonction du sexe et de l'âge.

- **Comprendre les déterminants environnementaux affectant ces traits.**

Les facteurs considérés sont multiples incluant les variations climatiques, la densité de population, les pressions de pêches et les effets parentaux. Ce point répond aux attentes sur l'amélioration des connaissances concernant les relations entre les jeunes oiseaux marins et leur environnement à des fins de protection, en abordant également des problématiques d'écologie évolutive.

- **Quantifier l'importance de l'hétérogénéité individuelle.**

Cet axe s'intéresse aux facteurs intrinsèques affectant les traits d'histoire de vie du début de vie. L'objectif est de documenter l'existence d'une l'hétérogénéité fixe et de rechercher les déterminants qui peuvent être à son origine.

4.2.2. Structure de la thèse

Cette thèse est rédigée sur articles. Après une présentation concise du matériel et des méthodes, le corps du manuscrit est constitué des cinq articles rédigés au cours de cette thèse sur les traits démographique en début de vie de l'albatros hurleur. En partant des facteurs biologiques fondamentaux que sont le sexe et l'âge, nous sommes conduits à considérer l'existence de stratégies individuelles puis de la qualité individuelle. Les principaux résultats obtenus au cours de ce travail sont repris dans une discussion générale qui ouvre sur de nouvelles perspectives. Chapitre par chapitre, cette thèse se structure de la façon suivante :

Le **premier chapitre** présente notre modèle d'étude et introduit la modélisation capture-marquage-recapture. Cette partie vise à présenter les principaux traits démographiques de l'albatros hurleur ainsi que le contexte écologique particulier de notre population d'étude. Les méthodes statistiques ne sont pas détaillées. Les modèles utilisés sont présentés en détail dans les articles constituant le corps de cette thèse.

Le **second chapitre** rassemble deux articles sur la description des traits démographiques de l'albatros hurleur en début de vie ainsi que les relations fonctionnelles entre ces paramètres démographiques et l'environnement. L'effet du sexe et de l'âge sur la survie et la probabilité de se reproduire pour la première fois sont investigués. Les variations d'âge de première reproduction sont également considérées. Les variations temporelles de ces paramètres démographiques sont estimées et mis en relation avec des facteurs climatiques reflétant la disponibilité alimentaires, la taille de population pour étudier le mécanisme de densité-dépendance et les pressions de pêche, cette activité étant une source importante de mortalité chez cette espèce. Ces articles abordent également l'existence potentielle d'effets parentaux à travers les conditions environnementales durant la période d'élevage, lorsque le jeune est encore sur le nid.

Le **troisième chapitre** approfondis l'étude des effets parentaux sur les performances des jeunes individus après leur envol. Cette partie se penche sur l'effet de l'âge des parents sur la survie et l'accès à la reproduction de leur descendant. Les albatros montrant une diminution de leurs performances biodémographiques après 30 ans, nous interrogeons ici les conséquences transgénérationnelles du vieillissement. L'effet de l'âge maternel et paternel sont considérés alternativement l'un et l'autre puis simultanément.

Le **quatrième chapitre** s'intéresse à la variabilité interindividuelle au sein de la population d'étude en recherchant l'existence de qualité individuelle et de différentes stratégies démographiques. Les stratégies sont envisagées ici comme une répétition du continuum rapide-lent à l'échelle individuelle. Ce questionnement est effectué dans le contexte des variations de l'âge de première reproduction. Ainsi, en plus d'étudier ces concepts généraux, cette partie vise à expliquer la variabilité importante observée pour ce trait d'histoire de vie.

Le **cinquième chapitre** approfondit la thématique de l'hétérogénéité individuelle en étudiant les relations entre des traits démographiques variés depuis le début de vie jusqu'à la sénescence. Il met en évidence l'importance de la qualité individuelle et questionne son origine. Les facteurs natals sont considérés à travers la taille de population l'année de naissance ainsi que les conditions climatiques reflétant la disponibilité alimentaire sur les aires de nourrissage des parents.

Une **discussion générale** clôt la rédaction de ce manuscrit.

CHAPITRE 1

Matériels et Méthodes

Crozet. Crédit: Florian Orgeret

1 Modèle d'étude : l'albatros hurleur

1.1 Présentation de l'espèce

1.1.1 Description et état de conservation

L'albatros hurleur *Diomedea exulans* (Linnaeus, 1758), est le plus grand des oiseaux volants actuels. Les mâles peuvent atteindre une envergure de 3m50. Cette espèce est caractérisée par un dimorphisme sexuel : les mâles sont plus grands et plus lourds que les femelles, atteignant 9-10kg pour les premiers contre 7-8kg pour les secondes (Shaffer et al. 2001). Le plumage est aussi différent en fonction des sexes. Bien que tous les jeunes aient une couleur brun chocolat à l'envol, le plumage s'éclaircit avec l'âge pour devenir presque entièrement blanc chez les mâles les plus âgés (Weimerskirch et al. 1989). Les femelles conservent quant à elles un plumage pommelé plus sombre (Figure 1.1). Avec une population reproductrice annuelle mondiale estimée à 8000 couples en 2010 (ACAP 2010), l'albatros hurleur est classé espèce vulnérable par l'UICN. La pêcherie industrielle à la palangre, avec les prises accidentelles qu'elle engendre, est la principale menace qui pèse sur l'espèce. Cette activité économique explique en grande partie le déclin des populations observé à l'échelle mondiale au cours des dernières décennies.

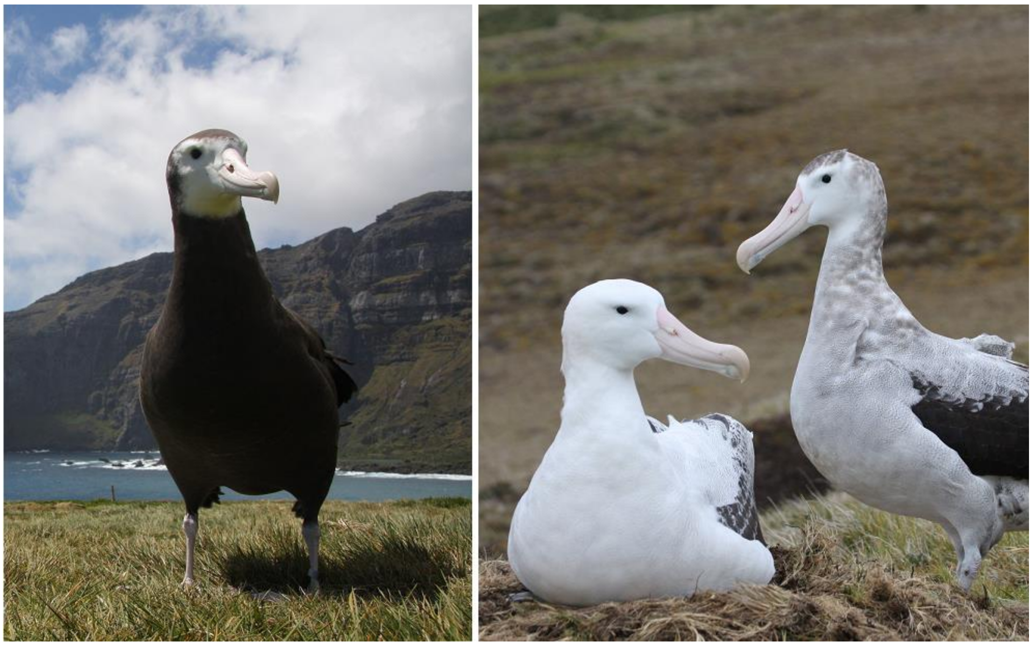

Figure 1.1 : Albatros hurleur Diomedea exulans. A gauche : Jeune prêt à l'envol. A droite : Couple d'albatros adultes, mâle assis et femelle debout. Crédit : Aurélien Prudor (Ile de la Possession).

1.1.2 Habitat et mode de vie

L’albatros hurleur est un oiseau marin océanique, que l’on retrouve dans tous les océans de l’hémisphère sud entre 30°S et 60°S (Figure 1.2). Il revient à terre uniquement pour se reproduire, différentes colonies étant réparties sur plusieurs archipels subantarctiques (Géorgie du Sud, îles de Princes Edouard, îles Crozet, îles Kerguelen, Macquarie). Généralement solitaire et erratique, il utilise au mieux les vents pour parcourir de très grandes distances afin de rechercher sa nourriture (Weimerskirch et al. 2000b). On estime qu’un albatros peut parcourir plusieurs millions de kilomètres au court de sa vie pour rechercher ses proies (Weimerskirch et al. 2014). Il se nourrit principalement en journée de calmars, poissons et autres débris organiques qu’il trouve à la surface des eaux (Cherel and Weimerskirch 1999). Plus charognard que prédateur, il est capable d’absorber de grandes quantités de nourriture en peu de temps et possède par ailleurs des sucs gastriques particulièrement acides qui lui permettent de digérer rapidement une large gamme d’aliments (Grémillet et al. 2012).

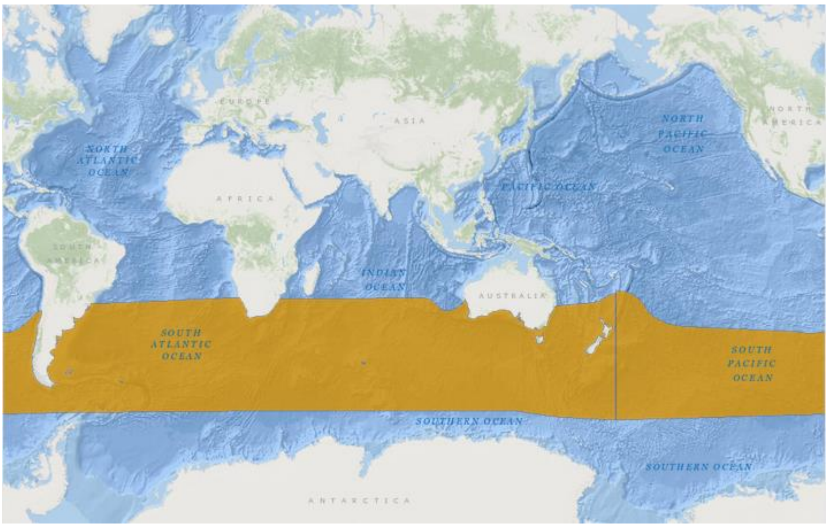

Figure 1.2 : Carte de répartition de l’albatros hurleur. Source : UICN (http://maps.iucnredlist.org)

1.2 Stratégie d’histoire de vie

1.2.1 Cycle de vie

La stratégie d’histoire de vie de l’albatros hurleur est l’une des plus lentes parmi les oiseaux. Bien que la maturité sexuelle semble atteinte à 5 ans (Hector et al. 1986), la première reproduction intervient généralement entre 8 et 11 ans (Croxall et al. 1990, Weimerskirch 1992). L’âge de la première reproduction est cependant très variable, certains individus débutant exceptionnellement à 6 ans alors que d’autres individus ne se sont toujours pas reproduits après l'âge de 15 ans. Lors de la reproduction, un seul œuf d'environ 500g est pondu. Les deux partenaires participent à l'incubation qui dure 80 jours. Durant les 30 premiers jours de sa vie, le poussin dépend de la présence de ses parents pour sa régulation thermique. Après cette période, le poussin seul sur le nid est nourrit alternativement par ses deux parents. La contribution du père est toutefois supérieure à celle de la mère d'environ un tiers, en raison notamment du dimorphisme sexuel (Weimerskirch et al. 2000a). Comme chez les autres espèces d'oiseaux, la croissance des poussins est rapide. Ils atteignent en un peu plus de 100 jours la masse des adultes. Le jeune prend son envol, seul, vers 270 jours, lorsque son développement est terminé. Entre les parades pré-copulatoires et l'envol du poussin, le cycle de reproduction chez cette espèce dure une année complète (Figure 1.3). Ainsi la reproduction est biennale ou quasi biennale (Barbraud and Weimerskirch 2012). La plupart des parents qui ont mené un jeune à l'envol prennent ensuite une année « sabbatique » passée en mer, avant de venir se reproduire de nouveau sur les colonies. Les individus forment des couples stables (Jouventin et al. 1999) et se reproduisent sur l'ensemble de leur vie qui peut durer plus de 60 ans. Le phénomène de vieillissement a été très clairement mis en évidence chez l'albatros hurleur et affecte les performances des individus au-delà de 25 ans (Lecomte et al. 2010, Froy et al. 2013).

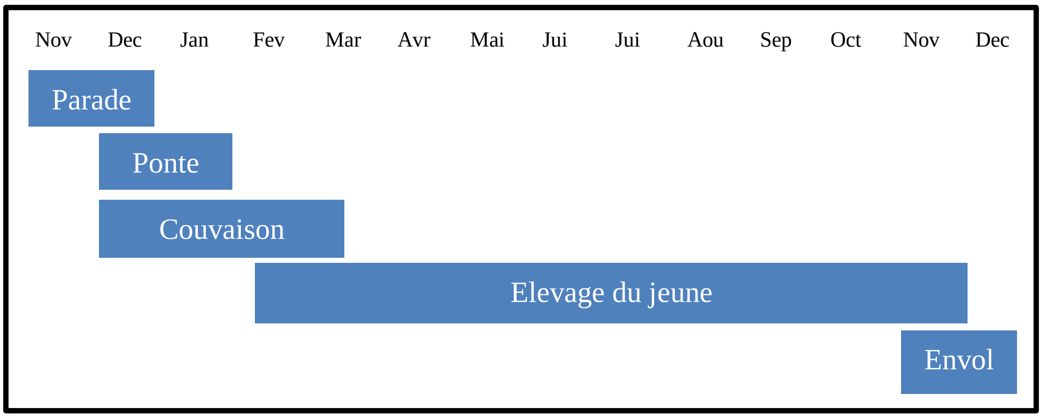

Fig. 1.3 : Cycle de vie reproduction de l'albatros hurleur

1.2.3 Reproduction et survie

La fécondité de l'albatros hurleur est particulièrement faible. Sa reproduction est strictement limitée à un seul œuf et il n'y a pas de ponte de remplacement. Le succès de reproduction, peu variable dans le temps, est en moyenne de 60 à 70 % selon les populations (Croxall et al. 1990, Rolland et al. 2010). Il évolue avec l'âge des individus, augmentant avec l'expérience en début de vie (Weimerskirch 1992) puis diminuant

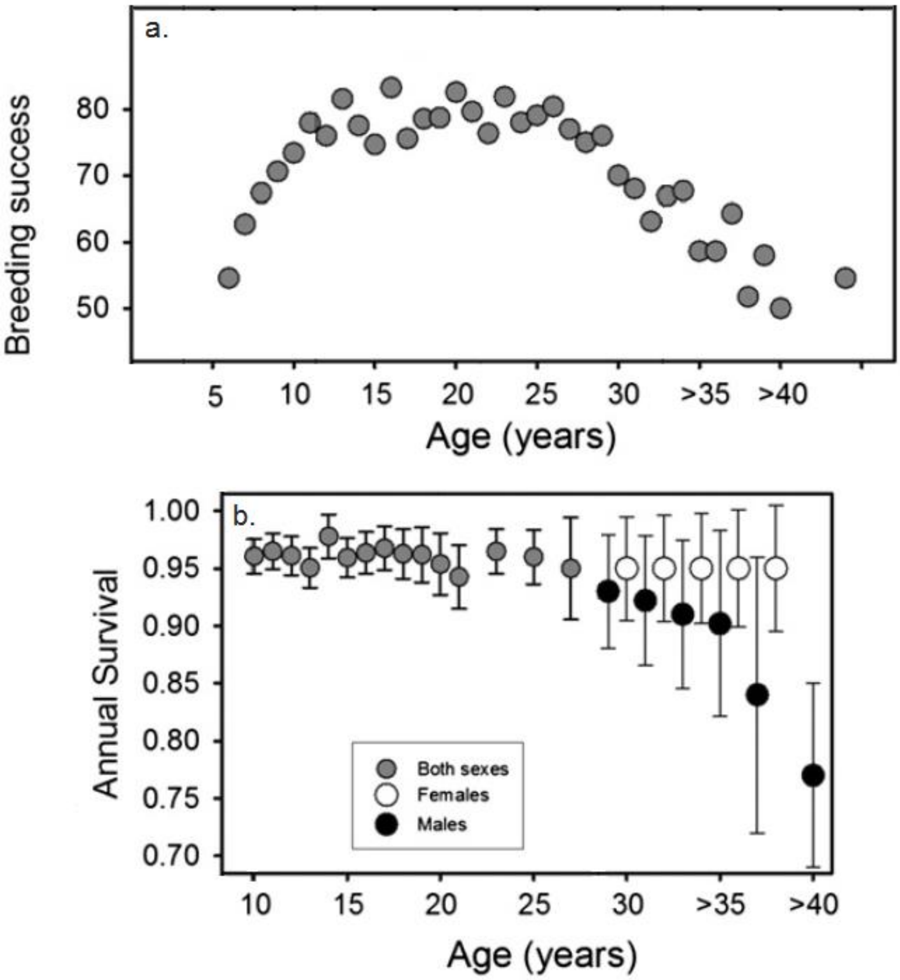

Figure. 1.4 : Variation du succès de reproduction (a) et de la survie (b) en fonction de l'âge et du sexe. Reproduit d'après Weimerskirch et al. 2014

progressivement après 25 ans du fait de la sénescence (Froy et al. 2013, Pardo et al. 2013b, Figure 1.4). Le taux de survie des albatros est l'un des plus forts chez les oiseaux. Il avoisine les 95% pour un adulte d'âge moyen et montre remarquablement peu de variations temporelles (Rolland et al. 2010). Ce taux est cependant variable en fonction de l'état des individus. En particulier les individus non reproducteurs ont une survie inférieure aux individus reproducteurs (Pardo et al. 2013c). Il faut également garder à l'esprit que ces taux de survie sont probablement affectés par de la mortalité induite par les activités de pêches industrielles (Rolland et al. 2010). Chez une population soumise à de fortes pressions de pêche, la survie est estimée autour de 94% (Croxall et al. 1990) alors que pour l'unique population d'albatros d'Amsterdam *Diomedea amsterdamensis*, une espèce très proche de l'albatros hurleur et chez laquelle la mortalité par prise accidentelle est probablement proche de zéro, la survie adulte moyenne est estimée à 97% (Rivalan et al. 2010). Ces exemples illustrent l'importance que les facteurs anthropiques pourraient avoir sur le taux de survie d'une population. Tout comme le succès de reproduction, la survie décroît chez les individus les plus âgés, surtout après 30 ans (Pardo et al. 2014). La sénescence est particulièrement marquée chez les mâles (Pardo et al. 2013b).

1.2.4 Dispersion

Après leur envol, les jeunes individus se dispersent rapidement à des milliers de kilomètres de leur île natale dans des directions multiples (De Grissac et al. 2016). Ils sont cependant extrêmement fidèles à leur localité de naissance et reviendront quasi systématiquement se reproduire, des années plus tard, sur l'île où ils sont nés (Charmantier et al. 2011). Une fois que les individus se sont reproduits sur un site, ils sont extrêmement philopatriques, la dispersion de reproduction étant extrêmement faible (Inchausti and Weimerskirch 2002).

2 La population de Crozet (Ile de la Possession)

2.1 Site d'étude et répartition en mer

La population d'étude se trouve sur l'île de la Possession, au sein de l'archipel de Crozet, au Sud-Ouest de l'Océan Indien. Les albatros nichent en plusieurs colonies sur les plateaux et pentes herbeuses balayés par les vents. Le climat océanique qui y règne se caractérise par une faible amplitude thermique et des précipitations importantes. L'archipel de Crozet se trouve en zone subantarctique, entre le front polaire au sud et les fronts subantarctique et subtropical au nord (Figure 1.5). Ces fronts représentent des barrières hydrologiques qui structurent l'océan en délimitant des masses d'eaux aux caractéristiques physico-chimiques et biologiques différentes. D'une manière générale, en milieu subtropical les eaux sont moins productives et les vents plus faibles qu'en milieu antarctique et subantarctique. Bien que certains individus exploitent les eaux pacifiques et atlantiques, les albatros de l'île de la Possession recherchent principalement leur nourriture dans le sud de l'Océan indien et dans l'Océan austral entre l'Afrique du Sud à l'ouest et la Tasmanie à l'est (Weimerskirch et al. 2014). Dans cette large zone, la distribution des individus s'effectue en fonction de leur âge et de leur sexe. Schématiquement on retrouve les jeunes individus plus au nord dans les eaux plus chaudes de l'Océan indien (Weimerskirch et al. 2006), les femelles adultes dans les eaux subantarctiques et les mâles adultes plus au sud encore dans les eaux subantarctiques et polaires. On note cependant que le recouvrement entre les classes d’âge peut être important et que de fortes variabilités individuelles existent (Weimerskirch et al. 2015).

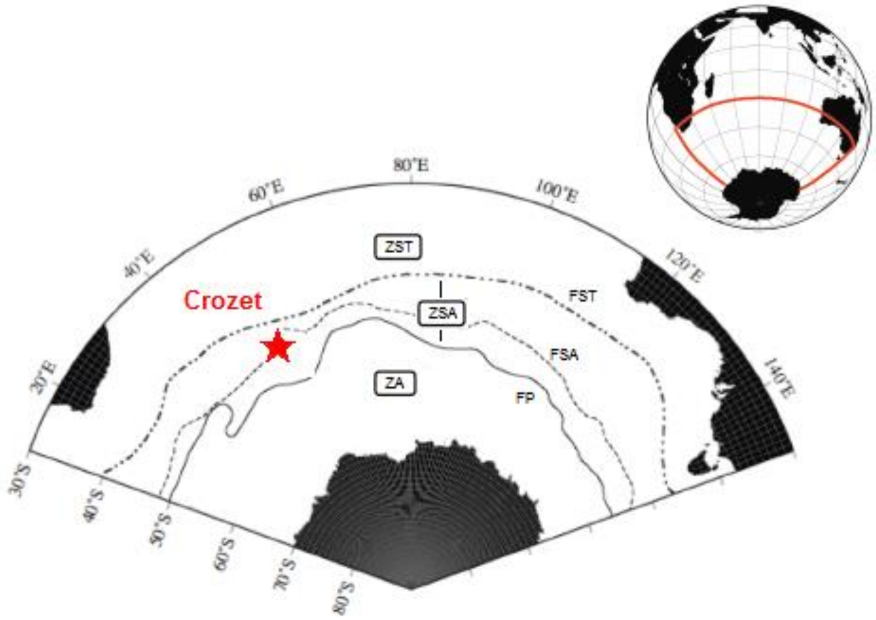

Figure 1.5 : Localisation de l’archipel de Crozet et des principaux fronts océanographiques. FST, front subtropical ; FSA, front subantarctique ; FP, front polaire ; ZST, zone subtropicale ; ZSA, zone subantarctique ; ZA, zone antarctique. Reproduit d’après Takao et al. 2012.

2.2 Dynamique de population

Les premières estimations de la taille de la population d’albatros hurleur de Crozet ont eu lieu dans les années 60. Ces premiers comptages rapportent qu’environ 500 couples d’albatros se reproduisent annuellement sur l’île de la Possession. Cependant, du fait qu’une partie importante de la population soit en mer, que ce soit les jeunes ou les adultes en année « sabbatique », le nombre de couples reproducteurs n’est qu’un indice de la taille de la population. En prenant en compte la distribution d’âge et les états reproducteurs des adultes, on peut estimer à l’aide de modèles matriciels une population totale d’environ 3300 individus. A partir des années 70, le nombre de couples reproducteurs dénombré chute rapidement pour atteindre 244 en 1984, soit une diminution de 51% (Delord et al. 2008). Cette chute des effectifs a été causée par une diminution de la survie des adultes en relation avec le développement des pêches industrielles à la palangre dans l’Océan Indien (Weimerskirch and Jouventin 1987, Weimerskirch et al. 1997). A partir de la fin des années 80, le nombre de couples ré-augmente progressivement pour atteindre 405 couples en 1998, avant de fluctuer autour de 350 couples jusqu'à aujourd'hui. En 2016, 330 couples reproducteurs ont été dénombrés sur l'île de la Possession. Différents déterminants environnementaux ont pu affecter simultanément la démographie de cette population. En plus des activités de pêche, les changements climatiques récents ont pu affecter les performances des individus. L'augmentation des vents aurait ainsi pu bénéficier aux albatros en améliorant leurs capacités de déplacement (Weimerskirch et al. 2012). On peut également évoquer la présence d'espèces introduites comme le rat noir *Rattus rattus* et la souris grise *Mus musculus*, qui sont connus pour affecter le succès de reproduction des albatros en d'autres localités bien qu'aucune preuve n'ait été documentée en ce sens pour ce qui concerne notre population d'étude.

3 Suivi démographique et analyses des données.

3.1 Suivi à long-terme

Le suivi démographique à long-terme de la population d'albatros hurleurs de l'île de la Possession a été initié en 1965. Depuis cette date, chaque année un observateur Volontaire au Service Civique (VSC) est envoyé sur l'île par le programme de recherche 109 « Oiseaux et mammifères marins sentinelles des changements globaux de l'Océan Austral » soutenu par l'IPEV. Le suivi implique le marquage systématique de tous les poussins nés sur l'île de la Possession à l'aide de bagues alphanumériques. Ces bagues permettent de suivre individuellement la présence et la reproduction des individus sur l'île tout au long de leur vie. Cependant, le suivi effectué ne permet pas d'observer avec certitude tous les individus reproducteurs. En particulier, lorsqu'un couple est en échec, il est possible de manquer un des partenaires. Si l'on peut observer un oiseau lors de l'échec, il y a de fortes chances que son partenaire abandonne le nid dès qu'il aura lui-même constaté l'échec. Les observateurs n'étant pas en permanence sur les colonies d'études, cet individu reproducteur peut être manqué. Ce type d'observation lacunaire est typique des suivis d'animaux en milieu naturel. Pour analyser ce type de donnée, il est indispensable de prendre en compte le processus de détection qui est sous-jacent aux observations. Ceci est possible grâce aux modèles de type Capture-Marquage-Recapture (CMR).

3.2 Méthodes de Capture-Marquage-Recapture

Les modèles traitant des données issues de la méthode CMR ont évolué sur plus d'un siècle en accompagnant le développement de l'écologie. La première application de la méthode CMR sur des populations sauvages a été effectuée sur des poissons par un biologiste marin danois nommé Carl G. J. Peterson (1860-1928). En observant qu'une partie des individus qu'il marquait étaient repris par les pêcheurs, Peterson compris que cette information constituait une opportunité pour estimer la taille de la population. Il publiera sa méthode en 1896 dans un article intitulé *The yearly immigration of young plaice into the Limfiord from the German Sea*. Durant le début du XX^{ème} siècle, la méthode de capture- marquage-recapture est utilisée uniquement pour estimer la taille de populations sous l'hypothèse que celles-ci soient démographiquement fermées. A partir des années 30, de nouveaux modèles directement dérivés de ces premiers modèles élargissent l'application de la CMR aux populations ouvertes. Il devient possible d'estimer la taille de populations qui varient dans le temps en considérant d'autres processus comme les migrations et la mortalité. Cependant, il faut attendre les années 60 pour voir apparaitre la formulation de modèles CMR plus complexes qui découplent explicitement le processus d'observation du processus démographique sous-jacent (Cormack 1964, Jolly 1965, Seber 1965). Le modèle dit de Cormack-Jolly-Seber réoriente l'utilisation de la méthode CMR non plus vers l'estimation de la taille de la population, mais vers l'étude des taux vitaux. Ce modèle pose les bases de nombreux outils statistiques utilisés jusqu'à nos jours pour estimer les paramètres démographiques en fonction du temps, de l'âge ou d'autres caractéristiques individuelles (Lebreton et al. 1992).

Le modèle de Cormack-Jolly-Seber a été généralisé par la suite pour prendre en compte différents états. Ces modèles dit multi-sites permettent d'étudier des dynamiques de transition entre des états de reproduction ou des localisations spatiales et de les associer à la survie des individus. Ces modèles correspondent à des modèles de Markov, la probabilité de transition vers un état au temps t+1 ne dépend que de l'état occupé au temps t. Les modèles utilisés au cours de cette thèse sont des modèles multi-évènements et font suite à une généralisation des modèles multi-sites (Figure 1.6). Les modèles multi-évènements permettent de prendre en compte l'incertitude dans les états auxquels appartiennent les individus (Pradel 2005). Dans notre cas, nous nous intéressons à des états biologiques liés au cycle de reproduction tel que le succès, l'échec et la non reproduction. L'appartenance d'un individu à un de ces états peut occasionnellement ne pas être connue avec certitude, par exemple lorsqu'un oiseau est observé en tant que reproducteur une année donnée sans que l'issue de la reproduction, succès ou échec, soit connue.

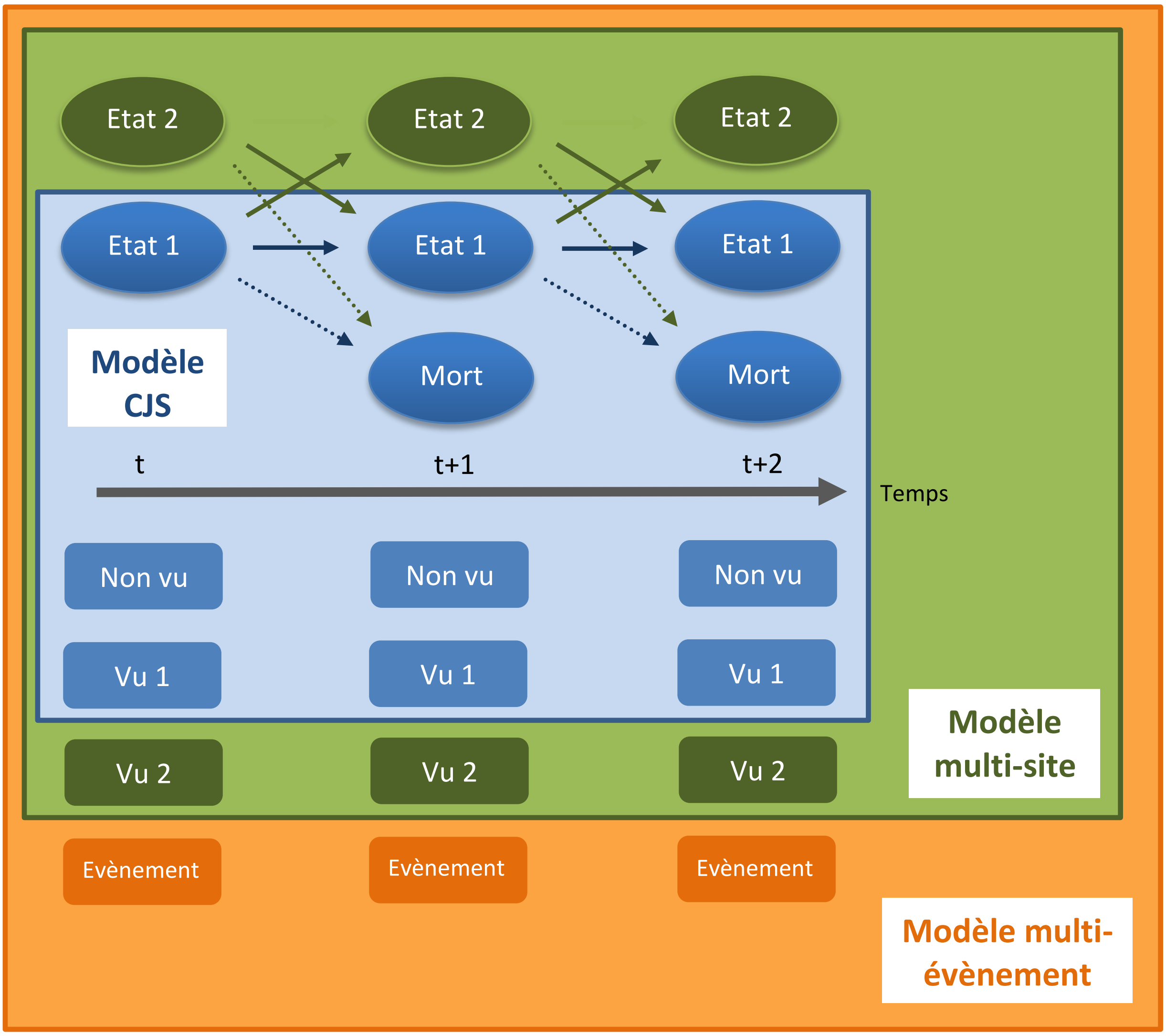

Figure 1.6 : Schéma présentant la généralisation du modèle de Cormack-Jolly-Seber (CJS) vers les modèles multi-sites et multi-évènements. Les états biologiques sont illustrés dans la partie supérieure de la figure par des ellipses. Les flèches symbolisent les processus biologiques c'est-à-dire les transitions entre ces états. Les processus d'observations sont représentés dans la partie inférieure par des rectangles.

Je ne présente pas plus en détails la structure et le fonctionnement de ces modèles qui nécessiteraient plusieurs pages de développement pour être abordé en profondeur. Pour une introduction générale à la modélisation capture-marque-recapture, les lecteurs intéressés peuvent se référer à l'ouvrage *Handbook of Capture-Recapture Analysis* de Amstrup et al. (2005).

CHAPITRE 2

Population density and climate effect on early-life demography

Crédit: Valentin Nivet-Mazerolles

- **Fay R**., Weimerskirch H., Delord K. and Barbraud C. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. **Journal of Animal Ecology**, 84:1423-1433.

- **Fay R**., Barbraud C., Delord K. and and Weimerskirch H. Contrasting effect of climate and population density over time and life-stages in a long-lived seabird. Accepted in **Functional Ecology**.

PARTIE 1 : Population density and climate shape early-life survival and recruitment in a long-lived pelagic

Abstract

1. Our understanding of demographic processes is mainly based on analyses of traits from the adult component of populations. Early-life demographic traits are poorly known mainly for methodological reasons. Yet, survival of juvenile and immature individuals is critical for the recruitment into the population and thus for the whole population dynamic, especially for long-lived species. This bias currently restrains our ability to fully understand population dynamic of long-lived species and life history theory.

2. The goal of this study was to estimate the early-life demographic parameters of a long-lived species with a long immature period (9-10 years), to test for sex and age effects on these parameters, and to identify the environmental factors encountered during the period of immaturity that may influence survival and recruitment.

3. Using capture-mark-recapture multi-event models allowing us to deal with uncertain and unobservable individual states, we analysed a long-term data set of wandering albatrosses to estimate both age and sex specific early-life survival and recruitment. We investigated environmental factors potentially driving these demographic traits using climatic and fisheries covariates and tested for density dependence.

4. Our study provides for the first time an estimate of annual survival during the first two years at sea for an albatross species (0.801±0.014). Both age and sex affected early-life survival and recruitment processes of this long-lived seabird species. Early-life survival and recruitment were highly variable across years although the sensitivity of young birds to environmental variability decreased with age. Early-life survival was negatively associated with sea surface temperature and recruitment rate was positively related to both Southern Annular Mode and sea surface temperature. We found strong evidence for density dependence mortality of juveniles. Population size explained 41% of the variation of this parameter over the study period.

5. These results indicate that early-life survival and recruitment were strongly age and sex-dependent in a dimorphic long-lived species. In addition, early life demographic parameters were affected by natal environmental conditions and by environmental conditions faced during the period of immaturity. Finally, our results constitute one of the first demonstrations of density dependence on juvenile survival in seabirds, with major consequences for our understanding of population dynamics in seabirds.

1 Introduction

Demographic processes have strong implications for both theoretical and applied research through life history theory on one hand and conservation biology and ecosystem management on the other hand. So far, most demographic studies focused on the vital rates of the adult component of populations (e.g. adult survival, fertility), whereas the vital rates of the immature component (e.g. juvenile survival, recruitment) have been manifestly less studied (Clutton-Brock, Albon & Guinness 1985; Quinn & Peterson 1996; Gaillard et al. 2000; Coulson et al. 2001), particularly in seabirds (Nevoux, Weimerskirch & Barbraud 2010). Yet, in long-lived species, younger age classes represent up to half of the total population and account for a large contribution to the total reproductive value and demographic stochasticity (Sæther et al. 2013). Thus, variations in vital rates of younger age classes are likely to have a high influence on the whole population dynamics and the rate of evolutionary change in long-lived species (Sæther et al. 2013). In addition, there is increasing evidence that conditions experienced in early-life may have long-term individual fitness consequences with important demographic and evolutionary effects (Lindström 1999; Gaillard et al. 2000; Metcalfe & Monaghan 2001; Monaghan 2008; Cam & Aubry 2011). Hence, our knowledge bias toward the adult compartment of populations currently restrains our ability to fully understand population dynamics of long-lived species and life history theory.

The lack of quantitative knowledge on demographic traits in the early-life of long-lived species is mainly due to methodological limitations. First, in most taxa such as insects, fishes or amphibians, juveniles are so small that they cannot easily be individually monitored. Only large vertebrates such as birds or mammals have sufficient size at independence to be tracked individually allowing estimation of juvenile survival. But even in this case, studying survival after young become independent from their parents is challenging since immature survival is typically low (Newton 1989) and highly sensitive to environmental variability (Gaillard & Yoccoz 2003) so that large sample sizes need to be monitored. Furthermore, juvenile dispersal if often higher than adult dispersal and juvenile mortality is commonly confounded with permanent dispersal, unless considerable large scale monitoring effort is undertaken, which is often not the case due to logistical constraints. Finally, although sex could affect both dispersal behavior (Clobert et al. 2001) and survival probability (Clutton-Brock et al. 1985), few studies controlled for offspring sex when estimating vital rates of younger age classes because of difficulties in determining offspring sex at independence before convenient molecular methods became available (Maness & Anderson, 2013).

At the interface between evolutionary and ecological processes, demographic traits in early-life may be affected both by natal conditions though parental care (Clutton-Brock 1991; Cam et al. 2003) and environmental variability encountered after independence (Sedinger, Flint & Lindberg 1995; Gaillard, Festa-Bianchet & Yoccoz 1998; Votier et al. 2008). Today, it is not clear whether environmental conditions between fledging and recruitment override the influence of conditions experienced during development. It is difficult to disentangle these two processes which probably interact with age (Cam & Aubry 2011). Identifying factors driving demographic traits in wild populations is especially challenging since it requires long-term data series without the possibility to control environmental parameters as for experimental studies. Furthermore, extrinsic factors such as climatic or anthropogenic variables may interact with intrinsic population processes, e.g. density dependence effects (e.g. Martínez-Padilla et al. 2014). Although intrinsic mechanisms may have a central role for the population dynamic of birds, affecting vital rates of the adult component (Barbraud & Weimerskirch 2003), density-dependence effects on early-life demographic traits has been little studied, especially for seabirds.

Although marine top predators such as seabirds and pinnipeds are convenient species for population demographic studies because they breed on discrete units, colonies, where large numbers of individuals can be tracked year after year given their high site fidelity, the study of their early-life demographic parameters implies coping with additional difficulties. Most seabirds do not breed until at least three years (Furness & Monaghan 1987; Gaston 2004), and for most species, juveniles are unavailable for detection remaining permanently at sea for several years before returning to breeding colonies (Warham 1990; Croxall & Rothery 1991). Consequently, our knowledge of vital rates in juvenile seabirds is very limited and was defined as a priority for seabird research (Lewison et al. 2012). Additionally, the status of the world’s seabirds has deteriorated rapidly over recent decades and has now become the most threatened group among birds (IUCN 2012). Thus, conservation management of seabirds requires new studies including the consideration of early-life stages (e.g. Finkelstein et al. 2010).

Here, we estimate the early-life demographic parameters of a seabird and investigate the environmental factors encountered during the period of immaturity that may influence survival and recruitment. We analysed mark-recapture data of 9685 known-age Wandering albatrosses (*Diomedea exulans*). In this long-lived species, the immature period is particularly long, lasting around 9-10 years (Weimerskirch 1992). Using capture-mark-recapture multi-event models (Pradel 2005) that allows dealing with unobservable states and age related recapture probability in early-life, we estimated early-life survival distinguishing the juvenile stage corresponding to the first two years at sea from later observable immature stages, as well as recruitment probability. Our models included both age and sex effects which are important factors to understand the demographic processes in long-lived species including wandering albatrosses (Barbraud & Weimerskirch 2012). We used climatic covariates and fisheries covariates to describe environmental conditions encountered by young animals and tested for density dependence on early-life demographic parameters.

Hypothesis and predictions

Prediction 1

According to the canalization theory, which predicts a stronger buffering against environmental stochasticity in the vital rates to which the population growth rate is the most sensitive (Gaillard & Yoccoz 2003), we expect juvenile survival to be more variable than adult survival and juvenile survival to be more affected by environmental variability.

Prediction 2

Theory predicts that when sexual size dimorphism occurs in birds and mammals, the larger sex may be more susceptible to food shortage after independence causing sex difference in juvenile mortality (Clutton-Brock et al. 1985; Kalmbach & Benito 2007). Wandering albatross present strong sexual size dimorphism when adult and at fledging, with males being in average 4% larger and 23% heavier than females, and juvenile males present faster growth rates and increased nutritional requirements than juvenile females (Weimerskirch, Barbraud & Lys 2000). We thus expect that juvenile survival was sex-specific, with lower survival probability for males.

Prediction 3

Wandering albatrosses suffer additional mortality through bycatch in longline fisheries (Brothers, Cooper & Lokkeborg 1999) and immature individuals appear to be captured in larger proportion than adults (Morant, Brooke & Abrams 1983; Gales, Brothers & Reid 1998). In addition earlier studies on wandering albatross populations have established negative relationships between population abundance and longline fishing effort (Croxall et al. 1990; Weimerskirch, Brothers & Jouventin 1997). We thus expect a negative effect of fishing effort on early-life survival.

Prediction 4

Juvenile seabirds are known to be less efficient foragers than adults and may be less able to compete with adults (Porter & Sealy 1982; Wunderle 1991; Daunt et al. 2007).

In addition for wandering albatrosses, decreasing age of recruitment has been reported simultaneously to declining breeding population size (Weimerskirch et al. 1997), suggesting density dependent recruitment as observed in others species when compensatory recruitment occurs after important breeder mortality (Pradel et al. 1997; Votier et al. 2008). We thus expect negative density dependence for early-life survival and annual recruitment rate.

2 Materials and Methods

2.1 Study species and site

We studied the wandering albatross population of Possession Island in the Crozet Archipelago (46°S; 52°E), southern Indian Ocean, from 1965 to 2012. Monitoring started in 1960, but all chicks were ringed each year with a stainless steel band just before fledging from 1965. The breeding cycle of this quasi-biennial species lasts almost one year, with pair formation in December, laying in early January, hatching of the egg in April and fledging of the chick in November (Tickell 2000). Clutch size is limited to one egg without replacement laying. There is no post-fledging care and the fledglings leave the colony alone remaining at sea continuously for the following 2 to 7 years (Weimerskirch 1992). Juvenile wandering albatrosses remain in the tropical and subtropical waters of the Indian Ocean with males moving more to the east than females (Weimerskirch et al. 2014). After 2 years at sea their range shifts southward, and young immature birds start to return to their natal colony before starting to breed when 6 year-old at the earliest (Weimerskirch 1992 and unpublished data). This population showed important changes in population size over the study period: with 500 breeding pairs in the 1960s, it declined steeply in the 1970s to reach 260 pairs in the mid-1980s, increased progressively to 380 pairs in the 2000s and declined slowly since then (Delord et al. 2008).

2.2 Field methodology

From early to mid-December, pre-breeding adults are checked over the whole island. From mid-January (just after egg laying is resumed) to mid-February at least 3 visits are made every 10 days to identify the two members of each pair and their breeding status. All new individuals are ringed with a uniquely-numbered stainless steel-band. In mid-April, June and August, nests are checked and the chick status recorded (alive/dead). During all visits, non-breeding individuals (mainly immatures) are searched for and their identity determined (from ring number) when possible. From mid-September to mid-October fledglings are ringed. Chicks that died on the colony between ringing and fledgling are noted during the first checks of the following breeding cycle and were excluded from our data set (0.3% of all individuals). Sex assignment methodology is given in supplementary materials (appendix A1).

2.3 General model

Individual encounter histories were modeled using a multi-event approach. The model consisted in 7 states, 1 immature state and 6 adult sates (Figure.1), and five events. To consider individuals during the period of immaturity, we defined the Pre-Recruitment state (PrR) after which immature birds can recruit, i.e. lay an egg for the first time into the breeding population. Adult birds can transit towards Successful Breeder state (SB), when the chick fledged, Failed Breeder state (FB), when the chick died before fledging, or recruited Non Breeder state (NB), when individuals that have recruited in the population (i.e. bred at least once) were observed as non-breeders at the colony. To model the sabbatical years spent continuously at sea, we added three unobservable states (Kendall & Nichols 2002; Lebreton & Pradel 2002) corresponding to the three previous adult states defined: Post Successful Breeder (PSB), Post Failed Breeder (PFB) and Post Non Breeder (PNB). Thus, adult which are at sea (i.e. not at colonies for a whole year), are distinguished based on their most recent breeding state, last time they were on a colony. In our study, state assignment was not always certain since between 1966 and 1986, state assessment was unknown for a number of breeders; some individuals were classified as breeders but the success or failure was not always ascertained. Multi-event models allowed us to deal with state uncertainty by assessing the likelihood of an individual state given the events (i.e. observations) (Pradel 2005). We considered five events, i.e. five types of observation in the field, 0 = “not observed”, 1 = “seen as non-breeder”, 2 = “seen as a failed breeder”, 3 = “seen as a successful breeder”, 4 = “seen as a breeder but successful status not ascertained”. Details of the parametrization of the general model can be found in appendix A2.

2.4 Environmental covariates

We used previous knowledge on seabird and wandering albatross ecology to select candidate covariates. Selected covariates included a large-scale climate index, the Southern Annular Mode (SAM), and a local climate index, the Sea Surface Temperature Anomaly (SSTA). Both have been linked to seabird demography (Barbraud et al. 2012), including in the wandering albatross (Weimerskirch et al. 2012). Long term effects of

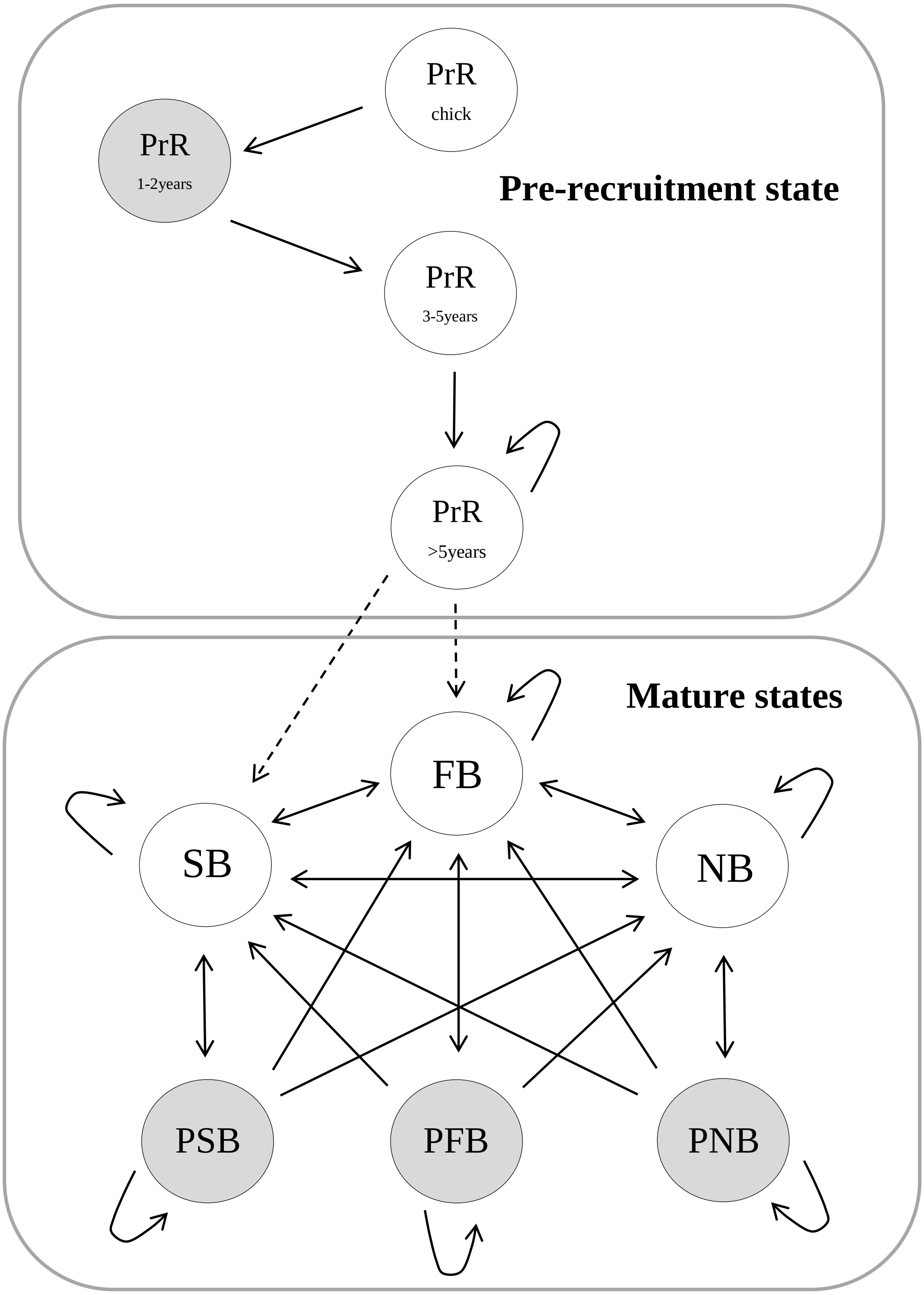

Figure 1 : Life cycle graph representing transitions between observable (white) or unobservable states (grey). As all birds are ringed as chicks, individuals start in the Pre-Recruitment state (PrR). After fledging, all birds remain at least two years continuously at sea and are thus unobservable. Pre-Recruitment state becomes observable from 3 years-old when birds start to return at the colony. Starting at 6-years-old, birds can transition into the breeding part of the population. This transition corresponds to recruitment and it is represented by the dashed arrows. Then mature birds irrespectively of age can make the transition between mature states: successful breeder (SB), failed breeder (FB), observable recruited non breeder (NB), post successful breeder (PSB), post failed breeder (PFB) and post observable recruited non breeder (PNB).

environmental conditions were assessed both with natal climatic conditions and with the breeding success of the colony (as a proxy for natal environmental conditions). Natal climatic conditions were considered during the chick rearing period (April-November), when parental investment, potentially affected by environmental fluctuations, could have a high impact on chick condition and future fitness components (Cam, Monnat & Hines 2003). Parental investment and foraging areas are sex-dependent in the wandering albatross (Weimerskirch et al. 2000). Thus, for natal SSTA we distinguished SSTA on the males' foraging grounds (SSTAma), SSTA on the females' foraging grounds (SSTAfe) and the SSTA on the foraging grounds of both sexes (SSTAma+fe) (see Figure A1). The impact of fishery activities on early-life survival was assessed using the numbers of hooks set as a proxy of fishing effort. To test for an effect of population density on pre-recruitment survival and recruitment, we used the number of breeding pairs observed annually at Possession Island as a covariate. More details on environmental covariates and their modelling are available in supplementary materials (appendix A3 and Figure A2). To make inference about temporal variability in early survival, we distinguished process variance from sampling variance as described in appendix A4.

3 Results

Goodness of fit tests ($\chi 2$ = 1003.4, df =749, P <0.001 for females and $\chi 2$ =1263.8, df =898, P <0.001 for males) indicated that the general JMV model did not fit the data correctly (see appendix A5 and Table A1 for detailed comments). We thus used a variance inflation factor ($\hat{c} = 1.37$) for model selection. As the general model included age effects, our model selection is conservative since these age effects accounted for a part of the variation not captured by the JMV model. Results indicated that early-life survival and recruitment probability were influenced by both age and sex (Table A2), showing high variability across years although the sensitivity of young birds decreased with age. Our study suggests that these variations could be explained both by climate and population density.

In early-life, both sexes showed a progressive increase in survival until 9-13 years, followed by a strong decrease after this age (Figure 2). The annual average juvenile survival during the first two years of life was 0.801±0.014 (0.770±0.020 for males and 0.829±0.025 for females), with consistent variations between cohorts over the study period following a quadratic pattern for both sexes (Figure 3). For the 3-8 age-class, sex differences in annual survival were reversed with males having higher

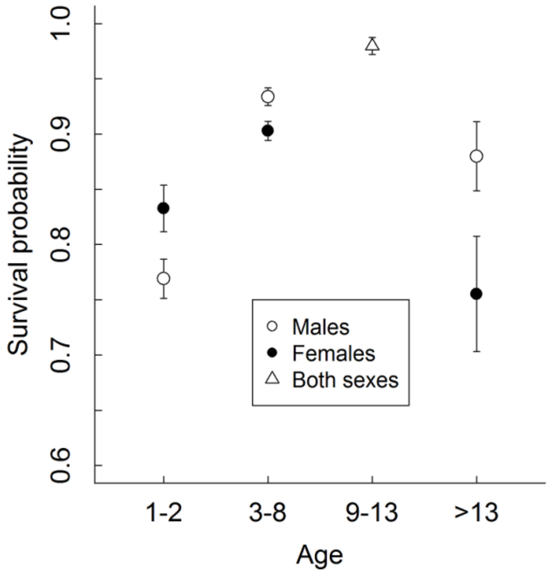

Figure 2 : Pre-recruitment survival estimates (±SE) as a function of age and sex for the wandering albatross population of Crozet. Open and filled dots correspond to males and females respectively. Open triangles correspond to the sex-independent parameter according to model selection. Estimates came from model 4 (Table A2).

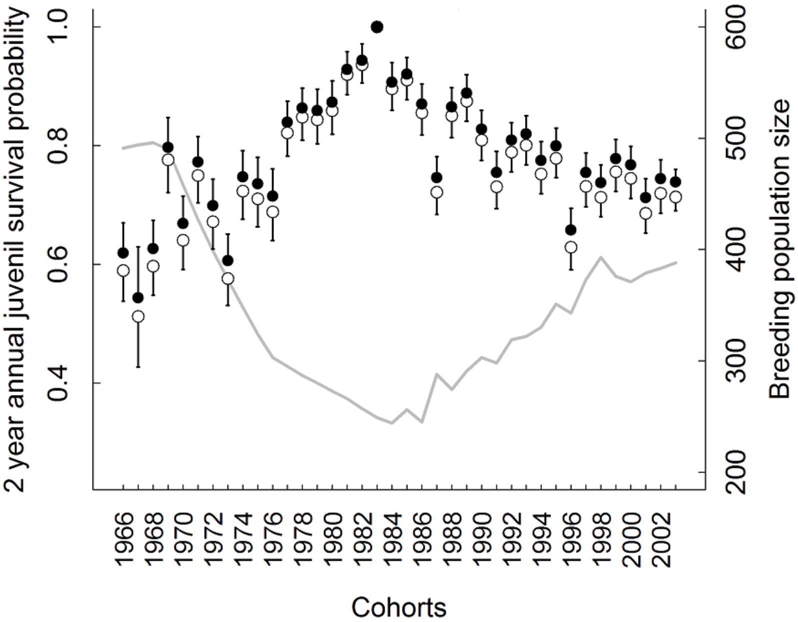

Figure 3 : Cohort-specific first 2-year annual juvenile survival and breeding population size (grey line, expressed as the number of breeding pair) from 1966 to 2002 of the wandering albatross population of Crozet. Open and filled dots correspond to males and females respectively. Survival estimates (±SE) came from model 10 (Table A2).

Table 1 : Relative process variances and SD of first 2-year juvenile survival and immature survival parameters for wandering albatrosses from Crozet Island from 1965 to 2012.

Age class	Estimate	Relative Process Variance	Relative Process SD
1-2 years	0.801±0.016	0.058	0.240
3-8 years	0.918±0.007	0.013	0.116
9-13 years	0.980±0.009	-0.111	0

survival than females (Figure 2). The 3-8 year-old immature survival was not related to birth cohort (Table A2, M8 vs M6, ΔQAIC=60) but showed interannual variations which were similar between sexes (Table S2, M7 vs M8, ΔQAIC=70).Between 9 and 13 years old, survival probability reached 0.980±0.008 without difference between sexes and remained stable over the study period (Table A2, M3 vs M4, ΔQAIC=1.5). After 13 year-old survival of individuals that had not yet recruited declined to 0.876±0.036 for males and 0.768±0.061 for females.

Model selection suggested that in early-life, survival temporal variability stabilized progressively with age. Time effect was strongly supported for the juvenile stage (ΔQAIC =153), weakly supported for the 3-8 year-old class (ΔQAIC=2), and not supported for older individuals. In accordance with this result, relative process variance decreased gradually with age (Table 1). Variation of juvenile survival was strongly related to natal environmental conditions. Breeding population size the year of birth was negatively related to juvenile survival, explaining 41% of the variation of this parameter over the study period (Table 2, M1, Figure 3). Additionally, we found an additive negative effect of SSTA on the male adults foraging grounds on juvenile survival which explained 6% of the total variation (Figure A3a). Neither SSTA on the female foraging grounds nor the global SSTA on the foraging grounds of both sexes were significantly related to juvenile survival (Table 2, Ftestcst/co/t=1.39 and 1.45 respectively, p-value>0.20). None of the other covariates had a statistically significant effect on juvenile survival (Table 2, p-value>0.15). The best model for the 3-8 year-old class retained a significant but weak effect of SSTA (Table 2, Ftestcst/co/t=3.10, p-value=0.05). This climatic covariate was negatively related to 3-8 year-old survival and explained 8% of the total variation (Table 2, M12). We did not find evidence for an impact of any other covariates on the 9-13 year-old class survival. Due to small sample sizes, we could not test whether survival variations for the oldest age-class were time or covariate dependent.

Table 2 : Testing for the effects of covariates on pre-recruitment survival and recruitment probability for wandering albatrosses from Crozet Island from 1965 to 2012. Results include the relative deviance corrected by the overdispersion factor (QDev), the statistic Ftestcst/co/t testing the null hypothesis that the focal climatic covariate has no effect on survival, the percentage of variation explained by the covariates (r^2) and the slope±SE. All covariates were standardized. * indicates one-sided tests (p-value / 2) since we expected bycatch to increase with fishing effort and thus to be negatively related to survival. Models with statistically significant covariate effects at the level of 5% are in bold characters.

No.	Pre-recruitment survival	QDev	F	p-value	r^2	slope
		1-2 years old class				
1	**N**	**80328.01**	**25.63**	**<0.001**	**0.41**	**-0.41±0.05**
2	N+SAM	80326.95	0.35	0.71	0.41	
3	N+SSTA	80327.35	0.22	0.80	0.41	
4	N+fishing effort	80326.74	0.42	0.33*	0.41	
5	N+SAMnatal	80327.79	0.07	0.93	0.41	
6	N+SSTAfe	80323.96	1.39	0.26	0.43	
7	**N+SSTAma**	**80315.15**	**4.78**	**0.01**	**0.47**	**-0.21±0.06**
8	N+SSTAfe+ma	80323.76	1.45	0.24	0.43	
9	N+BS	80322.80	1.80	0.17	0.43	
		3-8 years old class				
10	N	80289.82	1.26	0.29	0.03	
11	SAM	80290.89	0.72	0.49	0.02	
12	**SSTA**	**80286.39**	**3.10**	**0.05**	**0.08**	**-0.20±0.07**
13	Fishing effort	80290.51	0.91	0.20*	0.02	
14	N+SAMnatal	80292.09	0.70	0.50	0.03	
15	N+SSTAfe	80292.31	0.12	0.89	<0.01	
16	N+SSTAma	80292.35	0.01	0.99	<0.01	
17	N+SSTAfe+ma	80292.10	0.67	0.52	0.03	
18	N+BS	80292.35	0.01	0.99	<0.01	
		9-13 years old class				
19	N	80214.07	0.67	0.42	0.02	
20	SAM	80213.79	1.45	0.24	0.04	
21	SSTA	80214.04	0.76	0.39	0.02	
22	Fishing effort	80213.40	2.52	0.06*	0.07	
23	N+SAMnatal	80214.25	0.16	0.85	<0.01	
24	N+SSTAfe	80214.26	0.13	0.87	<0.01	
25	N+SSTAma	80213.71	1.30	0.30	0.07	
26	N+SSTAfe+ma	80214.31	0.05	0.95	<0.01	

Table 2 continued : Testing for the effects of covariates on pre-recruitment survival and recruitment probability for wandering albatrosses from Crozet Island from 1965 to 2012. Results include the relative deviance corrected by the overdispersion factor (QDev), the statistic Ftestcst/co/t testing the null hypothesis that the focal climatic covariate has no effect on survival, the percentage of variation explained by the covariates (r^2) and the slope±SE. All covariates were standardized. * indicates one-sided tests (p-value / 2) since we expected bycatch to increase with fishing effort and thus to be negatively related to survival. Models with statistically significant covariate effects at the level of 5% are in bold characters.

No.	Recruitment	QDev	F	p-value	r^2	slope
28	**SSTA**	**80245.87**	**11.59**	**<0.001**	**0.28**	**0.28±0.05**
29	**SAM**	**80276.66**	**3.10**	**<0.001**	**0.10**	**0.16±0.05**
30	detrendedSAM	80276.55	0.02	1	0.01	
31	**N**	**80224.75**	**12.28**	**<0.001**	**0.41**	**0.33±0.03**
32	N+SAMnatal	80292.34	<0.01	1	<0.01	
33	N+SSTAfe	80292.23	0.03	1	<0.01	
34	N+SSTAma	80292.36	0	1	0	
35	N+SSTAfe+ma	80291.70	0.17	1	<0.01	
36	N+BS	80292.33	<0.01	1	<0.01	

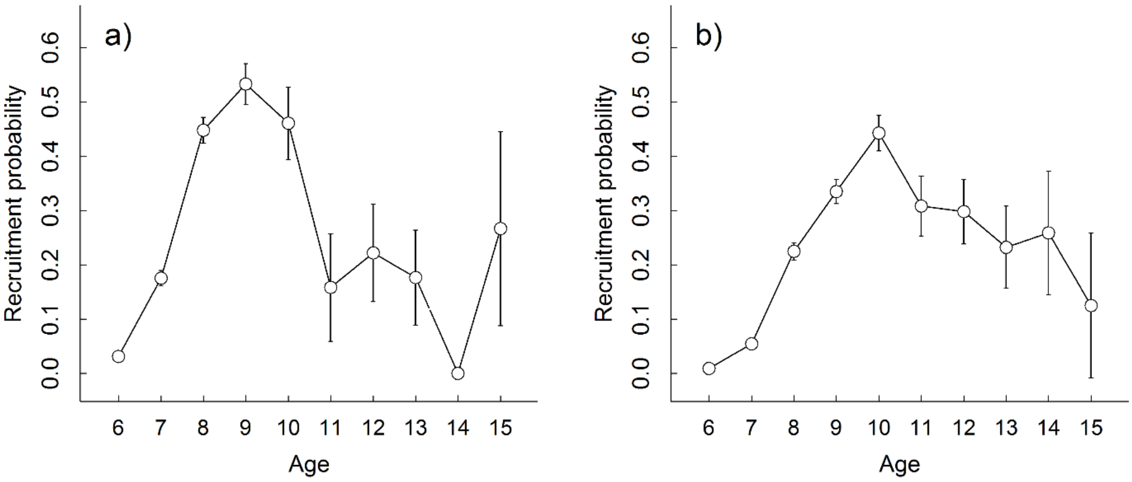

Figure 4 : Estimates of age-specific probability of recruitment for females (a) and males (b) of the wandering albatross population of Crozet. Estimates (±SE) came from model 15 (Table A2).

Concerning recruitment, females bred earlier than males. At 9 year-old the probability to be recruited was 80% for females whereas it was only 50% for males (Figure A4). Nevertheless, the probability to be recruited at age 15 was very similar between sexes reaching 95%. Both sexes showed increasing recruitment probability from 6 to 10 year-old and a decrease in recruitment probability at older ages (Figure 4).Constraining the recruitment probability to be constant after 10 years improved significantly our model reducing the AIC of 14 points, probably due to large SEs resulting from the smaller sample size of these ages. To assess the relationships between recruitment and the covariates we used this more parsimonious model structure. Results suggest that recruitment was not limited by population density since recruitment probability was positively correlated to breeding population size (Table 2, M25, slope=0.33±0.03). SSTA was positively related to the probability to start to breed, explaining 28% of the variation of recruitment rate (Table 2, M28). We found an additive positive effect of SAM (Figure A3c). However, SAM presented a linear temporal trend as did our estimated recruitment rate between 1982 and 2000 (Figure 5). After removing the linear trend from SAM using the residual regression technique and reanalyzing the relationship between recruitment rate and this climatic covariate, the SAM effect was no longer significant (Table 2, M24, Ftestcst/co/t=0.02, p-value=1).

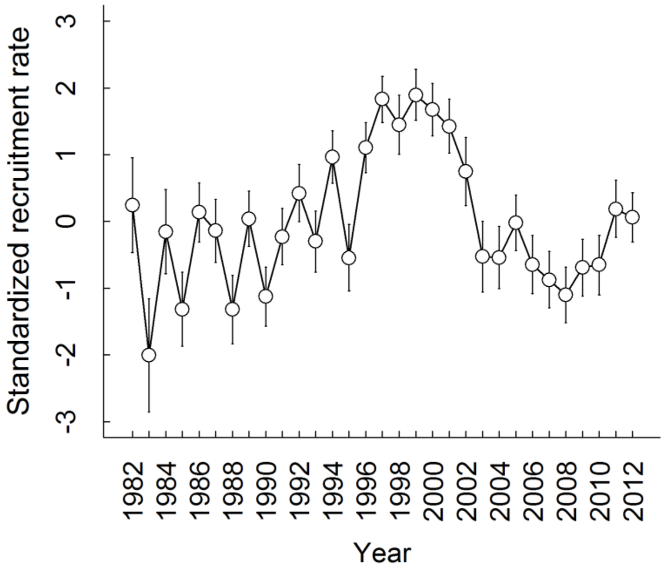

Figure 5 : Recruitment rate between 1982 and 2012 of the wandering albatross population of Crozet. The proportions of new recruits are expressed as standardized difference from the average recruitment rate. Estimates (±SE) came from model 19 (Table A2).

4 Discussion

This study demonstrated that sex, population density and climatic conditions can strongly influence survival during early-life, and to a lesser extent recruitment, of a long-lived marine top predator. In addition it provides for the first time an estimate of juvenile survival (during the first two years at sea) for an albatross species.

4.1 Early-life survival

Previous studies in mammals and birds suggested that most of the mortality between fledging and recruitment occurs during the first months of life (Gaillard et al. 2000; Naef-Daenzer, Widmer & Nuber 2001; Martìn et al. 2007; Riotte-Lambert & Weimerskirch 2013). This pattern has been linked to progressive improvement of flight abilities and foraging skills in early-life (Marchetti & Price 1989; Thornton & Clutton-Brock 2011). In wandering albatrosses, juvenile survival over the first two years of life was 0.64 (annual survival of 0.801), which is one of the highest values of early-life survival estimated for a bird species, but still lower than adult survival. Given that long-distance natal dispersal is very rare in this highly phylopatric species (Inchausti & Weimerskirch 2002; Charmantier et al. 2011), we are confident that our apparent survival estimates are close to the true survival probabilities.

As predicted, we found that juvenile survival was highest for females. Male wandering albatrosses which are structurally larger and heavier than females could be more sensitive to starvation during this critical step of independence due to their higher food requirements for self-maintenance (Clutton-Brock et al. 1985). Males of larger size at fledging are those that better survive, whereas females in better body condition survive better (Weimerskirch et al. 2000). However, after the juvenile stage, the sex difference in survival was surprisingly reversed. Different hypotheses could explain this pattern. First, it could be the result of a selective process. Indeed, sex-specific juvenile mortality potentially removed disproportionately low quality individuals according to genders during the first year at sea, providing more high quality males than females in older age classes. Nevertheless, this hypothesis suggests that such survival shifts between sexes during early-life would be regularly observed in wild populations, which is not currently supported by the literature. On the other hand, immature birds show sex-specific distributions at sea with male wandering albatrosses from Possession Island moving more to the east of the southern Indian Ocean than females (Weimerskirch et al. 2014). Thus, environmental conditions experienced by immature individuals could be different between sexes and females may experience less favorable climatic and trophic conditions than males. Non exclusively, immature females could be more exposed to long line fisheries with associated bycatch mortality due to different overlap with fisheries or different susceptibility (Barbraud & Weimerskirch 2012), as it has been suggested to explain higher male survival in adults due to their differential overlapping distribution with fisheries at sea (Weimerskirch et al. 1997).

Early-life survival increased with age and reached adult survival value at 9 years. As predicted by the environmental canalization theory (Gaillard & Yoccoz 2003), survival stabilized progressively against temporal variability with aging. In 3-8 year-old individuals, immature survival appeared less variable than juvenile survival and we did not detect a delayed effect of natal conditions on immature survival. However, we observed a decrease in immature survival after 13 year-old. This decrease may be due to individual heterogeneity (Vaupel & Yashin 1985; Cam & Aubry 2011). Birds that have not yet recruited after 13 years are probably individuals of lower quality. Although very few studies estimated age specific survival during early-life in interaction with breeding status by distinguishing non-recruited from recruited individuals, declining survival associated with late recruitment could be a common pattern in long-lived species.

In contrast with adult survival which was not affected by climatic covariates (Rolland, Weimerskirch & Barbraud 2010), we detected significant correlations between environmental covariates and survival of young birds. Juvenile survival appeared highly related to conditions at sea during chick rearing. We found that SSTA on the males' foraging grounds during breeding was negatively related to future juvenile survival. SSTA anomalies are widely used as an indicator of food availability for seabirds, and high SSTA may negatively affect food resources favouring more stable density stratification of the water column associated with a strong decrease in net primary production (Behrenfeld et al. 2006). Thus, during positive SSTA years, breeders may face low abundance of food resources. This would reduce food provisioning to the chick, which may be in poorer body condition at fledging, compromising their survival. Concordant results have been provided in the yellow-nosed albatross *Thalassarche carteri*. In this species, positive SSTA have been related to increasing foraging trip duration, affecting negatively the provisioning rate of adults to their chick, with negative effects on chick body condition at fledging (Weimerskirch, Zimmermann & Prince 2001). Additionally, the ability of wandering albatrosses to increase their foraging effort may be limited by the unpredictability of their foraging success due to the extreme scattered distribution of their food resources (Weimerskirch, Gault & Cherel 2005). Male wandering albatrosses provision more food to their offspring than females (Weimerskirch et al. 2000). Our study supported the main role of male parental investment since the relationship between SSTA and juvenile survival was only found for adult males' foraging grounds. Early-life survival seemed to be more affected by natal environmental conditions since we did not detect an influence of the climatic conditions encountered during the first year of life at sea on juvenile survival. As found in other long-lived species, survival in early-life might be more strongly related to the initial conditions rather than to the severity of environmental conditions after independence (Gaillard et al. 2000; Reed et al. 2003; Beauplet et al. 2005).

Three to eight year-old immature survival was negatively related to SSTA on their foraging grounds. This effect was again consistent with the literature since most of the relationships between SSTA and seabird demographic parameters in the Southern Ocean are negative owing to unfavorable effect of warm water temperature on food resources (Barbraud et al. 2012). Finally, the effect of SSTA on 1-2 year-old and 3-8 year-old individuals was similar with no significant difference between slope estimates (z-test = 0.128, p = 0.898).

Contrary to expected, we found no effect of long line fishing effort on juvenile and immature survival variations. Barbraud et al. (2012) reported that 24% of studies (n=33) investigating the effects of fisheries activities in the Southern Ocean on seabird demography focusing mainly on the mature state found no significant relationship. Several hypotheses could explain this surprising result. First, our assumption of proportionality between bycatch rates and fishing effort may be false. This could be due to the implementation of mitigation measures to reduce albatross bycatch in long line fisheries, in which case fishing effort would become independent of bycatch rates. However, preventive measures to reduce seabird mortality in longline fisheries occurred mainly in Antarctic and sub-Antarctic waters whereas young albatrosses remained in sub-tropical waters and thus did not benefit from mitigation measures. Second, we cannot exclude that our analysis using fishing effort data was biased due to the varying quality of fishing effort data that we could not control. Finally, young albatrosses could interact less with fishing vessels than previously expected. In contrast to our results, studies conducted on the adult component of this population reported a negative relationship between survival and fishing effort (Rolland et al. 2010). Young albatrosses might be excluded from longline fishing vessels by older individuals since they are probably less competitive (Morant et al. 1983, Weimerskirch et al. 1997).

4.2 Recruitment

As documented in other species, the recruitment process seemed highly influenced by current environmental condition without persistent observable effects of natal conditions (Reid et al. 2003; Stauffer, Rotella & Garrott 2013). In contrast to survival, the highest recruitment rate was associated with warmer sea surface temperatures during the previous year. This relatively strong relationship (r^2=28%) was difficult to interpret since it is generally expected that positive SSTA depress food resources and thus affect negatively demographic traits, and studies that reported negative relationships between SSTA and survival reported the same effect on recruitment probabilities (Votier et al. 2008; Oro et al. 2010). Yet, similarly to our findings, studies on the black-browed albatross *Thalassarche melanophrys* found opposite associations between survival and recruitment for the same climatic variable (Nevoux, Weimerskirch & Barbraud 2007; Nevoux et al. 2010). Although wandering albatrosses are sexually mature at age 6 years (Hector, Croxall & Follett 1986), and some breed at this age in our population, most individuals recruit several years later. As suggested for survival, decreasing recruitment probabilities beyond 10 year-old were probably the result of individual heterogeneity with accumulating low quality non-recruited birds at later age.

4.3 Density dependence

Density dependent mortality has been found in terrestrial mammals and birds (Durell et al. 2000; Gaillard et al. 2000) but was rarely documented in seabirds and marine mammals (Frederisken & Bregnballe 2000; Barbraud & Weimerskirch 2003; Rotella et al. 2009). Although adult survival and reproductive parameters (i.e. breeding and success probability) in this albatross population appeared density independent (Rolland 2009), our study suggested that juvenile survival was strongly density dependent with a clear negative relationship between breeding population size the year of birth and juvenile survival. These results support the paradigm of Eberhardt (Eberhardt 2002), suggesting that in long-lived species, juvenile survival is the first parameter affected by increasing population density. The effect of breeding population was restricted to very early-life since immature survival was not affected, and was nearly 2 times stronger than the effect of natal SSTA (significant difference between slope estimates: z-test = 3.123, $p = 0.002$). Two different processes may explain density dependence in this species. First, juvenile survival could be affected by parental investment variations depending on intraspecific competition for food during the breeding season. In seabirds, foraging competition among breeders may be important, affecting colony distribution (Furness & Birkhead 1984) and foraging trip duration (Lewis et al. 2001). In long-lived species, life-history theory predicts that breeders minimize their energetic costs to preserved future breeding attempts (Stearns 1992). Thus, in cases when increasing breeding population size implies a higher foraging effort, parents may shunt this additional cost on their chick, reducing chick food supply, with negative consequences on the chick condition at fledging and its subsequent survival probability. In agreement with this expectation, Gaston, Chapdelaine & Noble (1983) showed that mass at fledging of thick-billed murre *Uria lomvia* chicks was negatively related to colony size. An alternative, but non-exclusive, hypothesis is that juvenile albatrosses may suffer from direct competition during early-life at sea. Recent studies on spatial ecology at sea revealed that offshore competition among seabirds may be an active process with strong consequences on populations, and juveniles could be more affected by competition than older birds (Navarro et al. 2010). Indeed, juveniles are known to be less efficient foragers than adults suggesting that they may be less competitive (Daunt et al. 2007; Riotte-Lambert & Weimerskirch 2013). For wandering albatrosses, the overall range of juvenile at sea is mainly situated in sub-tropical waters at lower latitudes than the adult range (Weimerskirch et al. 2014). These differences in spatial distribution may be the result of selective pressures to avoid competition.

Results did not support density dependence for recruitment rate. Indeed, we found a positive relationship between annual variation in the number of recruits and the breeding population size. Thus, it appears the effects of density-dependence are limited to the first step in the sequence of changes in vital rates as population density increases as proposed by Eberhardt (2002). In colonial birds, a negative influence of breeders' density on recruitment probability was reported in a handful of species (Pradel et al. 1997; Tavecchia et al. 2007). Thus, it is likely that the population size of wandering albatrosses of Crozet was below the threshold for which density dependence recruitment may occur. Indeed, present numbers (350 pairs) are much lower than the original population size in the 1960s (500 pairs) (Delord et al. 2008).

5 Conclusion

To conclude, we found that early-life demographic traits were sex-specific, highly sensitive to environmental variability and stabilized progressively with aging, as predicted by the life-history theory. Our study provided strong evidence for density dependence in juvenile survival in a pelagic seabird. This result has important consequences for our understanding of population dynamics in seabirds. Indeed, the effects of population density and climate factors on juvenile survival are generally not considered explicitly into projection population models for seabirds and other long-lived species (e.g. Finkelstein et al. 2010) whereas our results demonstrate that the juvenile compartment may be strongly impacted by population density and climate fluctuations. Including the effects of density into projection population models will have important consequences on the projected population growth rates and trajectories (Caswell 2001). Furthermore, the mechanisms proposed here to explain this density effect are not restricted to albatross species suggesting that density dependent juvenile mortality may occur across a higher number of seabird species than currently suspected.

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PARTIE 2 : Contrasting effect of climate and population density over time and life-stages in a long-lived seabird.

Abstract

1. Although population responses to environmental variability have been extensively studied for many organisms, few studies have considered early-life stages owing to the inherent difficulties in tracking the fate of young individuals. However, young individuals are expected to be more sensitive to environmental stochasticity owing to their inexperience and lower competitive abilities. Thus, they are keys to understand demographic responses of an age-structured population to environmental variability.

2. In this study, we used capture-recapture modelling, based on a 49 year-long individual-based longitudinal monitoring dataset, to investigate climatic and population density effects on immature demographic parameters in a long-lived seabird, the wandering albatross.

3. We provide evidence that climate and population size affected both survival and recruitment age of young individuals although in different ways according to the trait. We found that early-life survival was mainly affected by population density, whereas recruitment age variation appeared to be better explained by climatic conditions, with a surprising long-term effect of climate. While population size explained 60% of the variation in juvenile survival, average Southern Annular Mode over the five previous years explained 52% of variation in recruitment age.

4. Additionally, although early-life survival was consistently negatively affected by population size, the relationship between recruitment age and population size shifted from negative to positive over time from the 1970s to 2000s, showing that density dependence mechanisms can temporarily disappear.

5. Finally, we found that similar climatic conditions may affect individual performances in opposite ways according to the life stage of individuals. This result underlines the critical need to assess age specific functional responses to environmental variability to allow accurate demographic predictions. By revealing the poorly known demographic process of younger age classes, the results of this study improve our understanding of population dynamics of long lived marine species.

1 Introduction

The impacts of global change are now well documented for several levels of biological organization from individual to ecosystem scales (Vitousek 1994; Walther et al. 2002; Parmesan 2006; Dillon, Wang & Huey 2010). At the population level, variation in demographic rates have been related to climatic and anthropogenic perturbations for diverse animal and plant populations (Coulson 2001; Grosbois et al. 2008; Inouye 2008; Barbraud et al. 2012). However, most of these studies focused on the vital rates of the adult component of populations (e.g. adult survival, fertility), whereas the demographic sensitivity of the immature component to climate perturbations (e.g. juvenile survival, recruitment) has been less widely investigated (Coulson 2001; Nevoux, Weimerskirch & Barbraud 2010; Dybala et al. 2013). However, younger age classes are generally more sensitive to environmental variation (Gaillard et al. 2000; Oro et al. 2010; Pardo et al. 2013) owing to their inexperience and lower competitive abilities (Wunderle 1991; Sol et al. 1998). Thus, to fully understand the effects of climatic change on age-structured populations and to be able to establish sound predictions from population models, the effects of environmental variability on the vital rates of the immature component of populations need to be considered. Because younger age classes represent a significant part of the population and account for a large contribution to the total reproductive value and demographic stochasticity (Sæther et al. 2013), early life stages are particularly important for long lived species.

Although there is an increasing need to predict a population’s responses to climate change for conservation purposes, investigating relationships between demographic processes and environmental conditions remains challenging for at least 4 reasons. First, such studies require long-term datasets which are difficult to run and maintain (Clutton-Brock & Sheldon 2010). Second, studies focusing on young individuals raise additional challenges since survival of early-life stages is typically low (Newton 1989) and accompanied by a high dispersal probability (Clobert et al. 2001). Estimating early-life survival under such constraints requires both large sample sizes and large scale monitoring over extended periods. Third, studying the relationships between population dynamics and environmental variation is often difficult owing to the simultaneous effects of different ecological factors (Gaillard et al. 2000; Constable et al. 2014). At the same time, studies based on the monitoring of wild populations cannot experimentally control environmental parameters. Intrinsic factors, such as density dependence, may also interact with external climatic constraints leading to complex ecological interactions (Coulson 2001). Finally, generalization of the results obtained from one population is often difficult since different populations of the same species may respond differently to the same environmental variation due to locally specific responses to environmental changes and complex ecological interactions (Walther et al. 2002; Constable et al. 2014).

Seabirds are frequent model species for biological population studies due to practical reasons, i.e. they breed in large colonies distributed in discrete units and show high site fidelity. However, while there are evidences that climate change can affect their abundance (Croxall, Trathan & Murphy 2002; Weimerskirch et al. 2003), the underlying demographic processes at the individual scale remain often unknown, in particular for the immature component. When compared to adult vital rates, juvenile traits have been much less well studied (Jenouvrier 2013; Oro et al. 2014). Since young individuals have an important impact on demographic variability in long-lived species (Sæther et al. 2013), understanding causal demographic mechanisms at the individual scale including all life stages is essential to predict future population trends in response to climate change. Seabirds are today one of the most threatened group among birds (IUCN 2014), and the improvement of our knowledge on juvenile vital rates has been defined as a priority for seabird research (Lewison et al. 2012).

In this article we investigated the climatic effects on immature demographic parameters in a long-lived seabird, the wandering albatross *Diomedea exulans*. An individual based study of 9685 birds, conducted on the Crozet Islands (Southern Indian Ocean) since 1965, allowed us to estimate early-life survival and age of first reproduction. The climate in the Southern Ocean is rapidly changing (Pendlebury & Barnes-Keoghan 2007) impacting seabirds and marine mammal populations (Weimerskirch et al. 2003; Constable et al. 2014). Previous studies have investigated climate effects on adult performances in the wandering albatross (Rolland, Weimerskirch & Barbraud 2010; Weimerskirch et al. 2012). However, very few focused on immature individuals and relationships with climatic factors remain equivocal (Fay et al. 2015). Using capture-mark-recapture modelling, we investigated the impact of climate and population density on early-life demographic traits (i.e. survival and recruitment age) testing for both linear and quadratic relationships and interactions between climate and population size. Our models controlled for age, sex and density dependence since all these factors are important to understand demographic processes of immature wandering albatrosses (Fay et al. 2015).

2 Materials and Methods

2.1 Study species and site

The wandering albatross population of Possession Island in the Crozet Islands (46°S; 52°E), southern Indian Ocean, has been monitored from 1960, and annual mark-recapture studies started in 1965. From 1965, chicks were ringed each year with a stainless steel band just before fledging. The breeding cycle of this quasi-biennial species lasts almost one year, with pair formation in December, laying in early January, hatching of the egg in April and fledging of the chick in November (Tickell 2000). Clutch size is limited to one egg without replacement laying. There is no post-fledging care and the fledglings leave the colony alone at the age of 9 months, remaining at sea continuously for the following 2 to 7 years (Weimerskirch 1992). Juvenile (aged 1-2 years) wandering albatrosses remain in the tropical and subtropical waters of the Indian Ocean (Weimerskirch et al. 2014). After 2 years at sea their range shifts southward, and young immature birds start to return to their natal colony before starting to breed when 6 year-old at the earliest (Weimerskirch 1992 and unpublished data). This population showed important changes in population size over the study period. From 500 breeding pairs in the 1960s it declined steeply in the 1970s to reach 240 pairs in the mid-1980s, and then increased progressively to 380 pairs in the 2000s with a subsequent decline thereafter (Delord et al. 2008).

2.2 Field methodology

From early to mid-December, pre-breeding adults were monitored across the whole island. From mid-January (just after egg laying) to mid-February at least 3 visits were made every 10 days to identify breeding pairs and their status. All new individuals were ringed with a uniquely-numbered stainless steel-band. In mid-April, June and August, nests were checked and the chick status recorded (alive/dead). During all visits, non-breeding individuals (mainly immatures) were searched for and their identity determined (from ring number) when possible. From mid-September to mid-October fledglings were ringed. Chicks that died on the colony between ringing and fledgling were noted during the first checks of the following breeding cycle and were excluded from our data set (0.3% of all individuals). Sex assignment was carried out as described in the supplementary materials (appendix A1).

2.3 General model

Individual encounter histories were modeled using a multi-event approach. The model comprised 7 states consisting of 1 immature state, 5 adult states and the state dead (Figure 1), and five events. To consider individuals during the period of immaturity, we defined the Pre-Recruitment state (PrR) after which immature birds can recruit, i.e. lay an egg for the first time into the breeding population. Adult birds can transit toward Successful Breeder state (SB), when the chick fledged, Failed Breeder state (FB), when the egg or chick are lost before fledging, or recruited Non Breeder state (NB), when individuals that have recruited in the population (i.e. bred at least once) were observed as non-breeders at the colony. To model the sabbatical years spent continuously at sea after reproduction, we added two unobservable states (Lebreton & Pradel 2002), corresponding to the two previous breeding states defined: Post Successful Breeder (PSB) and Post Failed Breeder (PFB). Thus, adults that are at sea (i.e. not at colonies for a whole year) are distinguished based on their most recent breeding state last time they were at a colony. In our study, state assignment was not always certain since between 1966 and 1986, state assessment was unknown for a number of breeders; some individuals were classified as breeders but the success or failure was not always ascertained. Multi-event models allowed us to deal with state uncertainty by assessing the likelihood of an individual state given the events (i.e. observations) (Pradel 2005). We considered five events, i.e. five types of observation in the field, 0 = “not observed”, 1 = “seen as non-breeder”, 2 = “seen as a failed breeder”, 3 = “seen as a successful breeder”, 4 = “seen as a breeder but successful status not ascertained”. Details of the parametrization with the biological constraints applied can be found in appendix B1. Capture-recapture modeling does not allow the direct estimation of the average age of first reproduction for each year. Thus, variation in the age of first reproduction was estimated indirectly through the probability of early recruitment (ψ^{early}). Early recruitment was defined as the first reproduction occurring before or equal to 8 year-old females and 9 year-old for males, corresponding approximately for both sexes to the average age of first reproduction (Fay et al. 2015).

2.4 Density dependence and climate variables

Juvenile survival was modelled as a function of population size since a recent study revealed that this parameter was strongly density dependent (Fay et al. 2015). For the recruitment process, the relationship with population size was more equivocal. Weimerskirch, Brothers & Jouventin (1997) reported decreasing age at first reproduction simultaneously to declining breeding population size, whereas a recent study, including additional years, concluded that the recruitment process was currently

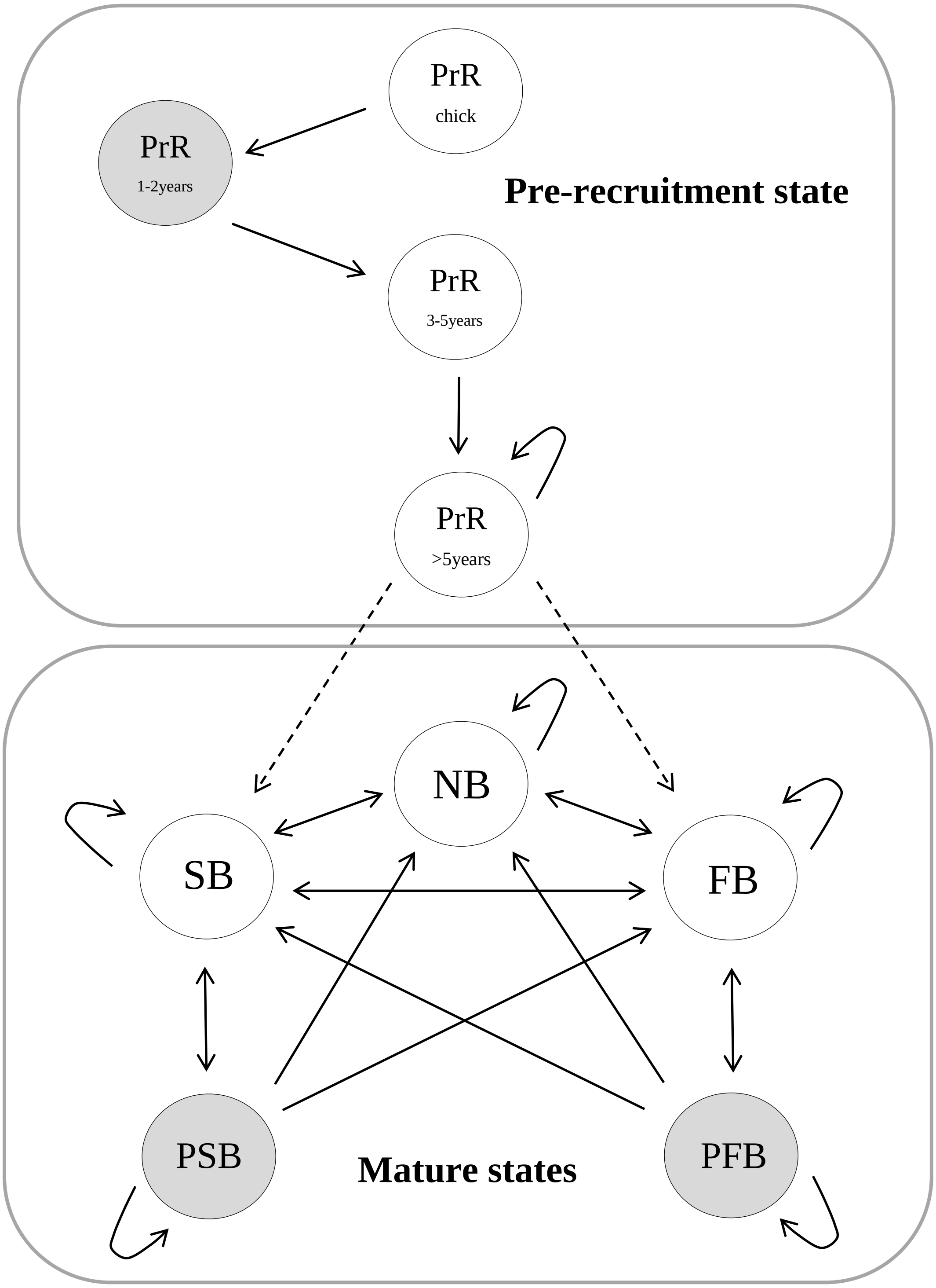

Figure 1 : Life cycle graph representing transitions between observable (white) or unobservable states (grey). All birds are ringed as chicks, thus individuals start in the Pre-Recruitment state (PrR). After fledging, all birds remain at least two years continuously at sea (i.e. juvenile stage). Pre-Recruitment state becomes observable from 3 years-old when birds start to return at the colony and are now considered as immature. From 6 years-old, birds can pass into the breeding group of the population though recruitment represented by dashed arrows. Then mature birds irrespectively of age can transit between mature states: successful breeder (SB), failed breeder (FB), recruited non breeder (NB), post successful breeder (PSB) and post failed breeder (PFB).

free from a density effect (Fay et al. 2015). Considered together, these studies suggest that a shift occurred in this population regarding density dependence effects on the recruitment process.We thus investigated the relationship between recruitment age and population size using 25 successive 10-year windows moving along the time series by a 1-year step (t1 to t10, t2 to t11,…, t25 to t35, Durant et al. 2004). Obtaining the same correlation between recruitment age and population size for all windows would support a single linear relationship over the whole study period. Otherwise, nonlinear processes and shifts in relationships may be supported. We used cohort specific recruitment estimates to have the largest temporal windows available. To model population density effects on early-life survival and recruitment, we used the number of breeding pairs observed annually at Possession Island as a covariate.

Our selected covariates included a large-scale climate index, the Southern Annular Mode (SAM) and a local climatic variable calculated over age specific ranges at sea (Figure A1), the Sea-Surface Temperature Anomaly (SSTA). SAM is the leading mode of atmospheric circulation variability in the Southern Hemisphere affecting the Southern Ocean (Marshall 2003). This climatic index may affect albatrosses both directly through wind speed (Weimerskirch et al. 2012), and indirectly, affecting primary productivity through large-scale impact on ocean mixed layer depth (Sallée, Speer & Rintoul 2010). SAM data were selected from the online database of the British Antarctic Survey (http://www.nerc-bas.ac.uk/icd/gjma/sam.html). At a regional scale, SSTA may determine the development and productivity of the whole trophic web, and hence may be used as a proxy of oceanographic conditions. SSTA have been related to demographic parameters for many seabird species in the Southern Ocean and elsewhere, probably through indirect mechanisms such as the abundance of food resources (Sandvik et al. 2005; Barbraud et al. 2012). SSTA data were obtained from the IRI Data Library http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn SmithOIv2/.monthly/.ssta/.

First, we assessed the impact of selected covariates on pre-recruitment survival considering their annual averages the previous year. We included the natal climatic condition for juvenile survival since this parameter is expected to be affected by climatic conditions both during chick stage and after fledging. A recent study suggested that high natal SSTA (i.e. SSTA during the chick rearing period) on parental foraging grounds has negative effects on post-fledging survival (Fay et al. 2015). This effect is expected to occur through decreasing paternal investment in chick rearing when they face poor environmental conditions leading to a negative impact on chick condition at fledging (McMahon & Burton 2005). In the absence of reliable data on the body condition of chicks, we tested this hypothesis indirectly, assessing the effect of

SSTA on parental foraging grounds by distinguishing the early rearing stage (April-July) from the late rearing stage (August-November) when chicks constituted their fat reserves (Reid, Prince & Croxall 2000). As parental investment and foraging areas are sex-dependent in the wandering albatross (Weimerskirch, Barbraud & Lys 2000), we distinguished SSTA on the males' foraging grounds (SSTAma) and SSTA on the females' foraging grounds (SSTAfe).

Knowing that access to reproduction may take many years in this species (Weimerskirch 1992), we investigated the effect of past climatic conditions on recruitment. We first assessed the effect of a climatic covariate on recruitment age by considering its annual average the previous year as a survival parameter. Then we assessed the longer term effect of this covariate by considering its average value calculated for the previous two years. If this new covariate improved our model, we tested a third covariate by considering its average value calculated for the three previous years, and so on until the percentage of variation explained by the climatic variable stabilized. Once this stage was reached, integrated additional years did not explain more residual variation, and we considered that the demographic parameter varied independently of these past climatic conditions.

All environmental variables were normalized prior to analysis. We fitted the logistic model: logit(Φ) = β0 + β1 * xn , where Φ is a demographic parameter, β0 is an intercept parameter, β1 is a slope parameter, and xn is the covariate x the year n. Significant relationships were assessed by an analysis of deviance test with a Fisher-Snedecor distribution (ANODEV; Grosbois et al. 2008). The percentage of variation that was explained by a covariate (r2) was estimated as: $r^2 = [(Dev(F_{cst}) - Dev(F_{cov})]/[Dev(F_{cst}) - Dev(F_t)]$ (Skalski 1996). To limit the number of tests, we investigated quadratic relationships and interaction effects between climatic variables and population size only for the covariates having received a minimum level of support (p-value≤0.10).

3 Results

Goodness of fit tests (χ2 = 1003.4, df =749, P <0.001 for females and χ2 =1263.8, df =898, P <0.001 for males) indicated that the general JMV model did not fit the data correctly (see appendix A5 and Table A1 for detailed comments). We thus used a variance inflation factor (ĉ = 1.37) for model selection.

Results indicated that early-life survival and recruitment processes were strongly influenced by environmental variability and population density. We found that population size constrained both early-life survival and recruitment age, although in different ways. Model selection confirmed density dependence for juvenile survival, with a better fit obtained with a quadratic relationship that explained 60% of the total variance (Table 1, Ftestcst/co/t=10.09, p-value<0.001 and Figure 2). Controlling for the effect of density, we found an additive linear negative effect of natal SSTA on paternal foraging ground,but not on maternal, during the late stage of chick rearing (Table 1, Ftestcst/co/t=4.24, p-value=0.03), that explained 31% of the residual variance (Figure 3). No relationship was supported for SSTA during the early stage of chick rearing (Table 1, Ftestcst/co/t=0.30, p-value=0.74). Model selection did not support an effect of natal SAM condition on juvenile survival or an effect of SAM and SSTA in the first year after fledging. We found no support for an interaction of natal SSTA with breeding population size. In contrast to juveniles, immature survival was not affected by population size (Table 1, p-value=0.76), and we did not find evidence for an impact of climatic condition on this parameter.

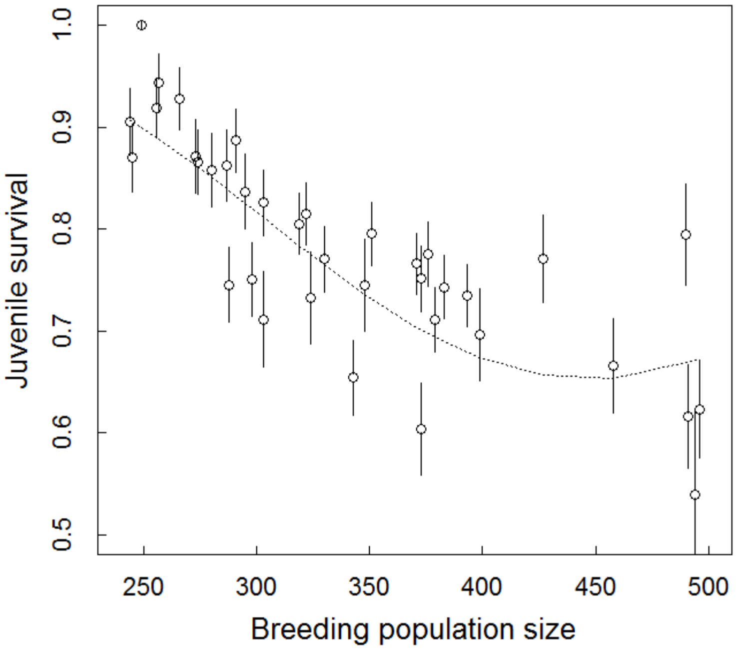

Figure 2 : Relationship between juvenile survival and breeding population size for the wandering albatross population of Crozet. Estimates of juvenile survival obtained from the time-dependent model (open circles ±SE) and juvenile survival modelled as a function of breeding population size (dotted line, Table 1 Model 2, PAnodev=0.01).

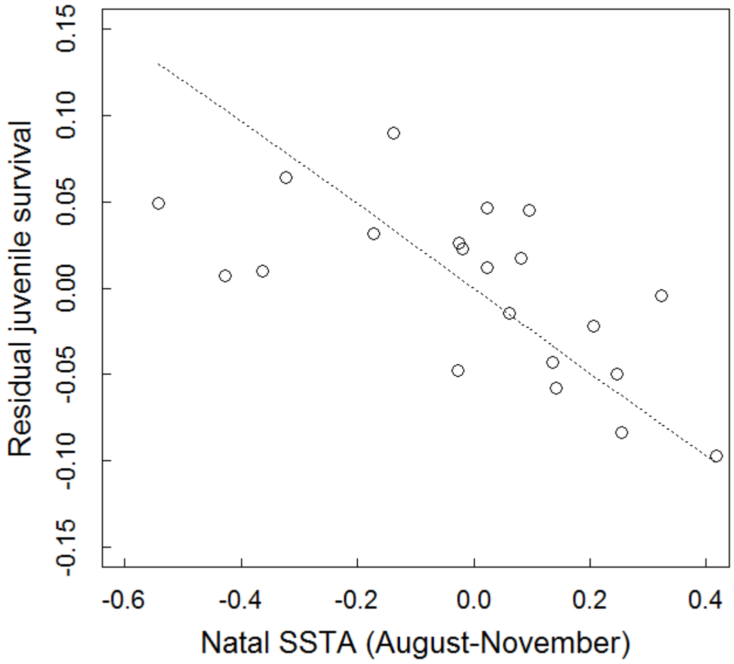

Figure 3 : Residual juvenile survival (open circles) modelled as a function of natal SSTA on male foraging grounds during the late rearing stage (August-November) for the wandering albatross population of Crozet (Dotted line, Table 1 Model 7, PAnodev=0.03). Residual survival estimates were calculated as the difference between survival estimates obtained from the time-dependent model and survival estimates obtained from the model where survival was modelled as a function of breeding population size.

The probability of early-recruitment was highly variable between years (Table 2, M2 vs M3, ΔQAIC=27.2), but these variations did not differ between sexes (Table 2, M1 vs M2, ΔQAIC=-20). Considering cohort specific early-recruitment probability, we found that recruitment age decreased continuously during the study period until the cohort born in 1994 (Figure. 4). We found a shift in the relationship between early-recruitment probability and population size. During the earlier part of the study, in 1970s when breeding population size decreased from 500 to 250 pairs, we found a negative relationship between recruitment age and population size (Figure 5). However, between the mid-1980s and the early 2000s when the population was recovering slowly to stabilize at around 380 pairs, recruitment age still decreased. Consequently, early recruitment was positively related to population size, suggesting that density dependence was no longer occurring.

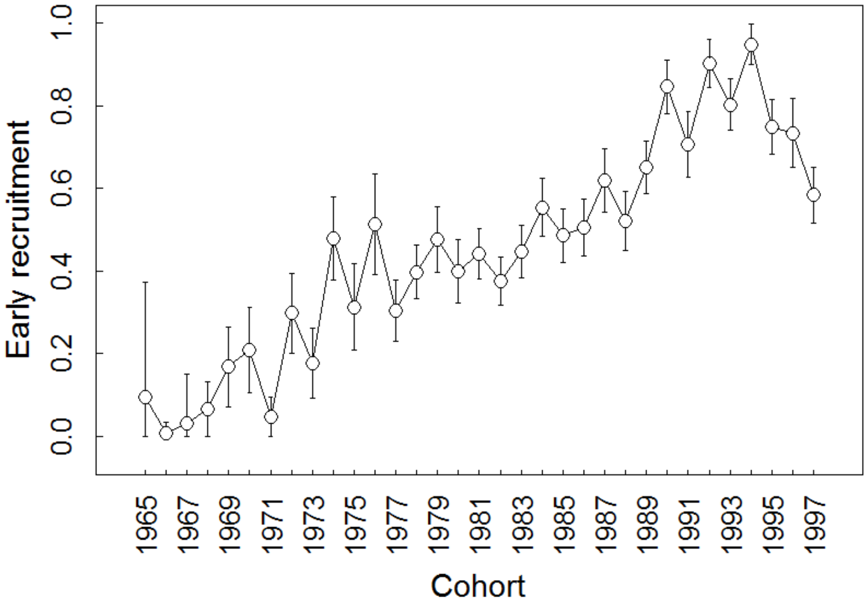

Figure 4 : Cohort specific early-recruitment probability (±SE) of the wandering albatross population of Crozet. Early recruitment was defined as first reproduction occurring before or equal to 8 year-old for females and 9 years-old for males (see figure A4).

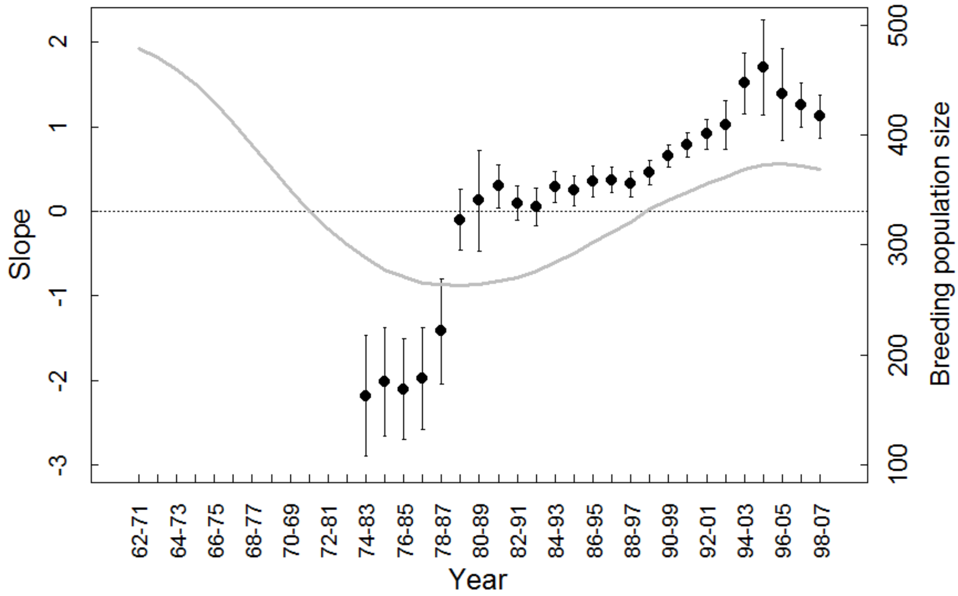

Figure 5 : Slope of the relationships over the successive 10-year windows between early recruitment probability and breeding population size for the wandering albatross population of Crozet. Values of the slopes of the relationships (filled circles ±SE) and 10-year moving average breeding population trend (grey line).

Table 1 : Testing for the effects of covariates on juvenile and immature survival for wandering albatrosses from Crozet Island from 1965 to 2012. Results include the relative deviance corrected by the overdispersion factor (QDev), the statistic Ftestcst/co/t testing the null hypothesis that the focal climatic covariate has no effect on survival, the percentage of variation or residual variation explained by the covariates or additive covariate respectively (r^2) and the 95% CI of the slope for linear relationships. Symbols ".", and "+" indicate interactive and additive effects respectively. All covariates were standardized. Models with statistically significant covariate effects at the level of 5% are in bold characters.

No.	Pre-recruitment survival	QDev	F	p-value	r^2	Slope [95% CI]
	1-2 years old class					
1	**N**	**79817.20**	**17.10**	**<0.001**	**0.49**	**-0.47 [-0.56; -0.37]**
2	**N_qua**	**79793.02**	**4.98**	**0.01**	**0.60**	
3	N_qua + SAM	79789.99	0.65	0.53	0.03	+0.07 [-0.01; +0.15]
4	N_qua + SSTA	79784.22	0.12	0.89	0.01	-0.04 [-0.16; +0.08]
5	N_qua + SAMnat	79785.12	1.79	0.18	0.09	+0.11 [+0.03; +0.19]
6	N_qua + SSTAmaAprJul	79783.45	0.30	0.74	0.03	-0.06 [-0.16; +0.05]
7	**N_qua + SSTAmaAugNov**	**79771.78**	**4.24**	**0.03**	**0.31**	**-0.25 [-0.39; -0.11]**
8	N_qua + SSTAmaAugNov_qua	79769.95	0.64	0.54	0.35	
9	N_qua + SSTAfeAprJul	79784.60	0.03	0.97	<0.01	-0.01 [-0.10; +0.08]
10	N_qua + SSTAfeAugNov	79784.46	0.06	0.94	0.01	-0.02 [-0.14; +0.09]
11	N_qua . SSTAmaAugNov	79773.94	0.41	0.67	0.34	
	3-8 years old class					
12	N	79675.77	0.28	0.76	0.02	-0.04 [-0.12; +0.05]
13	SAM	79674.29	0.88	0.42	0.05	-0.13 [-0.31; +0.04]
14	SSTA	79667.74	1.66	0.19	0.11	-0.17 [-0.30; -0.04]

Table 2 : Recruitment age (early vs late recruitment) modelling as a function of sex and time (t) of the wandering albatross population of Crozet Island from 1965 to 2012. Results of model selection include: number of mathematical parameters (k), the relative deviance corrected by the overdispersion factor (QDev) and Akaike Information Criterion value corrected by the overdispersion factor (QAIC). Symbols ".", and "+" indicate interactive and additive effects respectively. The best supported model is in bold characters.

No.	Recruitment age	k	QDEV	QAIC
1	**sex+t**	**154**	**79562.21**	**79870.21**
2	sex.t	186	79518.28	79890.28
3	sex	122	79673.48	79917.48
4	cst	121	79677.51	79919.51

Additionally, recruitment age was strongly related to climatic factors. Results support a positive linear effect of SAM on early-recruitment probability with a long-term effect of this large-scale climate index. Indeed, model fit increased continuously until the integration of the SAM value over the five previous years (Table 3), which explained 52% of the variation of recruitment age (Figure 6). SAM presented a linear temporal trend (slope=0.04, p-value=0.02) as well as early-recruitment probability over the study period (Figure 4). To check for the robustness of our result, we removed the linear trend of SAM using the residual regression technique and reanalyzed the relationship between early-recruitment and this detrended climatic covariate. We found again strong support for a long term effect of SAM on recruitment process (Ftestcst/co/t=7.24, p-value=0.003). Focusing on local climatic covariates, model selection supported a positive linear effect of SSTA (Table 3). Long term effects of SSTA appeared weaker in this case receiving support only for the two previous years (Table 3). No interactions were supported between climatic covariates and breeding population size.

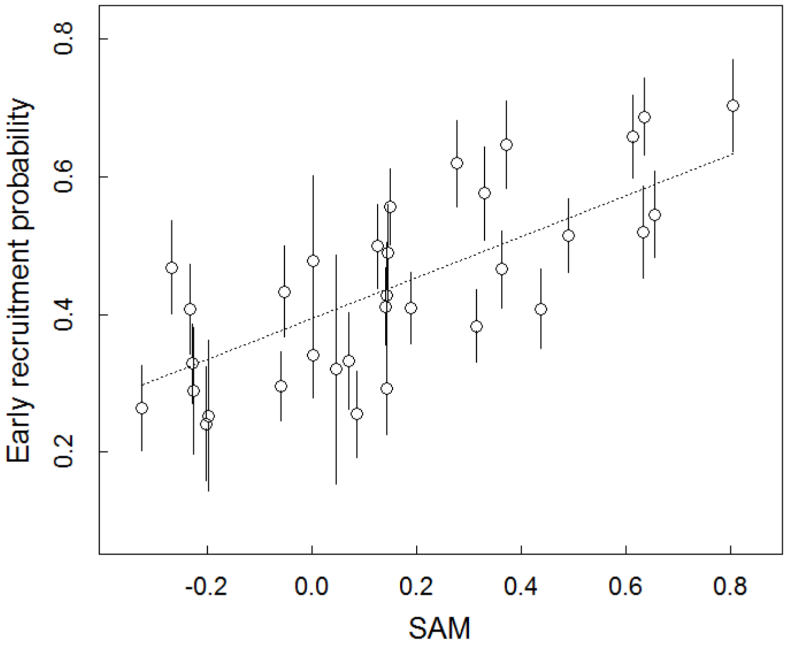

Figure 6 : Relationship between early recruitment probability and Southern Annular Mode (SAM) averaged over the five previous years for the wandering albatross population of Crozet. Estimates of early recruitment obtained from the time-dependent model (open circles ±SE) and early recruitment probability modelled as a function of standardized SAM averaged over the five previous years (dotted line, Table 3 Model 9, PAnodev<0.001).

Table 3 : Testing for the effects of covariates on recruitment age for wandering albatrosses from Crozet Island from 1965 to 2012. Results include the relative deviance corrected by the overdispersion factor (QDev), the statistic Ftestcst/co/t testing the null hypothesis that the focal climatic covariate has no effect on recruitment age, the percentage of variation explained by the covariates (r^2) and the 95% CI of the slope for linear relationships. Symbols ".", and "+" indicate interactive and additive effects respectively. All covariates were standardized. Models with statistically significant covariate effects at the level of 5% are in bold characters.

No.	Pre-recruitment survival	QDev	F	p-value	r^2	slope
	Single covariate model					
1	SAM(t-1)	79655.19	3.05	0.06	0.16	+0.22 [+0.12, +0.33]
2	SAM(t-1)_qua	79654.47	0.12	0.89	0.17	
3	**SAM(t-2)**	**79647.38**	**4.75**	**0.02**	**0.23**	**+0.25 [+0.15; +0.35]**
4	SAM(t-2)_qua	79646.42	0.17	0.84	0.24	
5	**SAM(t-3)**	**79631.52**	**9.38**	**<0.001**	**0.38**	**+0.33 [+0.22; +0.43]**
6	SAM(t-3)_qua	79630.48	0.24	0.79	0.39	
7	**SAM(t-4)**	**79624.02**	**12.40**	**<0.001**	**0.44**	**+0.35 [+0.25; +0.45]**
8	SAM(t-4)_qua	79623.23	0.20	0.82	0.45	
9	**SAM(t-5)**	**79615.54**	**16.84**	**<0.001**	**0.52**	**+0.38 [+0.28; +0.48]**
10	SAM(t-5)_qua	79613.93	0.48	0.62	0.54	
11	**SAM(t-6)**	**79614.34**	**17.58**	**<0.001**	**0.53**	**+0.38 [+0.28; +0.49]**
12	SAM(t-6)_qua	79612.01	0.73	0.49	0.55	
13	**SSTA(t-1)**	**79648.94**	**4.22**	**0.02**	**0.22**	**+0.25 [+0.14; +0.36]**
14	SSTA(t-1)_qua	79648.69	0.04	0.96	0.23	
15	**SSTA(t-2)**	**79638.23**	**7.06**	**0.003**	**0.33**	**+0.30 [+0.20; +0.40]**
16	SSTA(t-2)_qua	79636.56	0.35	0.71	0.34	
17	**SSTA(t-3)**	**79638.87**	**6.86**	**0.04**	**0.32**	**+0.30 [+0.19; +0.40]**
18	SSTA(t-3)_qua	79632.74	1.36	0.26	0.38	
	Multiple covariate model					
19	SAM(t-5) + SSTA(t-2)	79612.06	1.19	0.32	0.54	
20	SAM(t-5) . N	79596.73	1.40	0.26	0.69	
21	SSTA(t-2) . N	79595.67	0.01	1	0.74	

4 Discussion

In this study, we provided evidence that climate and population size affected both the survival and recruitment age of young individuals but in different ways according to the trait. We found that early-life survival was mainly affected by population density whereas recruitment age variation appeared better explained by climatic conditions with a long-term effect of climate. Furthermore, results suggested that similar climatic conditions had opposite effects on individual performance according to the life stage.

4.1 Density dependence

While population density as a regulating process of populations has been often mentioned in terrestrial environments (Bonenfant et al. 2009), it is less commonly considered in marine species, especially for seabirds that frequently range over vast oceanic areas (Lewis et al. 2001). In this study we showed that both early-life survival and recruitment age could be constrained by population density in wandering albatrosses. Density effects seemed higher for juvenile survival than for recruitment age, supporting Eberhardt's idea that vital rates have different sensitivities to changes in population density (Eberhardt 2002).

A negative effect of population size on early-life survival was clearly established in wandering albatrosses (Fay et al. 2015), but we showed that recruitment age could be affected as well. Earlier studies for the same study population reported decreasing age at first reproduction in the early 1970s associated with decreasing population size, and concluded a density dependent effect (Weimerskirch & Jouventin 1987; Weimerskirch et al. 1997). However, a recent study based on a different but larger time-window from the 1980s to current years suggested contrasting patterns with overall positive relationships between population size and recruitment (Fay et al. 2015). Here, by investigating the effect of population size on recruitment age over the whole study period, we showed that the effect of population density on this parameter shifted over the course of time. In the 1970s, recruitment age decreased simultaneously to decreasing breeding population size. Such negative relationships have been found for other long-lived species. In these organisms, young individuals delayed reproduction beyond the minimum age of sexual maturity, waiting for vacant breeding sites or territories (Sæther, Engen & Matthysen 2002). The result is a queuing process that allows massive recruitment when an important adult mortality event occurs (Pradel et al. 1997, Votier et al. 2008). Such mechanisms, known as compensatory recruitment, could be associated with decreasing recruitment age (Reid et al. 2003; Ferrer, Otalora &

GarcÍa-Ruiz 2004). In our study population, a similar queuing process may explain decreasing age at first reproduction occurring after the population crash in the 1960s, when adult survival decreased substantially (Weimerskirch & Jouventin 1987). However, for wandering albatross, which breeds in loose aggregations on the grassy plateaus of oceanic islands, nests or territories are probably not limiting (Tickell 2000). Rather, in this species, recruitment seems mainly constrained by body condition since immatures must attain a threshold condition to be able to recruit into the population (Weimerskirch 1992). With decreasing population size, immature birds may have been able to attain this condition earlier because of a reduction in competition at sea. However, after a phase of stabilization during the 1980s, recruitment age continued to decrease while the population recovered progressively from the mid-1990s to the early 2000s, resulting in positive relationships between early recruitment probability and breeding population size. This result is not expected since, other things being equal, the age at first reproduction in long-lived species usually increases with population size (Gaillard et al. 2000; Reid et al. 2003; Ferrer et al. 2004). However, the effect of population density could be nonlinear and demographic traits could be impacted by density only at high population levels (Strong 1986). Thus, we speculate that in recent decades, population size was below the threshold for which density dependent recruitment may occur, since the population had not yet recovered to its original size of the 1960s. With the effect of density dependence being relaxed, this albatross population then showed a positive relationship between recruitment and breeding population size that is characteristic of short-lived species. In short-lived species, survival, and not territory occupancy, is the main limiting factor restricting recruitment rate, and favorable environmental conditions increase both the return rate of adults and the number of recruits (Sæther et al. 2002). In this context, decreasing recruitment age since the 1990s may reflect continuing favorable environmental conditions allowing birds to reach the good body condition required for breeding at younger ages (Weimerskirch 1992; Weimerskirch et al. 2012).

Alternatively, although non-exclusive, decreasing age at first reproduction with increasing population size could be interpreted as an Allee effect (Allee 1931), i.e. positive a density effect at low population level. At low population densities, mating processes can be disturbed leading to positive relationships between population size and recruitment rates (McCarthy 1997; Angulo et al. 2007). Long-lived species adopting monogamous breeding systems with high mate fidelity such as the wandering albatross (Bried, Pontier & Jouventin 2003) could be particularly sensitive to the Allee effect.

4.2 Climate effect

We found that both early-life survival and recruitment age was strongly affected by climatic variation. Much of the variation in the first two years juvenile survival was explained by natal conditions, with a negative effect of SSTA on paternal foraging grounds. Thus natal effects may be mediated by parental investment. In long-lived species, breeders facing poor environmental conditions are expected to decrease their breeding investment to protect their own survival, resulting in poor chick condition at independence and lower survival in early-life (McMahon & Burton 2005). Consequently, the negative effect of natal SSTA was only been supported during the late stage of chick rearing when young accumulate fat stores before fledging (Reid et al. 2000). Climatic conditions on maternal foraging grounds were not related to juvenile survival whatever the rearing stage. This result confirm previous studies suggesting that paternal characteristics, in wandering albatrosses, have a major importance for post fledging juvenile performances due to the higher investment of male parent during chick provisioning (Fay et al. 2015, 2016).

Recruitment age appeared to be highly variable in relation to climatic conditions. In particular, we found a positive relationship between SAM and early recruitment, with an unexpected long-term effect of this climatic variable. Although little information is available to understand the underlying proximate mechanisms linking SAM to immature albatross, this long-term climatic effect on recruitment age may be related to the progressive increase in weight observed in this species through immaturity (Weimerskirch 1992). In long lived species, body condition is an important factor determining whether a young individual engages in reproduction or not (Martin & Festa-Bianchet 2012). Bearing in mind that climatic effects on seabird demography are usually mediated by food availability (Ainley, Sydeman & Norton 1995; Durant, Anker-Nilssen & Stenseth 2003; Bost et al. 2015), environmental conditions encountered several years before the first reproduction could impact the individual growth trajectory by affecting the time at which an individual reached the body condition required to breed (Weimerskirch 1992).

Increasing sea surface temperature had a positive effect on the recruitment process, which is in contrast to results reported for juvenile survival. This suggests that similar climatic conditions may lead to different demographic responses according to the life stage considered. We suggest that these surprising results could be explained by the age specific segregation shown by our study population. When aging, wandering albatrosses progressively shift their foraging areas southward from subtropical to Subantactic water (Weimerskirch et al. 2014). The Southern Ocean is highly heterogeneous with many sub-systems that do not respond equally to climatic variability

(Tréguer & Jacques 1992; Lovenduski 2005). Relationships between SST and primary productivity seem heterogeneous in relation to location (Fauchereau et al. 2011), and lower temperatures may limit phytoplankton growth rates in some areas (Reay et al. 2001). In Antarctic and subtropical tropical zones, SST increases are usually negatively related to demographic performances, suggesting that in both areas increasing SST decreased food availability (Barbraud & Weimerskirch 2001; Weimerskirch, Zimmermann & Prince 2001; Jenouvrier, Barbraud & Weimerskirch 2003; Beauplet et al. 2005). In contrast, in the subantactic zone, where adult and immature wandering albatrosses are found before recruitment stages, the negative effects of warm waters seem less clear (Fauchereau et al. 2011; Takao et al. 2012). In this area, studies report both positive (Nevoux, Weimerskirch & Barbraud 2007; Rolland et al. 2009; Oosthuizen et al. 2015) and negative (Guinet et al. 1998; Bost et al. 2015) relationships between SST and top predator demography. The latitude at which species forage within the subantactic zone seems critical to the sign of these relationships. Species foraging in the north of this area seem to have better demographic performances than those foraging to the south when facing positive SSTs (Inchausti et al. 2003). Consistently, we found that adult male wandering albatrosses foraging in the south of the subantactic zone, close to the Polar Front, were negatively affected by positive SSTs, whereas immature individuals staying at higher latitudes responded positively to the same climatic conditions (Weimerskirch et al. 2014). Thus, we suggest that age-specific demographic responses to SSTs observed in wandering albatrosses may be caused by the large range of this population in relation to local oceanic responses to climatic variation. Such result shows that it is essential to consider age effects to understand population responses to climate change, since similar climatic conditions may have opposite effects on individual performances according to the life stage considered (Dybala et al. 2013; Pardo et al. 2013; Radchuk, Turlure & Schtickzelle 2013).

5 Conclusion

In this study, we have shown that early-life survival and recruitment could be affected by both population density and climatic variation although in different ways according to the life stages. Such results highlight the need to assess age specific functional responses to environmental variability to allow accurate demographic prediction. Furthermore, we found a shift in the effect of density dependence with the recruitment age of our study population. In the context of global decreasing seabird abundances, this suggests that density dependence mechanisms can temporarily disappear, especially when decreasing population size is not related to food depletion.

In such circumstances, while density dependent processes could be less evident, it may still be essential to consider them when constructing long term population size projections. More importantly, in the context of climate change and rising temperatures, shifts in frontal zones and the forcing of wind speed in the southern ocean, the response of juvenile, immature and adult albatrosses will be different. Being able to estimate the respective influences of environmental parameters in different water masses on the survival of age classes as we did in our study will be critical to be able to make robust predictions on the impact of climate change on marine predators.

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CHAPITRE 3

Parental age effects in a long-lived seabird

Crédit: Valentin Nivet-Mazerolles

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Paternal but not maternal age influences early-life performance of offspring in a long-lived seabird

Abstract

Variability in demographic traits between individuals within populations has profound implications for both evolutionary processes and population dynamics. Parental effects as a source of non-genetic inheritance are important processes to consider to understand the causes of individual variation. In iteroparous species, parental age is known to influence strongly reproductive success and offspring quality, but consequences on offspring fitness component after independence are much less studied. Based on a 37 years longitudinal monitoring of a long-lived seabird, the wandering albatross, we investigate delayed effects of parental age on offspring fitness components. We provide evidence that parental age influences offspring performance beyond the age of independence. By distinguishing maternal and paternal age effects, we demonstrate that paternal age, but not maternal age, impacts negatively post-fledging offspring performance.

1 Introduction

Heterogeneity in demographic traits within populations has strong implications for both long-term evolutionary processes and actual population dynamics (Bolnick et al. 2011). Today, there is increasing evidence that conditions experienced during development explain an important part of the heterogeneity in demographic traits observed after independence (Lindström 1999; Cam & Aubry 2011). Interactions between parental genotype, phenotype and environment may strongly influence offspring realized fitness independently of its own genome. This source of non-genetic inheritance, called parental effects (Mousseau & Fox 1998), is a consequence of a large variety of mechanisms ranging from DNA methylations to parental behaviors such as parental favouritism, with profound impacts for future offspring performance. Such parental effects, which are at the interface of developmental, ecological and evolutionary processes, are fundamental mechanisms to understand individual variability in demographic traits (Benton, St Clair & Plaistow 2008).

In iteroparous species, parental age strongly influences reproductive success (Forslund & Pärt 1995). Variation in breeding success resulting from individual changes typically follows a dome-shaped curve pattern along the parental life (Rebke et al. 2010), due to accumulating experience in early life (Komdeur 1996) and senescence at older age (Nussey et al. 2013). Studies have shown that the variation in parental breeding abilities have important consequences for offspring quality, especially for older parents in relation to reproductive senescence (Descamps et al. 2008; Saino et al. 2012). Although there is evidence that parental age impacts negatively offspring lifespan, referred to as the Lansing effect (Priest, Mackowiak & Promislow 2002), the relative effects of parental age on different offspring fitness components remain little documented in wild populations (Table 1). Yet, accurate estimation of demographic traits is important to disentangle different processes implying different biological mechanisms which can lead to the same general pattern (Bouwhuis, Vedder & Becker 2015). For example, reduced life span of individuals from old parents may emerge from decreasing survival probability through the life or accelerating senescence rate in late life. However, few studies are able to assess accurately offspring performance after independence. Furthermore, studies on parental effects are biased toward maternal effects (Table 1), although it was recently recognized that both maternal and paternal effects are common and important in a large variety of organisms (Crean & Bonduriansky 2014). In the wild, assessing the effects of parental age on offspring performance requires high quality longitudinal datasets with known age individuals and pedigree information. Such conditions are rare due to technical and financial limitations, which explain why evidence of delayed parental effects on offspring performance in wild populations remains limited to date.

Table 1: Review of studies investigating the effect of parental age on offspring performance after independence in wild populations. * indicates apparent survival. For recruitment traits, recruitment rate, confounding early-life survival with recruitment, is distinguished from recruitment probability which is conditional on survival until maturity. LRS indicates lifetime reproductive success. Paternal and maternal age can have no effect (no), linear negative effect (-), linear positive effect (+), positive quadratic effect (qua) or is not assessed (/). For studies distinguishing male (m) from females (f) offspring performance, sex specific effects are indicated.

Species	Offspring trait	Paternal age effect	Maternal age effect	Reference
Birds				
Blue footed booby *Sula nebouxii*	Recruitment rate	qua	qua	Torres et al. 2011
Great tit *Parus major*	Age at last reproduction	/	no (f)	Bouwhuis et al. 2010
Great tit *Parus major*	LRS	/	no (f)	Bouwhuis et al. 2010
Red-billed Chough *Pyrrhocorax pyrrhocorax*	Juvenile survival*	no	no	Reid et al. 2010
Common tern *Sterna hirundo*	LRS	- (m) no (f)		Bouwhuis et al. 2015
Common tern *Sterna hirundo*	lifespan	- (m) no (f)	no (m,f)	Bouwhuis et al. 2015
House sparrows *Passer domesticus*	LRS	- (m) no (f)	- (f) no (m)	Schroeder et al. 2015
House sparrows *Passer domesticus*	lifespan	no (m,f)	no (m,f)	Schroeder et al. 2015
Mammals				
Red squirrel *Tamiasciurus hudsonicus*	Juvenile survival*	/	qua	Descamps et al. 2008
Weddell seals *Leptonychotes weddellii*	Survival to maturity*	/	+ (f)	Hadley et al. 2007
Weddell seals *Leptonychotes weddellii*	Recruitment probability	/	- (f)	Hadley et al. 2007
European rabbit *Oryctolagus cuniculus*	Survival to maturity	/	+ (f)	Rodël et al. 2009
European rabbit *Oryctolagus cuniculus*	LRS	/	qua (f)	Rodël et al. 2009
Rhesus macaque *Macaca mulatta*	Juvenile survival	/	- (m,f)	Hoffman et al. 2010
Rhesus macaque *Macaca mulatta*	Age at first reproduction	/	no (f)	Hoffman et al. 2010
Rhesus macaque *Macaca mulatta*	Reproductive rate	/	no (f)	Hoffman et al. 2010
Preindustrial humans *Homo sapiens*	LRS	/	- (m,f)	Gillespie et al. 2013
Preindustrial humans *Homo sapiens*	Survival to maturity	/	qua (m,f)	Gillespie et al. 2013
Preindustrial humans *Homo sapiens*	Recruitment probability	/	- (m,f)	Gillespie et al. 2013

In this study we investigated the effects of both paternal and maternal age on the long-term post-fledging offspring performance of the wandering albatross *Diomedea exulans*. In this species, age affects parental care with strong senescence effects (Froy et al. 2013; Pardo, Barbraud & Weimerskirch 2013, 2014). Delayed effect of parental age on offspring performance was assessed through juvenile survival, recruitment probability and age of recruitment. First, due to senescence in male and female breeding performance, we predict that parental age should be negatively related to offspring survival and recruitment. Second, knowing that parental care during chick rearing is strongly biased toward males (Weimerskirch, Barbraud & Lys 2000), and that senescence effects are stronger for males than for females in wandering albatross (Pardo et al. 2013), we predict a larger effect of paternal age on offspring performance than of maternal age.

2 Materials and Methods

2.1 Study species and field method

The study was conducted on Possession Island (46.8 °S, 51.8 °E), Crozet Island in the Indian Ocean, where long-term monitoring of wandering albatrosses, based on annual capture-mark-recapture methodology, has been carried out annually since 1960. Sex assignments were performed based on both field observations (i.e. sexual size and plumage dimorphism, mating behaviours) and genetic analyses since 1999 (appendix A1). Wandering albatrosses show a typical slow life history strategy with high adult survival rates and low productivity (i.e. quasi biennial reproduction and clutch size limited to one egg without replacement laying). The period of parental care is especially long, lasting about 10 months, from laying in January to fledging in November. Parental care is shared by both sexes although male involvement is more important during chick-rearing (Weimerskirch et al. 2000). Fledglings do not receive post-fledging care and leave the colony alone remaining at sea continuously for the following 2 to 7 years.

2.2 General model

Individual encounter histories were modeled using a multi-event approach. The model consisted in 7 states, 1 immature state, 5 adult states and the state dead (Figure C1), and five events. To consider individuals during the period of immaturity, we defined the Pre-Recruitment state (PrR) after which immature birds can recruit, i.e. lay an egg for the first time into the breeding population. Adult birds can transit toward Successful Breeder state (SB), when the chick fledged, Failed Breeder state (FB), when the chick died before fledging, or recruited Non Breeder state (NB), when individuals that have recruited in the population (i.e. bred at least once) were observed as non-breeders at the colony. To model the sabbatical years spent continuously at sea after reproduction, we added two unobservable states (Lebreton & Pradel 2002) corresponding to the two previous breeding states defined: Post Successful Breeder

(PSB) and Post Failed Breeder (PFB). Thus, adult that are at sea (i.e. not at colonies for a whole year) are distinguished based on their most recent breeding state last time they were at a colony. In our study, state assignment was not always certain since between 1966 and 1986, state assessment was unknown for a number of breeders; some individuals were classified as breeders but the success or failure was not always ascertained. Multi-event models allowed us to deal with state uncertainty by assessing the likelihood of an individual state given the events (i.e. observations) (Pradel 2005). We considered five events, i.e. five types of observation in the field, 0 = "not observed", 1 = "seen as non-breeder", 2 = "seen as a failed breeder", 3 = "seen as a successful breeder", 4 = "seen as a breeder but successful status not ascertained". Our model allowed us to estimate the probability of survival (φ), the probability of recruitment given survival (ψ^{rate}) and the probability of early recruitment given recruitment (ψ^{early}). Early recruitment was defined as first reproduction occurring before 8 year-old for females and 9 years-old for males corresponding for both sexes to the first quartile of age recruitment frequency distributions (Fay et al. 2015). Details of the parametrization with the biological constraints applied can be found in appendix B1.

2.3 Parental age and model selection

For our analyses, we used the capture histories of 4538 chicks from 1107 fathers of known age (from 6 to 41 year-old with an average of 4.1 chicks per father) and of 4294 chicks from 1060 mothers of known age (from 6 to 45 year-old with an average of 4.0 chicks per mother) (Figure C2). Among those chicks, 3454 came from known aged mothers and fathers (Figure 1). All chicks were ringed and resighted between 1977 and 2013. Impact of parental effects was assessed on juvenile survival, i.e. the two first years of life from fledging, probability of recruitment, and probability of early recruitment. We fitted the logistic model: $\text{logit}(\Phi) = \beta0 + \beta1 * xi$, where Φ is a demographic parameter, $\beta0$ is an intercept parameter, $\beta1$ is a slope parameter, and xi is the age of the parent of individual i at birth. We tested both linear and quadratic relations owing to the dome-shaped curve pattern observed for breeding success variation with age (Weimerskirch, Lallemand & Martin 2005). When parental age effect was supported, we tried, as a second step, to fit threshold models (Table C1). In our dataset, different offspring could have the same parents introducing non-independence between individuals. To check the robustness of the results, models that provided a better fit with parental age effect (ΔAIC > 2) were run a second time with parental identity as a random effect. We calculated a likelihood ratio test (LRT) between a model where the demographic trait was constant [φ(cst+random(PI)] and a model where the demographic trait was a function of parental age (a) [φ(a+random(PI)], considering for both parental identity (PI) as a random effect. The p value of the LRT corresponded to halving the p value from using a χ^2 distribution with 1 degree of freedom (Gimenez & Choquet 2010). This random effect was not used systematically in our model selection due to large computation time required. We tested the effect of paternal, maternal and average age of both parents on offspring performance. In wandering albatross, pair bonds usually last until one member of the pair dies. Thus, when individuals grow older, age effect could be confounded with the effect of age difference within a breeding pair. To avoid spurious conclusions, we tested if the age difference within a pair provided better support to explain early-life offspring performance.

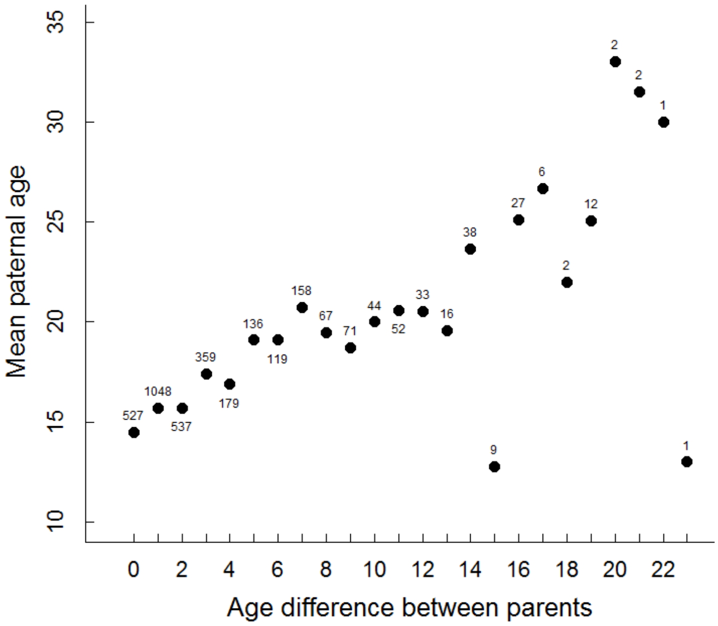

Figure 1: Age difference between parents in relation to paternal age. Numbers indicate sample sizes.

Between-individual heterogeneity may lead to detecting an effect of an individual covariate more often than it should be (Lin 1997). To take into account individual variation that cannot be measured, models that provided a better fit with parental age effect (ΔAIC > 2) were run a second time with individual as random effects on the focus demographic trait (Gimenez & Choquet 2010). To test for the hypothesis of unaccounted individual heterogeneity on the demographic trait, we calculated a LRT between a model where the demographic trait was constant [φ(cst)] and a model where the demographic trait was modelled as a function of heterogeneity [φ(cst+h)], where h indicates between-individual heterogeneity. To test for the hypothesis of an effect of parental age (a) on the demographic trait while accounting for heterogeneity we calculated a LRT between a model where the demographic trait was modelled as a function of heterogeneity [φ(cst+h)], and a model where the demographic trait was modelled as a function of parental age and heterogeneity [φ(a+h)]. Finally, we estimated the importance of within-individual effects (i.e. individual deterioration due to senescence) and between-individual effects (i.e. progressive appearance or disappearance of individuals) in the observed pattern using the methodology described by van de Pol and Wright (2009).

All models were run using the program E-SURGE (Choquet, Rouan & Pradel 2009). There is no test available to assess the goodness-of-fit (GOF) of multi-event models. Hence, we performed GOF tests using program U-CARE (Choquet et al. 2009a) on a simplified dataset which distinguished solely successful breeders and failed breeders and assigning randomly a reproductive status, i.e. failed or successful, to each individual for which no information was available.

3 Results

Goodness of fit tests ($\chi^2_{284} = 235.37$, p = 1.00 and $\chi^2_{309} = 311.32$, p = 0.75 for females and males from known paternal age respectively, and $\chi^2_{291} = 230.29$, p = 1.00 and $\chi^2_{300} = 317.52$, p = 0.51 for females and males from known maternal age respectively) indicated that the general model fitted the data correctly (Table C2).

We found that juvenile survival but not recruitment varied in response to parental age. Model selection indicated a strong linear negative effect of paternal age on offspring survival (Table 1, M1 vs M2: ΔAIC = 7.8), with no clear evidence for a quadratic relationship (Table 1, M2 vs M4: ΔAIC = -1.5). Knowing that no chicks from father older than 32 years of age have been recaptured, we tested the robustness of this result by reanalysing the data after removing these individuals. Consistently, we still found support for a negative relationship between paternal age and juvenile survival (ΔAIC = 5.6). Although threshold models did not provide a better fit (Table C1), they suggested that the negative relation between paternal age and juvenile survival was less supported before 15 years. Indeed, models with a threshold at 10, 15 or 20 year-old had as much support as a strictly linear model (ΔAIC<2), and the slopes of models with thresholds at 10 or 15 year-old were not meaningfully different from 0. Model averaging, accounting for uncertainty in model selection, suggested no relationship in young paternal age and a negative effect of paternal age after 20 years on juvenile survival (Figure 2). This result was robust with both the addition of parental identity as a random effect (Table C3, M3 vs M2: Likelihood Ratio Test $\chi_1^2 = 9.5$, p = 0.002), and the addition of a random effect to cope with unexplained variability in juvenile survival (Table C3, M5 vs M4: LRT $\chi_1^2 = 4.9$, p = 0.027). This result was not induced by increasing age difference within a breeding pair with age. Indeed, this variable was less supported than paternal age only (Table C4, M1 vs M2: ΔAIC = 3) despite the high correlation between these variables (Figure 1).

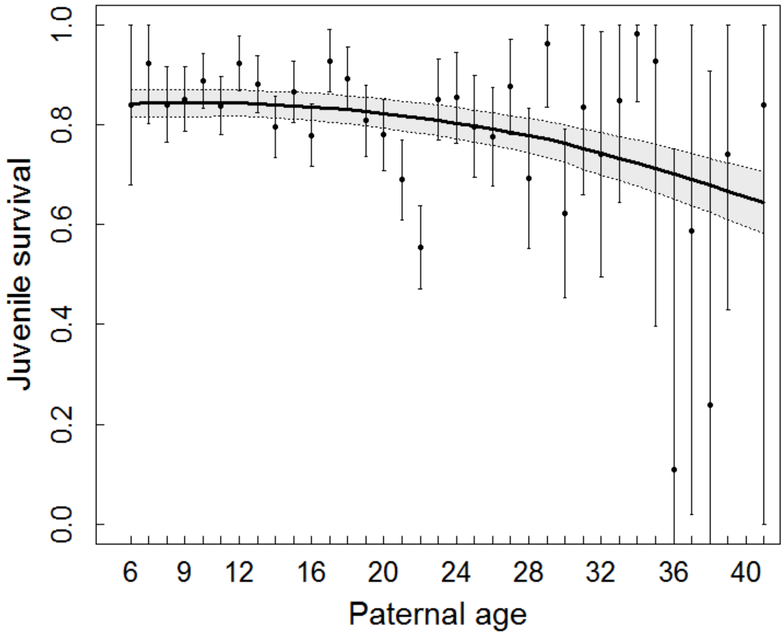

Figure 2: Relationship between juvenile survival and paternal age. The plain line represents the predicted relationship obtained from a model averaging procedure on constant, linear, quadratic and all tested threshold models (Table 1 and C4). For illustration the relationship is shown for female juvenile survival. Dashed lines and bars indicate ± s.e.

There was no evidence for a relationship between maternal age and juvenile survival (Table 1, M5 vs M6: ΔAIC = -1.5), neither between average age of both parents and juvenile survival (Table C5, M1 vs M2: ΔAIC = -0.7). The predominant effect of paternal age was less clear-cut when considering the analysis integrating simultaneously the age of both parents (Table C6 and C7), but this could be explained by the lower sample size used for these specific analyses, and by the difficulty to distinguish maternal from paternal age effects since parental ages are correlated due to assortative mating. Once juvenile survival was considered, we did not find any evidence of an impact of paternal, maternal or average age of both parents on the recruitment process. The effect of paternal but not maternal age on offspring performance was supported by the observed recruitment rate in relation to parental age. This demographic parameter was negatively related to paternal but not maternal age (Paternal age: slope=-0.025 ± 0.008, p=0.003; Maternal age: slope=-0.006 ± 0.008, p=0.529, figure 3). This transgenerational effect came from within-individual effects of senescence and not from the progressive appearance or disappearance of particular individuals (Table C8).

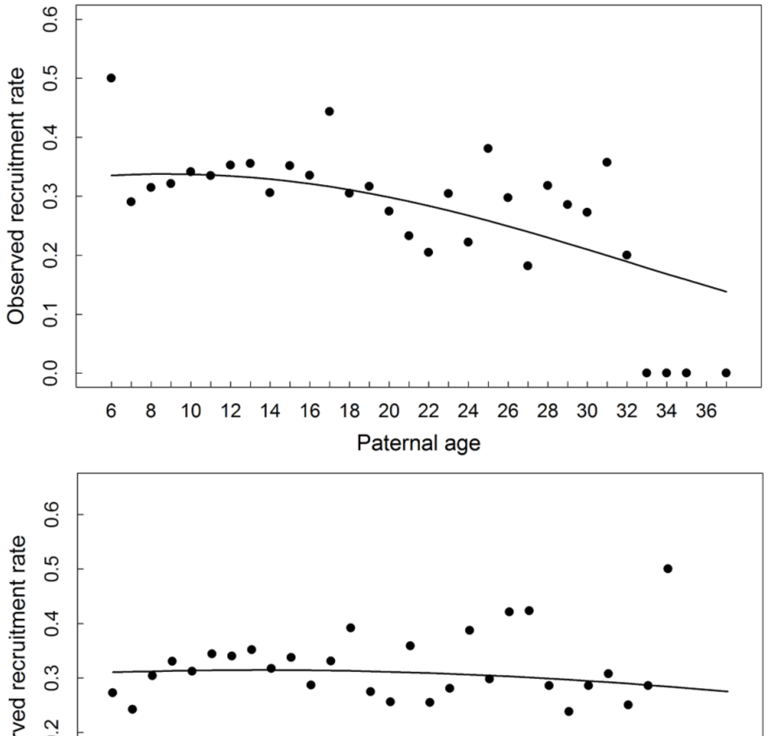

Figure 3: Observed recruitment rate in relation to paternal (a) and maternal (b) age. To model recruitment rate as a function of parental age, we used generalized linear mixed models (GLMM) with a binomial error-structure and a logit link function fitted to a binary response variable (recruited = 1, not recruited = 0), with parental identity as random effect. Recruit was assessed 15 years after fledging, when most of the recruitments have occurred. Plain lines represent curves derived from a model averaging procedure performed on models with constant, linear and quadratic relationships between parental age and offspring recruitment rate.

Table 2: Testing for the effects of paternal and maternal age (a) on early life survival (φ), recruitment rate (ψ^{rate}) and early recruitment probability (ψ^{early}) for wandering albatrosses, Possession Island, 1977-2013. k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion. cst = constant, a = age of the parent, a.sex = interaction between age of the parent and sex of the juvenile. Best supported models are in bold characters.

No.	Model	k	DEV	AIC	Slope ± s.e.
Survival					
	Paternal age				
M1	$\varphi(\text{cst})$	68	28597.4	28733.4	
M2	**$\varphi(\text{a})$**	**69**	**28587.6**	**28725.6**	**-0.17±0.05**
M3	$\varphi(\text{a.sex})$	70	28586.9	28726.9	
M4	$\varphi(\text{a}+\text{a}^2)$	70	28587.1	28727.1	
	Maternal age				
M5	**$\varphi(\text{cst})$**	**68**	**27540.2**	**27676.2**	
M6	$\varphi(\text{a})$	69	27539.7	27677.7	-0.04± 0.06
M7	$\varphi(\text{a.sex})$	70	27539.1	27679.1	
M8	$\varphi(\text{a}+\text{a}^2)$	70	27539.7	27679.7	
Recruitment					
	Paternal age				
M12	**$\psi^{\text{rate}}(\text{cst})$**	**68**	**28597.4**	**28733.4**	
M13	$\psi^{\text{rate}}(\text{a})$	69	28597.0	28735.0	-0.01±0.06
M14	$\psi^{\text{rate}}(\text{a.sex})$	70	28595.9	28735.9	
M15	$\psi^{\text{rate}}(\text{a}+\text{a}^2)$	70	28596.4	28736.4	
	Maternal age				
M16	**$\psi^{\text{rate}}(\text{cst})$**	**68**	**27540.2**	**27676.2**	
M17	$\psi^{\text{rate}}(\text{a})$	69	27539.5	27677.5	0.05±0.06
M18	$\psi^{\text{rate}}(\text{a.sex})$	70	27538.8	27678.8	
M19	$\psi^{\text{rate}}(\text{a}+\text{a}^2)$	70	27539.4	27681.4	
Early recruitment					
	Paternal age				
M20	**$\psi^{\text{early}}(\text{cst})$**	**69**	**28595.5502**	**28733.55**	
M21	$\psi^{\text{early}}(\text{a})$	70	28595.3158	28735.32	-0.02±0.09
M22	$\psi^{\text{early}}(\text{a.sex})$	71	28595.095	28737.10	
M23	$\psi^{\text{early}}(\text{a}+\text{a}^2)$	71	28594.4419	28736.44	
	Maternal age				
M24	**$\psi^{\text{early}}(\text{cst})$**	**69**	**27542.4**	**27680.4**	
M25	$\psi^{\text{early}}(\text{a})$	70	27542.2	27682.2	-0.02± 0.10
M26	$\psi^{\text{early}}(\text{a.sex})$	71	27542.0	27684.0	
M27	$\psi^{\text{early}}(\text{a}+\text{a}^2)$	71	27541.8	27683.8	

4 Discussion

This study of a long-lived seabird provided evidence that paternal age affects offspring fitness components after independence. Juvenile survival was negatively related to paternal age, with no effect of maternal age. Given that long-distance natal dispersal is exceptional in this highly philopatric species (Charmantier et al. 2011), we are confident that our apparent survival estimates are close to the true survival probabilities. Few studies estimated offspring survival after independence in relation to parental age in wild populations, and they report contrasting results including quadratic patterns [Red squirrel *Tamiasciurus hudsonicus* (Descamps et al. 2008); Blue footed booby *Sula nebouxii* (Torres, Drummond & Velando 2011)], positive relationships [Weddell seals *Leptonychotes weddellii* (Hadley et al. 2006); European rabbit *Oryctolagus cuniculus* (Rödel, von Holst & Kraus 2009)], negative relationships [Rhesus macaque *Macaca mulatta* (Hoffman et al. 2010)] and no relationship [Great tit *Parus major* (Bouwhuis et al. 2010); Red-billed Chough *Pyrrhocorax pyrrhocorax* (Reid et al. 2010)]. Note that these results could be sex-specific and that some studies did not control for offspring sex (Table 1). Our model selection supported continuous decreasing juvenile survival with paternal age for offspring of both sexes. This linear effect is probably more a simplification from modeling rather than the expression of a biological pattern. Indeed, for young fathers, increasing age was not clearly linked to decreasing offspring survival and was even slightly positive when considering recruitment rate, a fitness component closer to real realized fitness than juvenile survival. In addition, results obtained with threshold models suggested that juvenile survival was not affected by paternal age until 15 years old. Finally, model averaging suggested that paternal age affected strongly juvenile survival mainly after 20 years (Figure 2). This pattern was very similar to the pattern observed in the same species for variation in breeding success with age (Weimerskirch et al. 2005).

The negative expected relation between parental age and offspring performance based on the general decline in parental performance due to senescence, has been documented in laboratory species (Kern et al. 2001) and human populations (Gillespie, Russell & Lummaa 2013). Previous studies on wandering albatross have shown that aging in this species involved deterioration in foraging ability (Lecomte et al. 2010) with strong consequences on reproductive performance including lower breeding probability, and given they breed, lower hatching and fledging probabilities (Pardo et al. 2014). In the wandering albatross, continuously decreasing chick pre-fledging weight has been reported to occur in relation to parental age (Froy et al. 2013). A bad start in early-life could be highly detrimental to survival over the first months after independence (Weimerskirch et al. 2000), when most of the mortality between fledging and recruitment is expected to occur (Riotte-Lambert & Weimerskirch 2013).

A pattern observed at the population scale may not result from within-individual changes, and could be produced by selective disappearance of individuals. However, in our case, the parental age effect was most probably caused by individual changes since the ageing pattern in parental care is assumed to be shaped by within-individual processes (Froy et al. 2013). Moreover, a recent study suggested the selective disappearance of poor-quality breeders (Fay et al. unpublished data) and therefore that long-lived parents were individuals of higher quality able to allocate more in reproduction than short-lived parents. This statement was supported by our analysis decoupling within-individual from between-individual effects, suggesting that the progressive disappearance of low quality breeders decreases the negative effect of paternal age on juvenile survival that we observed at the population scale.

Interestingly, we found that paternal but not maternal age was related to post-fledging survival. Two complementary mechanisms can explain this pattern. First, the rate of senescence is sex-specific in wandering albatrosses, the fitness cost of senescence being 2.3 times larger in males than in females (Pardo et al. 2013). Old males forage in different waters than prime-aged males, making longer trips at sea, and failing to restore baseline corticosterone levels which suggest that their level of stress remains high at old age when foraging (Lecomte et al. 2010). Second, parental care is biased toward males in the wandering albatross, i.e. males perform more frequent visits provisioning more food to their offspring than females (Weimerskirch et al. 2000). This bias may be due to sexual size dimorphism, males being larger and heavier than females (Shaffer, Weimerskirch & Costa 2001), and sex specific foraging areas, since males forage over the continental shelf edge while females move farther off in oceanic waters bordering the shelf edge. Thus, chick characteristics at fledging probably depend more on paternal than maternal foraging abilities. Our results also suggest that paternal effects do not persist until recruitment. Similarly, in rhesus macaque, maternal age was negatively related to early life survival but did not affect age of first reproduction (Hoffman et al. 2010). In a long-lived species such as the wandering albatross, owing to the very long period of immaturity, i.e. 9-10 years, inter-individual heterogeneity could be gradually weakened by viability selection (Nevoux, Weimerskirch & Barbraud 2010).

To conclude we found that paternal but not maternal age impacted offspring performance beyond the age of independence. Such paternal effects are rarely documented in wild populations and this result was, to our knowledge, the first to suggest a predominant effect of paternal age over maternal age. We suggest that this effect could be explained by sex-specific senescence in relation to ecological constraints. Since senescence seems to be widespread in animal populations (Nussey et al. 2013), we may expect transgenerational effects, having implications for both population dynamics and evolutionary processes, to be common in the wild.

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CHAPITRE 4

Variation in age of first reproduction

Crédit: Valentin Nivet-Mazerolles

- **Fay R.**, Barbraud C., Delord K. and and Weimerskirch H. 2016. Variation in the age of first reproduction: different strategies or individual quality? **Ecology**, 97(7), 1842-1851.

Variation in the age of first reproduction: different strategies or individual quality?

Abstract

Although age at first reproduction is a key demographic parameter which is probably under high selective pressure, it is highly variable and the cause of this variability is not well understood. Two non-exclusive hypotheses may explain such variability. It could be the expression of different individual strategies, i.e. different allocation strategies in fitness components, or the consequences of individual difference in intrinsic quality, i.e. some individuals always doing better than others in all fitness components. We tested these hypotheses in the Wandering albatross investigating relationships between the age at first reproduction and subsequent adult demographic traits. Using finite mixture capture recapture modeling, we demonstrate that the age at first reproduction is negatively related to both reproductive performances and adult survival, suggesting that individual quality was an important factor explaining variation in the age at first reproduction. Our results suggest that age at first breeding is a good predictor of quality in this long-lived seabird species.

1 Introduction

Age at recruitment (i.e. age at first reproduction) is a key demographic trait shaping life-history strategies (Stearns 1976; Gaillard et al. 2005). Variations in this parameter have strong impact for both evolutionary and ecological processes from individual to population level (McGraw & Caswell 1996; Ferrer, Otalora & GarcÍa-Ruiz 2004; Acker et al. 2014). Theoretical works showed that fitness is highly sensitive to changes in age at first reproduction (Stearns 1976) and this result was confirmed by empirical studies (McGraw & Caswell 1996; Oli, Hepp & Kennamer 2002; Krüger 2005). Intuitively, recruiting as early as possible should be the best strategy. Not only does early recruitment increases the number of lifetime reproductive attempts, it also increases fitness by shortening generation time (McGraw & Caswell 1996). Consequently, early reproduction should be at first glance favored by natural selection (Oli et al. 2002; Martin & Festa-Bianchet 2012). However, because individuals have a limited amount of energy available, life-history theory predicts that the advantages of early breeding could be balanced by associated costs (Stearns 1992). High breeding investment in early-life may depress survival probability (Clutton-Brock 1984; Viallefont, Cooke & Lebreton 1995) and accelerate senescence in old age (Kim et al. 2011; Nussey et al. 2006; Gustafsson & Pärt 1990). Such tradeoffs are particularly important in long-lived species because of high residual reproductive value in early-life. Indeed, in species with slow life history strategy and thus high life expectancy, early mortality is very costly since life-time reproductive success varies primarily with breeding longevity (Reid et al. 2003). The high early-life reproductive value in long-lived organisms probably explains why delayed reproduction is generally the rule in these species. Although age at recruitment seems to be under high selective pressure (McGraw & Caswell 1996; Oli et al. 2002; Krüger 2005), long-term studies regularly showed that age at recruitment can be highly variable within wild populations (Reed et al. 2003; Hadley et al. 2006). The variability in the age at first reproduction between populations or between years are usually explained by variations in environmental conditions and food availability, recruitment being often related to body condition (Gaillard et al. 2000; McMahon, Burton & Bester 2003). However, these environmental effects hardly explain the variations in recruitment age observed between-individuals that share the same environment. In such cases, individual variability is expected to arise from intrinsic factors that can be considered independently of environmental effects (Becker & Bradley 2007).

Two non-exclusive intrinsic mechanisms can explain heterogeneity in age at first reproduction. First, allocation strategies among different fitness components may differ between individuals (Roff 1992; Stearns 1992). Individual variations in life-history may emerge when environmental fluctuations are important because the best genotype in one environment is not necessarily the best in another environment (Reznick, Nunney & Tessier 2000), or when different strategies provide equivalent solutions to an ecological problem (Shuster & Wade 1991). Some studies suggested that the life-history continuum hypothesis described at the interspecific level may occur at the intraspecific level, with some individuals favoring survival compared to others investing more in reproduction (Reid et al. 2010; Meunier et al. 2012). Empirical studies have reported positive genetic covariance between the age at first reproduction and the later adult performances, providing support for the existence of the fast-slow continuum within populations (Charmantier et al. 2006; Blomquist 2009). In this context, age at first breeding could be linked to individual strategies, early recruitment occurring in individuals investing more in reproduction and late recruitment occurring in individuals favoring survival, resulting in a negative correlation between age at recruitment and survival.

Alternatively, but not exclusively, variations in the age at first reproduction may be explained by individual quality, i.e. “an axis of among-individual heterogeneity that is positively correlated with individual fitness” (Wilson & Nussey 2010). In the wild, the hypothesis of variations in individual quality is supported by observations of individuals having different performance levels that are consistent throughout life (Reid et al. 2003; McCleery et al. 2008; Lee et al. 2013). Positive correlations between life-history traits, e.g. survival and reproduction, are frequently reported although they are not predicted by life-history theory (Cam et al. 2002; Hamel et al. 2009). Such positive correlations between life history traits make sense if individuals vary in their abilities to acquire resources (Van Noordwijk & de Jong 1986). Since recruitment is expected to occur according to a tradeoff between current and future reproduction, variation in individual quality in relation to resource acquisition may strongly affect the recruitment process and age at first reproduction. As a consequence, it is expected that individuals of different quality recruit at different ages (Becker & Bradley 2007). In long-lived species, low quality individuals may recruit at old age, and some may not recruit at all as indicated by the observation of lower survival and recruitment probability for oldest immature age-class (Hadley et al. 2006; Aubry, Cam & Monnat 2009).

In practice, investigating how intrinsic factors affect recruitment is particularly challenging since it requires monitoring known-aged animals individually. Such individual-based data can generally only be obtained by marking individuals at birth. In this case, estimating recruitment into the natal population requires large sample sizes owing to commonly high juvenile mortality and dispersal rate in early-life (Clobert et al. 2001). Moreover, obtaining unbiased estimates of age at first reproduction may be challenging due to imperfect age-related detection and uncertainty in the assignment of reproductive status which are inherent in studies of wild populations. Finally, because the highest variations in recruitment age occur typically in long-lived species delaying their first reproduction, studying recruitment processes necessitates very long-term studies carried out over several decades, which are often complicated to run and difficult to maintain (Clutton-Brock & Sheldon 2010).

In this study, we analyzed a mark-recapture data set of 9685 known-aged Wandering albatrosses (*Diomedea exulans*) born over 48 years to explore the importance of individual quality and individual strategy on the age at first reproduction. To do this, we investigated the relationships between age at first reproduction and breeding success at recruitment, adult breeding probability, adult breeding success, and adult survival. In this long-lived species, recruitment ranges between 6 to 15 years with a peak around 9-10 year-old (Weimerskirch 1992). According to the trade-off hypothesis, we predicted that early recruitment should be associated with high adult breeding performances and low adult survival (Figure 1). Alternatively, based on the individual quality hypothesis, we predicted that early recruitment should be associated with both high breeding performances and high survival (Figure 1). Finally, we tested the prediction derived from both hypotheses that breeding success at first reproduction should decrease with recruitment age. Note that this last prediction is in contradiction with the common expectation that the breeding success of first time breeder increased with age owing to accumulating competence and experience in early-life (Forslund & Pärt 1995).

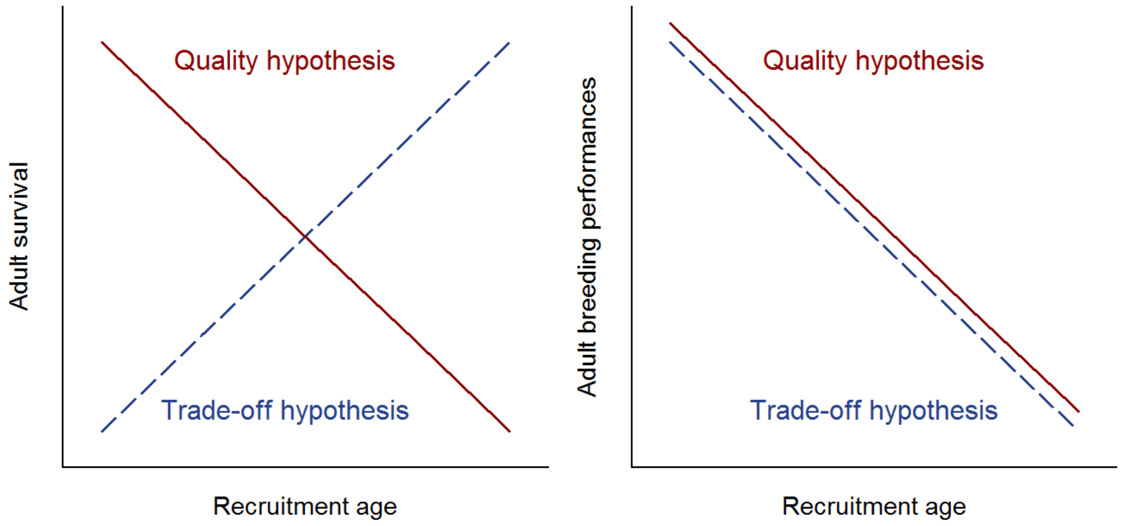

Figure 1: Variation of adult survival (a) and adult breeding performances (b) as a function of recruitment age predicted by the trade-off hypothesis and by the individual quality hypothesis.

2 Materials and Methods

2.1 Study species and field method

We studied the wandering albatross population of Possession Island in the Crozet Archipelago (46°S; 52°E), southern Indian Ocean, from 1965 to 2013. Monitoring started in 1960, but all chicks were ringed each year with a stainless steel band just before fledging from 1965. From early to mid-December pre-breeding adults are checked over the whole island. From mid-January (just after egg laying is resumed) to mid-February at least 3 visits were made every 10 days to identity the two members of each pair and their breeding status. All new individuals were ringed with a uniquely-numbered stainless steel-band. In mid-April June and August, nests were checked and the chick status recorded (alive/dead). During all visits, non-breeding individuals (mainly immatures) were searched for and their identity determined (from ring number) when possible. From mid-September to mid-October fledglings were ringed. Sex assignments were performed based on both field observations (i.e. sexual size and plumage dimorphism, mating behaviours) and genetic analyses since 1999 (appendix A1). Wandering albatrosses show a typical slow life history strategy with high adult survival rates and low productivity (i.e. quasi biennial reproduction and clutch size limited to one egg without replacement laying). Fledglings leave the colony alone, remaining at sea continuously until they return to their colony of birth from 3 year-old at the earliest (Weimerskirch 1992 and unpublished data). Recruitment occurs between 6 to 15 year-old. Females recruit earlier than males but both sexes show increasing recruitment probability until 9-10 year-old followed by a decrease at older age (Fay et al. 2015).

2.2 General model

Individual encounter histories were modeled using a multi-event approach (Pradel 2005). The model consisted in 7 states, 1 immature state, 5 adult states and the state dead (Figure 2), and five events. To consider individuals during the period of immaturity, we defined the Pre-Recruitment state (PrR) after which immature birds can recruit into the breeding population, i.e. lay an egg for the first time into the breeding population. Adult birds can transition into Successful Breeder state (SB), when the chick fledged, Failed Breeder state (FB), when the chick died before fledging, or recruited Non Breeder state (NB), when individuals that have recruited into the population (i.e. bred at least once) were observed as non-breeders at the colony. To model the sabbatical years spent continuously at sea after a year of reproduction, we added two unobservable states (Lebreton & Pradel 2002) corresponding to the two

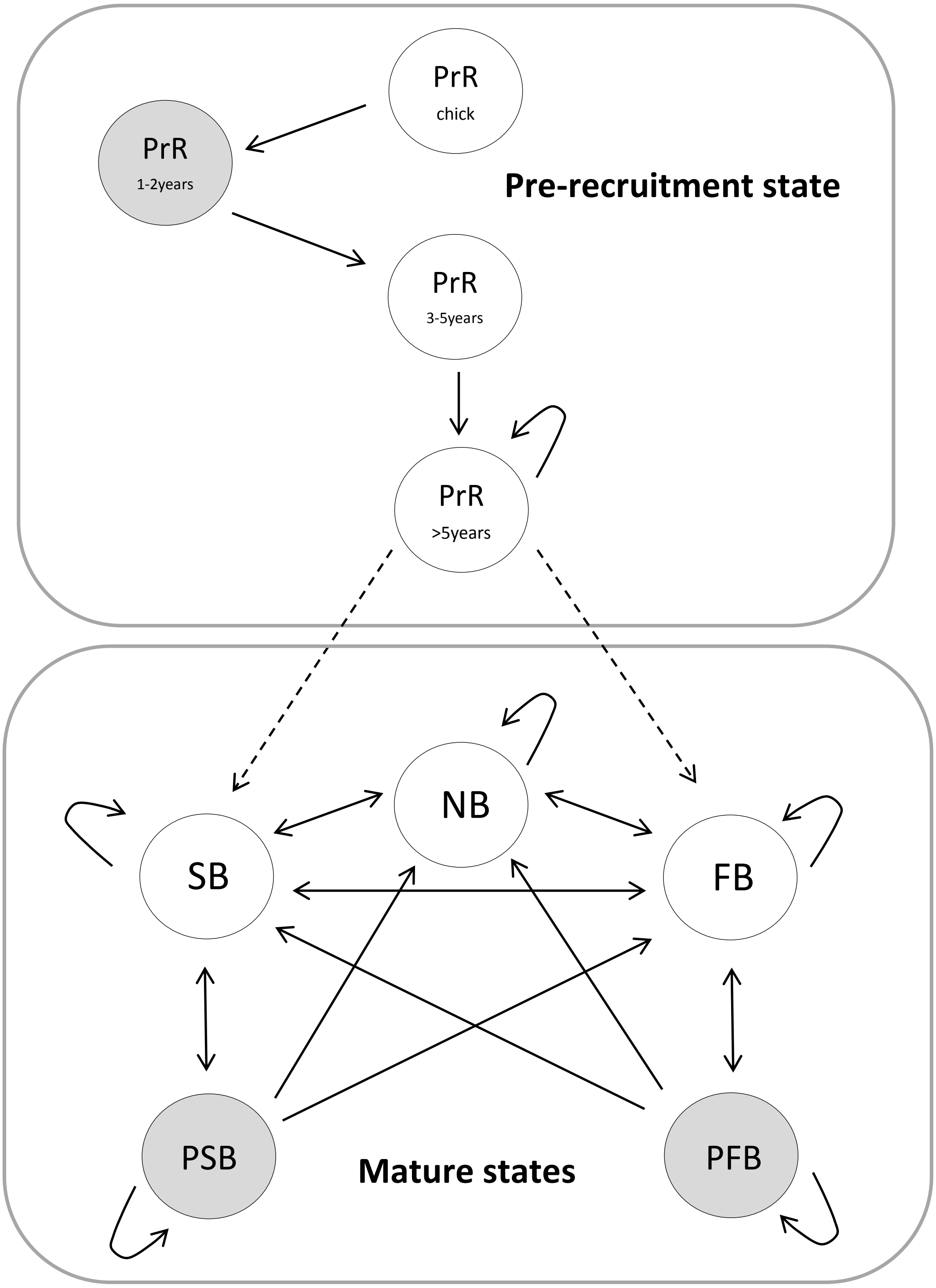

Figure 2 : Life cycle graph representing transitions between observable (white) or unobservable states (grey). All birds are ringed as chicks, thus individuals start in the Pre-Recruitment state (PrR). After fledging, all birds remain at least two years continuously at sea (i.e. juvenile stage). Pre-Recruitment state becomes observable from 3 years-old when birds start to return at the colony and are now considered as immature. From 6 years-old, birds can pass into the breeding group of the population though recruitment represented by dashed arrows. Then mature birds irrespectively of age can transit between mature states: successful breeder (SB), failed breeder (FB), recruited non breeder (NB), post successful breeder (PSB) and post failed breeder (PFB).

previous breeding states defined: Post Successful Breeder (PSB) and Post Failed Breeder (PFB). Thus, adults which are at sea (i.e. not at colonies for a whole year), are distinguished based on their most recent breeding state, the last time when they were observed at a colony. In our study, state assignment was not always certain since between 1966 and 1986, state assessment was unknown for a number of breeders; some individuals were classified as breeders but the success or failure was not always ascertained. Multi-event models allowed us to deal with state uncertainty by assessing the likelihood of an individual state given the events (i.e. observations) (Pradel 2005). We considered five events, i.e. five types of observation in the field, 0 = "not observed", 1 = "seen as non-breeder", 2 = "seen as a failed breeder", 3 = "seen as a successful breeder", 4 = "seen as a breeder but successful status not ascertained".

2.3 Pre-recruitment state and biological constraints

The initial state was constrained to the pre-recruitment state because all birds were banded as chicks. Then, from the first year of life to the fifth, transition probability to the pre-recruitment state was fixed to 1 because no recruitment occurred before 6 year-old. To model the pre-recruitment period we defined two stages: the juvenile stage, which was an unobservable stage, corresponding to the first 2 years of life spent continuously at sea (i.e. no individual of 1 or 2 year-old were observed at the colony), and the immature stage corresponding to non-recruited birds older than 2 years that started to visit the colony and could be potentially observed. Based on previous results from Fay et al. (2015), the immature stage was decomposed into three age classes: 3-8 years, 8-13 years and >13 years corresponding to the most parsimonious age structure to model the progressive change of survival rate in early life. Juvenile survival was set to be cohort dependent and both juvenile and immature survivals were assumed to be sex-dependent (Fay et al. 2015). Recapture probability of the immature stage was modelled as age dependent to fit the progressive return of individuals at the breeding colony before recruitment. From 6 years of age birds may recruit and transition into the mature states SB and FB depending both on sex and age. Recruitment rate was constrained to be constant after age 10 (Fay et al. 2015). For mature birds, following the results of Barbraud and Weimerskirch (2012), survival was assumed sex-dependent. Based on Pardo et al. (2014), we distinguished different survival probabilities for breeders and post reproductive breeders on one side and recruited non-breeders on the other side. Transitions were set to be state dependent. Since wandering albatrosses are monogamous and both sexes exhibit a quasi-biennial breeding, transitions were constrained to be equal between sexes. Recapture probabilities were assumed state dependent due to lower detection probability for observable non-breeders and failed breeders compared to successful breeders. Details of the models implemented with E-Surge are given in appendix D1.

2.4 Heterogeneity

To model individual heterogeneity in the age at first reproduction and its relation with adult demographic traits, we used finite mixture models (Pledger, Pollock & Norris 2003). These models allowed us to detect positive or negative correlation between demographic traits and thus to test our predictions. Based on the general model, we considered heterogeneity for adult states for both transition and survival parameters. Each mature state was duplicated (i.e. SB, FB, NB, PSB, PFB) into two groups with specific transition probabilities and adult survival. Individual birds would be split between groups in the likelihood framework based on how they transit between adult states (i.e. breeding frequencies, breeding success) and how they survive. At recruitment, each individual has a probability $\psi_{cst}^{R\to G1}$ to transition into the group 1 and a probability $\psi_{cst}^{R\to G2}(= 1 - \psi_{cst}^{R\to G1})$ to transition into the group 2, both being constant (cst). Once recruited in the breeding population in group Gj (= 1, 2) each individual has transition probabilities $\psi_{state}^{adGj\to adGj}$ and survival probabilities $\phi_{sex.state}^{adGj}$ (Figure 3).

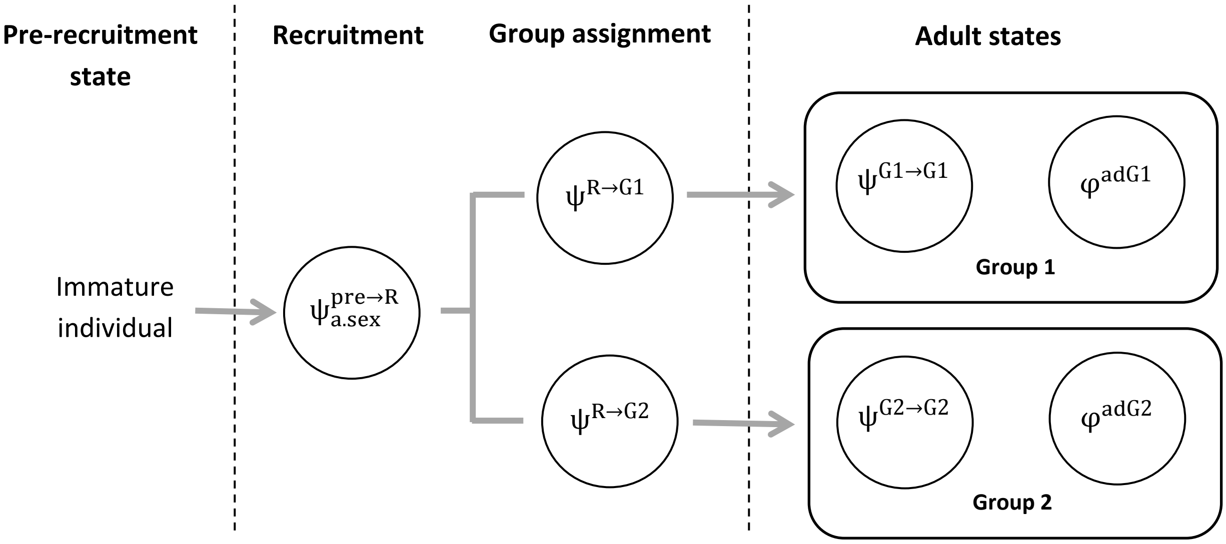

Figure 3: Graph summarizing the finite mixture model used. Immature individuals recruit differently according to their age and sex ($\psi_{a.sex}^{pre\to R}$), and may transition into group 1 or 2 ($\psi^{R\to Gj}, j = 1,2$) based on how they transit between adult states ($\psi^{adGj\to adGj}$) and how they survive (ϕ^{adGj}).

This model has the potential to detect correlations between survival and breeding processes, i.e. breeding probability and breeding success. If individuals differ in their strategies or level of performances, they would be separated in each group according to their pattern of transition between mature states. Thus, $\psi^{R\to G1}_{cst}$ is the key parameter at the interface between recruitment and adults traits that allowed us to investigate the covariations between age at first reproduction and adult performances. By investigating the age effect on this parameter, we could test if individuals recruiting at different ages adopted different strategies during adulthood or showed differences in quality, i.e. had consistently high or low breeding and survival performances. To summarize, our initial finite mixture model was: $\Phi^{pre}_{a_{(1to2)}.sex.cohort,age_{(3to8,>13)}.sex,age_{(9to13)}}$ $\Psi^{pre\to R}_{age.sex}$ $\Psi^{R\to G1}_{cst}$ for the immature component and $\Phi^{adG1}_{sex.state}$ $\Phi^{adG2}_{sex.state}\Psi^{G1\to G1}_{state}\Psi^{G2\to G2}_{state}$ $p^{pre}_{age}p^{ad}_{state}$ for the adult component, where the pre-recruitment (pre) survival probability (Φ) was age, sex and cohort dependent, the adult (ad) survival probability was sex and state dependent, the probability of transition (Ψ) from pre-recruitment to adult through recruitment (R) was age and sex dependent, the probability of transition into the group 1 (G1) given recruitment was constant, the pre-recruitment capture probability (p) was age dependent, and the adult capture probability was state dependent. In this model notation, symbol "." indicates interactive effects, "1to2" and "3to8" indicate that age classes were grouped and ">13" indicates that age classes were grouped after 13 years.

2.5 Estimation of breeding performances

Since our model had full state dependent transitions, we did not have direct access to breeding probability and breeding success estimates. Both were calculated from the outputs of the multievent modeling. For a given state, breeding probability is the probability to be in success plus the probability to be in failure. The breeding success is the ratio between the probability to be in success and the probability to reproduce (with success or not). 95% confidence intervals for these derived estimates were obtained with a bootstrap method as described in appendix D2.

2.6 Model selection and goodness-of-fit

All models were run using program E-SURGE (Choquet, Rouan & Pradel 2009b). Model selection was done using Akaike Information Criteria (AIC, Burnham & Anderson 2002). A model averaging approach was used to estimate demographic parameters when models had a $\Delta AIC < 2$ since they were not considered meaningfully different (Burnham & Anderson 2002). Model selection was done for parameters modelling the breeding success at recruitment ($\psi^{R\rightarrow BS}$), and group assignment ($\psi^{R\rightarrow Gj}, j = 1,2$). To investigate the relation between the age at first reproduction and both breeding success at recruitment and adult performances, we used a logistic model: logit(ψ) = β0 + β1 * xi , where ψ is a demographic parameter, β0 is an intercept parameter, β1 is a slope parameter, and xi is the age of individual i at recruitment. We tested linear, quadratic and log inverse relationships for breeding success at recruitment, and both linear and quadratic effects for group assignment. There is no test available to assess the goodness-of-fit (GOF) of multi-event models. Hence, we performed GOF tests using program U-CARE (v.2.3.2, Choquet et al. 2009a) on a simplified dataset which distinguished solely successful breeders from failed breeders and assigned randomly a reproductive status, i.e. failed or successful, to each individual for which no information was available (Pradel 2005). A variance inflation factor (ĉ) was taken into account by correcting AIC for extra-binomial variation.

3 Results

Goodness of fit tests (χ2 = 1003.4, df =749, P <0.001 for females and χ2 =1263.8, df =898, P <0.001 for males) indicated that the general JMV model did not fit the data correctly (see Table A1 for detailed comments). We thus used a variance inflation factor (ĉ = 1.37) for model selection. Results suggest that the breeding success at recruitment varied with age without significant differences between sexes. Individuals that recruited at 6 year-old appeared to be significantly less successful than those recruiting at older ages (Table D1 SM1 vs SM3: ΔAIC = 3, Figure 4). For individuals recruiting at 7 year-old and older, we found, based on multi-model inference accounting for uncertainty in model selection (AIC weight), that the breeding success at recruitment was negatively related to recruitment age. Model averaged estimates indicated that breeding success at recruitment declined from 0.519±0.039 at 7 year-old to 0.385±0.131 at 15 year-old (Figure 4).

Using finite mixture models we found strong support for individual heterogeneity (Table 1, M1 vs M2: ΔAIC = 272). We found a positive covariation between adult survival, breeding probability and breeding success. Individuals from the first group (1, higher quality individuals) had high breeding probabilities whatever their previous state, i.e. post-success, failed or non-breeder, associated with a high survival probability (0.973±0.003). In contrast, individuals from the second group (2, lower quality individuals) had lower breeding frequency with breeding probabilities varying

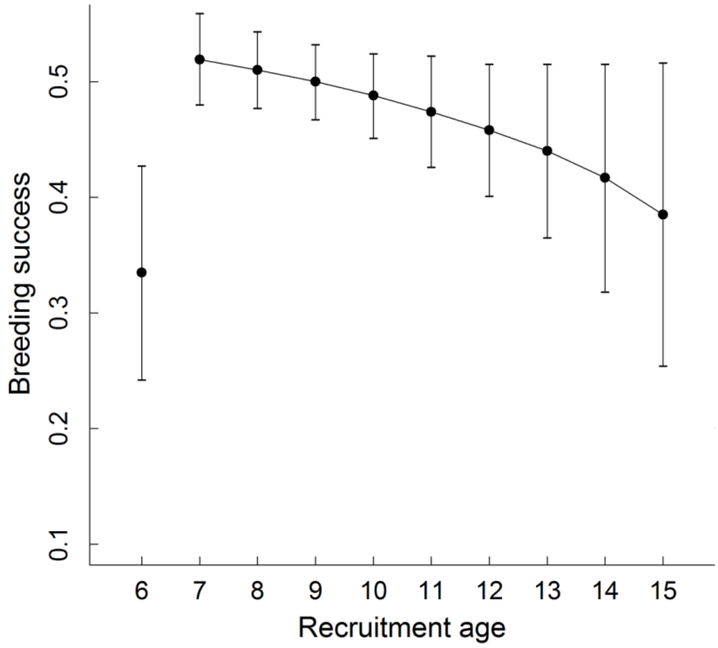

Figure 4: Breeding success at first breeding event in relation to recruitment age for wandering albatrosses from Crozet Island from 1965 to 2012. Estimates (±SE) came from the model averaging over all the models presented in table 1.

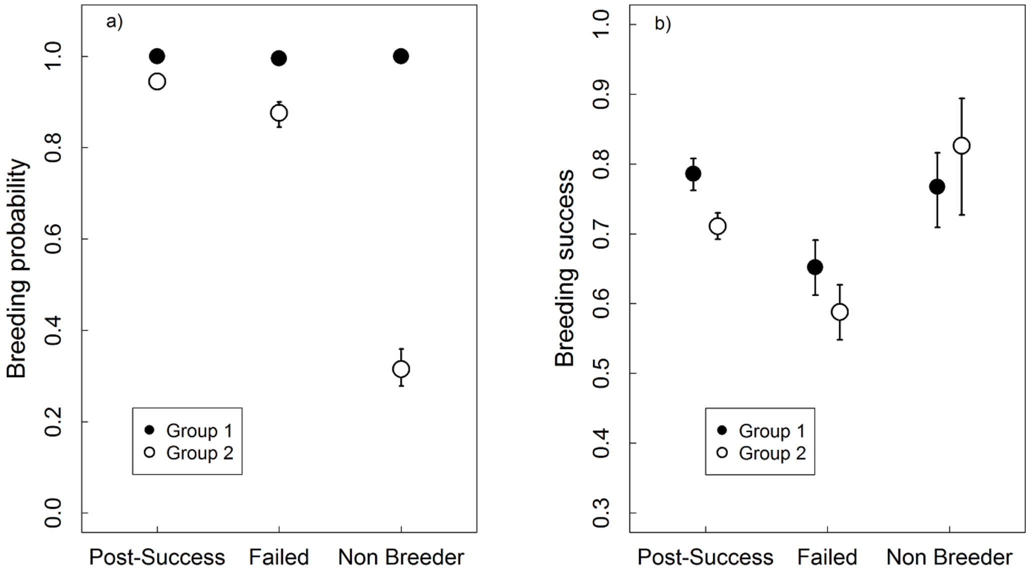

Figure 5: Heterogeneity in breeding probability (a) and breeding success (b) considering the previous breeding state for adult wandering albatrosses from Crozet Island from 1965 to 2012. Estimates were calculated from the outputs of M6 (Table 1) and ±95% confidence intervals were obtained with a bootstrap method (appendix D2).

between 0.315±0.026 to 0.944±0.010 depending on the previous state (Figure5a), and lower survival probability (0.959±0.003).Furthermore, given reproduction, breeding success was higher for individuals from the first group than for those from the second group (Figure 5b), except for observed non breeders but this latter state represented less than 7% of all adults. Average breeding success weighted by the proportion of individuals in each state was 0.735 for individuals in the first group and 0.684 for individuals in the second. On average, 36.1% ± 0.5% of birds belonged to the first group and 63.9% ± 0.5% to the second group with no clear evidence for differences between sexes (Table 1, M2 vs M3: ΔAIC = 0.45). Allowing this proportion to vary as a function of age at recruitment improved significantly our model (Table 1, M2 vs M5 & M6: ΔAIC = 4), suggesting a negative relationship between the age at first reproduction and adult performances (survival, breeding probability, breeding success). The probability to be in the first group declined rapidly after 8 year-old, both linear and quadratic trends being equivalently supported (Figure 6). This negative relationship was consistent both between years and cohorts suggesting that this pattern was independent of environmental conditions (Figure D1).

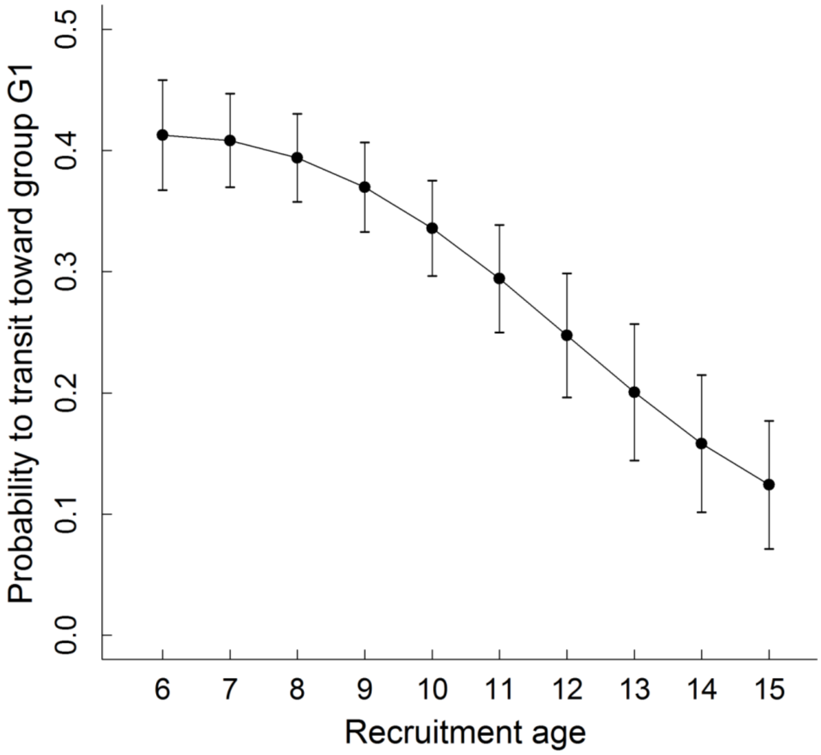

Figure 6: Heterogeneity in relation to the age at first reproduction: transition probability into group 1 (±SE) in relation to recruitment age. Estimates were derived from model averaging of M5 and M6 (Table 1).

4 Discussion

Our study suggested that individual quality was an important factor to explain variations in the age at first reproduction. Age at recruitment was negatively related to both reproductive and survival adult performances, as predicted by the *individual quality hypothesis*. The *trade-off hypothesis* was not supported by our analyses, since age at recruitment was negatively related to adult survival performances.

4.1 Heterogeneity in adult demographic traits

Our results provide strong support for individual heterogeneity in adult demographic traits with positive covariations between reproductive rate, breeding success and survival. Such positive covariations at the intra-population level are not predicted by life-history theory, although they have been reported in a number of taxa and interpreted as a consequence of variability in individual quality (Cam et al. 2002; Hamel et al. 2009). Theoretically, positive correlations between life-history traits at the individual level could be explained by variations in the ability of individuals to find resources (Van Noordwijk & de Jong 1986). Thus, variations are expected to derived from between-individual phenotypic differences which are often difficult to define consistently (Moyes et al. 2009).

In our model, individual heterogeneity was modelled through two classes where adults had their proper demographic parameters. Importantly, although our model used two classes, the results should not be interpreted as providing evidence of the existence of two classes (Pledger et al. 2003). Rather, individual quality may be viewed as a continuous variable, similarly to “frailty” (Vaupel, Manton & Stallard 1979), that we partly captured with our model through two classes. The detection of a strong individual heterogeneity within each group supports this interpretation. For example, the breeding success of individuals from the failed-breeder state was still lower than those from the post-success state in both groups. This result suggests that within each group, failed breeders may be individuals of lower quality since they had higher probability to fail again compared to birds being successful in their last breeding attempt.

4.2 Recruitment age and adult performances

In accordance with the hypothesis of individual quality, we found a negative relationship between recruitment age and adult performances. Individuals that recruited early had both higher breeding performances and higher adult survival than those that recruited at advanced ages. Previous studies have suggested that individual recruiting early in life are not a random subgroup of the population and could be individuals of higher quality (Viallefont et al. 1995; Oli et al. 2002; Zhang et al. 2015). Early recruiting females red deer *Cervus elaphus* calved earlier in the season and produced heavier offspring at birth (Nussey et al. 2006), and common terns *Sterna hirundo* recruiting at younger ages showed a stronger increase in body mass and a better improvement of breeding performance in early-life (Becker et al. 2008). Recruitment age has also been linked to long-term adult performances. It was reported that young recruits produced more offspring over their life span (Descamps et al. 2006; Dugdale et al. 2011; Kim et al. 2011; Martin & Festa-Bianchet 2012) and that late recruitment was associated with higher adult mortality rate (Hawn, Radford & du Plessis 2007; Aubry et al. 2011; Bosman et al. 2013). In our study, we reported positive correlation between early recruitment and four life history traits. Early first-time breeders had higher breeding success at recruitment, higher reproductive rate and breeding success after recruitment, and higher adult survival probability.

Individual quality is assumed to be related to the ability of individuals to find resources (Van Noordwijk & de Jong 1986). Such variations may affect the body condition of non-recruited individuals which is a determining factor for the decision to engage or not into the breeding population (Martin & Festa-Bianchet 2012). Indeed, individuals should recruit when their condition allows them to avoid any cost of reproduction. This is particularly important in long-lived species where survival is strongly canalized against temporal variability (Sæther & Bakke 2000). In such context, delayed recruitment is interpreted as a life-history adaptation that maximizes fitness under given constraints (McNamara & Houston 1996). This theoretical hypothesis was largely developed into the reaction norm literature (Stearns & Koella 1986) and is supported by empirical studies. For example, early reproducers were larger for their age in African elephant *Loxodonta africana* (Lee et al. 2013) and bighorn sheep *Ovis canadensis* (Martin & Festa-Bianchet 2012), suggesting that immature individuals delaying recruitment are individuals that have not accumulate enough resources to reach breeding condition. Concordant results have been provided for wandering albatross with breeders being heavier than non-recruited birds at the same age, and only individual attaining a certain mass threshold being able to reproduce (Weimerskirch 1992). Low quality individuals recruiting later in life are thus expected to make “the best of a bad job”.

Although this adaptive interpretation, equivalent to the restraint hypothesis, is robustly based on theoretical and empirical evidence, delayed recruitment of low quality individuals may also be due to constraints (Curio 1983). Beyond adaptive decision, low quality individuals could suffer from poorer access to breeding territories or nest sites due to competition (Camacho, Canal & Potti 2013) and/or have limited access to mating because of a lack of attractiveness due to condition-dependent expression of secondary sexual character (Andersson 1994).

4.3 Breeding success at recruitment

Contrary to the predictions from the individual quality hypothesis and from the trade-off hypothesis, we found that the breeding success of 6 year-old first-time breeders was lower than those that recruited later. In long-lived species, breeding success for first time breeders is often expected to increase with age owing to age-related improvements of competence (Forslund & Pärt 1995). As individuals become older, they improve their foraging efficiency, arrive earlier at the breeding grounds, acquire higher quality territories and lay earlier in the breeding season; all having positive effects on breeding success [foraging efficiency (Limmer & Becker 2009); quality territory (Pärt 2001); timing (Verhulst & Nilsson 2008)]. In accordance with these expectations, studies focusing on breeding success at recruitment documented increasing breeding success of first-time breeders with age (Krüger 2005; Aubry et al. 2009). However, for wandering albatrosses, this improvement was only observed between age 6 and 7. For those recruiting after 6 years of age, as predicted by our tested hypothesis, model selection supported a decreasing breeding success with recruitment age. This pattern concerned most of the recruitments since 98% of birds recruit after 6 years-old (Fay et al. 2015). In such long-lived species with long immature stage, first-time breeders may have the same foraging skills as experienced breeders, birds starting to breed only when they have attain a mass threshold, and good foraging skills. Also, wandering albatrosses are very long-lived and have overall a very high breeding success compared to most other species, making them extreme cases. It appears that the more a species delays reproduction, the less breeding success increases with age at first reproduction (Newton, Marquiss & Moss 1981; Krüger 2005; Aubry et al. 2009; Blas, Sergio & Hiraldo 2009). However, this age related pattern has rarely been investigated and seems difficult to detect. The negative relationship that we showed between recruitment age and breeding success was not found in a previous study on the same population (Weimerskirch 1992) and was here rather subtle even with large sample sizes. This might be explained by the conservative strategy adopted by young individuals in long-lived species. If each individual recruits when it reaches a condition at which costs of reproduction can be avoided, between individual differences in breeding success in the first reproductive event could be attenuated. Indeed, lower quality individuals could offset their intrinsic inferiority by delaying their first reproduction for longer, increasing in this way their experience and body condition.

5 Conclusion

Our study suggests that variability in individual quality may be an important factor explaining variations in recruitment age. Intrinsic individual differences associated with a conservative reproductive strategy could explain the high variability of recruitment age in the wandering albatross, leading to strong relationships between this trait and adult demographic rates. Finally, although there is increasing evidence of individual demographic heterogeneity in wild populations, very few studies assessed the impact of individual heterogeneity on demographic processes. More studies are needed to better understand the ecological effects of trait variations within species, and the different pattern occurring between species.

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CHAPITRE 5

Individual heterogeneity in a long-lived seabird

Crédit: Valentin Nivet-Mazerolles

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From early-life to senescence: individual heterogeneity in a long-lived seabird.

Abstract

Although population studies have long assumed that all individuals of a given sex and age are identical, ignoring among-individual differences may strongly bias our perception of eco-evolutionary processes. Individual heterogeneity, often referred as individual quality, has been an increasing research area in the last decade. However, there are still substantial gaps in our current knowledge. For example, there is little information on the relationship between individual heterogeneity for various life-history traits taken into consideration simultaneously and studies describing individual heterogeneity in wild populations are generally not able to jointly identify possible sources of this variation. Here, based on a mark-recapture data set of 9,685 known-aged wandering albatrosses *Diomedea exulans*, we investigated the existence of individual quality over the whole life cycle of this species, from early-life to senescence. Using finite mixture models, we investigated the expression of individual heterogeneity between various demographic traits and the origin of these among-individual differences considering the natal environmental conditions. We found that some individuals consistently outperformed others during most of their life, except at older age since senescence was stronger in individuals that showed high performances. Variations in individual quality seemed strongly affected by extrinsic factors experienced during the ontogenetic period. We found that individuals born in years with high population density tended to have lower performances during their lifespan, suggesting delayed density dependence effects through individual quality. Our study showed that between-individual differences could be importance features structuring individual life history trajectories with substantial consequences at higher ecological level such as population dynamics. Although age at first reproduction is a key demographic parameter which is probably under high selective pressure, it is highly variable and the cause of this variability is not well understood. Two non-exclusive hypotheses may explain such variability. It could be the expression of different individual strategies, i.e. different allocation strategies in fitness components, or the consequences of individual difference in intrinsic quality, i.e. some individuals always doing better than others in all fitness components. We tested these hypotheses in the Wandering albatross investigating relationships between the age at first reproduction and subsequent adult demographic traits. Using finite mixture capture recapture modeling, we demonstrate that the age at first reproduction is negatively related to both reproductive performances and adult survival, suggesting that individual quality was an important factor explaining variation in the age at first reproduction. Our results suggest that age at first breeding is a good predictor of quality in this long-lived seabird species.

1 Introduction

Population studies have long implicitly assumed that all individuals of a given sex and age are identical, but between-individual differences are widespread within species in all biological aspects of an individual (Bolnick et al. 2011). Neglecting individual heterogeneity may affect our understanding of empirical observations leading to spurious conclusions. For instance, processes acting at the individual scale may be very different from the average patterns observed at the population scale (Vaupel & Yashin 1985). Ignoring among-individual differences could hide fundamental biological processes such as senescence (Nussey et al. 2008) or trade-offs between life-history traits (Hamel et al. 2009a). Consequences of individual heterogeneity are not limited to individual patterns since it could also affect population dynamics (Benton, Plaistow & Coulson 2006), including asymptotic population growth rate and population stability (Kendall et al. 2011). Thus, the working assumption considering that all individuals are identical within a population or a component of a population is not sustainable since it could be the source of important bias in our perception of ecological processes.

Although individual differences leading to contrasting life history trajectories constitute a fundamental condition of the theory of natural selection (Darwin 1859), heterogeneity among individuals appears to be a concept difficult to define and a trait hard to measure (Wilson & Nussey 2010; Bergeron et al. 2011; Cam et al. 2012). This elusive aspect of individual heterogeneity has been explicitly formulated through the expression of latent or unobservable individual heterogeneity (Cam et al. 2002). Depending of their field, the authors have tackled individual heterogeneity in different ways using various terms such as frailty (Vaupel, Manton & Stallard 1979), state (McNamara & Houston 1996), or quality (Wilson & Nussey 2010), but all these authors agree that intrinsic individual factors, independently of age and sex, modify consistently reproduction and survival performances. Recently, this biological interpretation of individual heterogeneity has been questioned by a series of articles adding a new level of difficulty (Tuljapurkar, Steiner & Orzack 2009; Steiner & Tuljapurkar 2012). These authors stated that chance alone accounted for most of the observed variations of individual life histories in the wild, without the necessity of an underlying individual heterogeneity in vital rates. They used the term dynamic heterogeneity to describe variation in individual performances that arise from the stochastic nature of individual life trajectories, equivalent to a Markovian transition among biological states. However, recent research has raised weaknesses in the inference methods used in these studies leading to question the relevance of their conclusion (Plard et al. 2012; Bonnet & Postma 2016; Cam, Aubry & Authier 2016). Both biological and dynamic heterogeneity are probably important to explain the high variability in individual life history trajectories (Cam et al. 2012; Plard et al. 2012; Chambert et al. 2013) and more importantly, both sources of variability need to be considered simultaneously to ensure reliable inferences (Cam et al. 2016).

The observation of fixed individual heterogeneity could be traced back to the seminal work of David Lack (Lack 1954) which noted consistent differences in clutch-size between individuals that shared the same environment. In the last decades, based on long-term individual monitoring in wild populations, numerous studies documented unexpected correlation between vital rates, showing that some individuals consistently outperformed others. Contrary to what is expected from life-history theory regarding trade-offs between life-history traits (Stearns 1992), it was found that breeding success and survival could be positively related (Bérubé, Festa-Bianchet & Jorgenson 1999; Cam et al. 2002), as well as previous reproductive state and current breeding probability (Hamel et al. 2009a; Jenouvrier, Peron & Weimerskirch 2015), secondary sexual character allocation and survival (Bergeron et al. 2008), or that age at first and last reproduction could be negatively related (Charmantier et al. 2006; Aubry et al. 2011). All these results are difficult to explain without involving individual differences. Theoretically, individuals showing high performances are expected to acquire more resources (Van Noordwijk & de Jong 1986). This prediction was empirically supported by studies demonstrating that consistent among-individual heterogeneity in reproductive and survival performances were related to diet specialization and foraging performance (Annett & Pierotti 1999; Lescroël et al. 2010). Thus, at least part of the differences in individual life-history trajectories may occur from individual biological differences affecting energy acquisition (Reznick, Nunney & Tessier 2000).

On the other hand, it could be argued that spatial heterogeneity alone may create such individual variation in life trajectories without involving intrinsic differences between the individuals. Indeed, individuals experiencing different environmental conditions can lead to individual heterogeneity in demographic rates (Griffen & Norelli 2015). However, there is strong evidence that local individual distribution of mobile organisms in heterogeneous habitats is not random at all. Spatial distribution seems closely related to individual features (Coulson 1968; Camacho, Canal & Potti 2013), more competitive individuals may access to high quality habitats constraining dominated individuals to settle in marginal habitats (van de Pol et al. 2007; Oro 2008). Therefore, spatial heterogeneity makes the comprehension of among-individual variation even more difficult, but does not bring into question the concept of fixed heterogeneity as intrinsic individual differences. Consistently, individual heterogeneity has been documented in laboratory populations under controlled environments and in wild populations in non-territorial species such as pelagic seabirds (Fay et al. 2016).

Individual heterogeneity has been an increasing research area in the last decade, but there are still substantial gaps in current knowledge. For example, it is generally accepted that among-individual difference arises from both genetic and non-genetic factors, but studies describing individual heterogeneity in wild populations are not able, in the vast majority of cases, to jointly identify possible sources of this variation. Furthermore, owing to the difficulties with measuring individual heterogeneity, in particular with the problems of parameters identification associated with multiple random effects (e.g. Knape et al. 2011), most of the studies investigated heterogeneity in one or two specific traits. Thus, there is little information on the relationship between individual heterogeneity for various life-history traits taken into consideration simultaneously.

Since the investigation of individual heterogeneity have been addressed in various ways leading to confusion and ambiguity (Wilson & Nussey 2010), we need to define accurately our conception of among-individual heterogeneity. The comprehensive approach adopted in this study is often referred as individual quality. We retain the working definition of Wilson and Nussey (2010), “an axis of among-individual heterogeneity that is positively correlated with fitness”. In our thinking of individual quality, we consider that it is an unmeasured feature of phenotype and thus a fixed property of each individual (Cam et al. 2012). The static character of individual quality was supported through individuals maintaining higher performances level across a large range of environmental conditions. Under extreme conditions, it appears that individual quality is not reversed or attenuated but exacerbated (Chambert et al. 2013; Jenouvrier et al. 2015).

Long-lived seabirds are a convenient model for population demographic studies because they breed in large colonies and show high philopatry. They are also suitable model species for studies on individual heterogeneity owing to their long life-span that allow to investigate the repeatability of demographic performances over time and their non-territorial foraging behavior that relax the potential effect of spatial heterogeneity. Here, based on a mark-recapture data set of 9,685 known-aged wandering albatrosses

Diomedea exulans, we investigated the existence of individual quality over the whole life cycle, from fledging to senescence. Using finite mixture models that allow us to deal with the elusive character of individual quality while taking into account both dynamic and fixed heterogeneity, our main objective was to gain insight into the expression of individual heterogeneity between various demographic traits including, early-life survival, recruitment rate, breeding success at first reproduction, adult breeding probability, adult breeding success and adult survival considering actuarial senescence. Since consistent individual variations in vital rates could come from early-life environment having long term effects on phenotypes (Lindström 1999), adverse conditions experienced during ontogeny may affect future mortality and fecundity. Thus, by estimating cohort average quality, we investigated the origin of this heterogeneity through natal environmental conditions considering climatic factors and population size. We predicted (1) that inferences made from mixture models would support the quality hypothesis with some individuals consistently outperforming others, (2) that there is cohort variation in average quality, i.e. cohort specific probability to be associated to quality groups of the mixture model, and (3) that a part of these variations could be explained by the early-life environmental conditions.

2 Materials and Methods

2.1 Study species and field method

We studied the wandering albatross population of Possession Island in the Crozet Archipelago (46°S; 52°E), southern Indian Ocean, from 1965 to 2013. Monitoring started in 1960, but all chicks were ringed each year with a stainless steel band just before fledging from 1965. From early to mid-December pre-breeding adults were checked over the whole island. From mid-January (just after egg laying is resumed) to mid-February at least 3 visits were made every 10 days to identity the two members of each pair and their breeding status. All new individuals were ringed with a uniquely-numbered stainless steel-band. In mid-April June and August, nests were checked and the chick status recorded (alive/dead). During all visits, non-breeding individuals (mainly immatures) were searched for and their identity determined (from ring number) when possible. From mid-September to mid-October fledglings were ringed. Sex assignments were performed based on both field observations (i.e. sexual size and plumage dimorphism, mating behaviours) and genetic analyses since 1999 (appendix A1).

Wandering albatrosses show a typical slow life history strategy with high adult survival rates and low productivity (i.e. quasi biennial reproduction and clutch size limited to one egg without replacement laying). Fledglings leave the colony alone, remaining at sea continuously until they return to their colony of birth from 3 year-old at the earliest (Weimerskirch 1992) and unpublished data). Recruitment occurs between 6 to 15 year-old. Females recruit earlier than males but both sexes show increasing recruitment probability until 9-10 year-old followed by a decrease at older age (Fay et al. 2015).

2.2 General model

The capture-recapture dataset was modeled with the same multi-event model (Pradel 2005) structure used by Fay et al. (2016) on the same population. Briefly, the model consisted in 7 states, 1 immature state, 5 adult states and the state dead (Figure C1) and five events. We defined the Pre-Recruitment state (PrR) to consider individuals during the period of immaturity, Successful Breeder state (SB), when the chick fledged, Failed Breeder state (FB), when the chick died before fledging, or recruited Non Breeder state (NB), when individuals that have recruited into the population (i.e. bred at least once) were observed as non-breeders at the colony, and finally two unobservable states, Post Successful Breeder state (PSB) and Post Failed Breeder state (PFB), to model the sabbatical years spent at sea after the reproduction. Then, biological constraints were applied regarding sex, age and time dependence, based on previous results from Fay et al. (2015), as follows. The PrR state was divided in two stages: the juvenile stage, which was an unobservable stage, corresponding to the first 2 years of life spent continuously at sea (i.e. no individual of 1 or 2 year-old were observed at the colony), and the immature stage corresponding to non-recruited birds older than 2 years that started to visit the colony and could be potentially observed. The immature stage was decomposed into three age classes: 3-8 years, 8-13 years and >13 years corresponding to the most parsimonious age structure to model the progressive change of survival rate in early-life. Juvenile survival was set to be cohort dependent and both juvenile and immature survival rates were assumed to be sex-dependent. From the age of 6, immature birds can recruit into the breeding population, i.e. lay an egg for the first time into the breeding population. Recruitment rate depended both on sex and age and was constrained to be constant after age 10. For adult states, survival was assumed sex and state dependent distinguishing between NB and the others states (Pardo, Barbraud & Weimerskirch 2014). Actuarial senescence was estimated modelling adult survival as a quadratic function of age. Actuarial senescence rate was constrained to be equal between states. Transitions were set to be state dependent, but since wandering albatrosses are monogamous and both sexes exhibit a quasi-biennial breeding, transitions were constrained to be equal between sexes. For more details on the starting general model and parametrization, readers are invited to consult Fay et al. (2016).

2.3 Heterogenity

We used finite mixture models to investigate individual heterogeneity (Pledger, Pollock & Norris 2003). These models, using clustering among-individuals, allowed dealing with a latent heterogeneity without a priori criteria (Hamel, Yoccoz & Gaillard 2016). Based on the general model, we investigated individual heterogeneity for both immature and adult states considering survival and transition parameters. Each immature and mature state (i.e. PrR, SB, FB, NB, PSB, PFB) was duplicated constituting two groups with specific survival and transition probabilities (Figure 1). In this model, individuals would be split between two groups in the likelihood framework based on their life history trajectory, i.e. how they survived and transited between states. The number of groups is a critical issue for mixture models but it was stated that two-heterogeneity groups could be used for hidden variable following a unimodal distribution (Pledger 2005). In our case, assuming a unimodal distribution for individual quality, as often suggested for frailty, seemed reasonable since we defined it as an individual phenotypic characteristic which is determined by many factors acting simultaneously.

Each mixture component being characterized by specific parameters, we anticipated according to the individual quality theory that one group will include individuals with higher vital rates, i.e. higher breeding probability, higher breeding success, higher survival, while the other group will bring together individuals with lower performances. Our model took into account both fixed and dynamic heterogeneity since within each mixture (fixed component), individual life trajectory was modelled as a Markovian process (dynamic component). Even if an individual is assigned to the group with higher performance probabilities, misfortune may theoretically results in lower life time reproductive success compared to a lucky individual in the second group. This versatility is reflected in the individual group assignment within a probabilistic framework. Individuals are not set in a particular group but have a probability to belong to the first or second group. Thus, in accordance with the conceptual view of individual quality adopted in this study, individual quality assignment is positively correlated, but not confounded, with fitness. This is consistent with our conception of quality as a fixed property of a phenotype that exists a priori, regardless of the individual’s realized history.

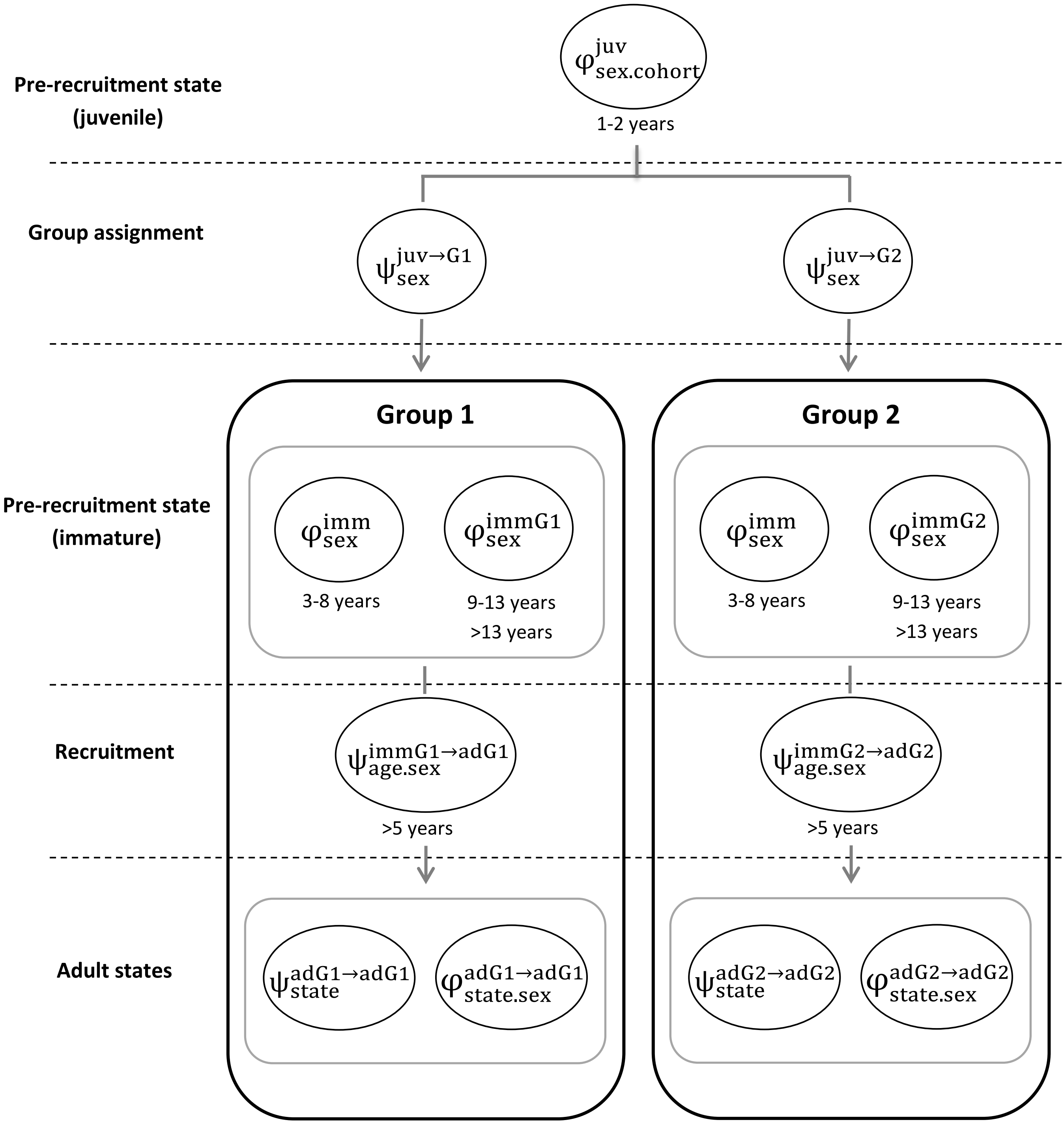

Figure 1: Graph summarizing the finite mixture model used. After juvenile mortality took place ($\varphi^{\text{juv}}_{\text{sex.cohort}}$), individuals may transition into group 1 or 2 ($\psi^{\text{juv}\rightarrow\text{Gj}}_{\text{sex}}$, j = 1,2) according to their life history trajectory including immature survival ($\varphi^{\text{immGj}}_{\text{sex}}$), recruitment probability ($\psi^{\text{immGj}\rightarrow\text{adGj}}_{\text{age.sex}}$), adult breeding parameters ($\psi^{\text{adGj}\rightarrow\text{adGj}}_{\text{state}}$) and adult survival ($\varphi^{\text{adG1}\rightarrow\text{adG1}}_{\text{state.sex}}$).

Preliminary analyses indicated that juvenile survival may drive individual assignment toward group 1 or 2 owing to the high variability of this parameter (Fay et al. 2015). Thus, group assignment was performed after modelling cohort specific juvenile survival (Figure 1). At this point, each individual has a probability $\psi_{sex}^{juv \to G1}$ to transition into the group 1 and a probability $\psi_{sex}^{juv \to G2} (= 1 - \psi_{sex}^{juv \to G1})$ to transition into the group 2, as a function of sex. Once assigned in group Gj (= 1, 2), each immature individual has survival probabilities $\phi_{age.sex}^{immGj}$ and recruitment probabilities $\psi_{age.sex}^{immGj \to immGj}$. For parameters to be identifiable, 3-8 years immature survival was constraint to be equal between groups. After recruitment, each individual has transition probabilities $\psi_{state}^{adGj \to adGj}$ and survival probabilities $\phi_{sex.state}^{adGj}$ (Figure 1). Once an individual is assigned in group j, defined by the set of parameters presented above, it cannot transition in the other group. Finally, to gain insight about the origin of individual heterogeneity, we estimated cohort specific assignment toward each mixture, i.e. $\psi_{sex+cohort}^{juv \to Gj}$. Environmental conditions experienced early in life may have long-term effects on individual fitness (Lindström 1999). Thus, we investigated the effect of natal environment condition on the cohort specific probability to belong to group j. We selected two variables which are expected to affect ontogeny at the pre-fledging and/or post-fledging stage: the Sea Surface Temperature on paternal foraging grounds during chick rearing, and the population density the year of birth estimated by the annual breeding population (Fay et al. 2015). We fitted the logistic model: logit($\psi_{sex}^{juv \to Gj}$) = β0 + β1 * xn , where $\psi_{sex+cohort}^{juv \to Gj}$ is the cohort specific transition probability into group j, β0 is an intercept parameter, β1 is a slope parameter, and xn is the covariate x the year of birth for the cohort n. We tested both linear and quadratic effects for group assignment. Significance of relationships were assessed by an analysis of deviance test with a Fisher-Snedecor distribution (ANODEV; Grosbois et al. 2008). The percentage of variation that was explained by a covariate (r^2) was estimated as: $r^2 = [(\mathrm{Dev}(F_{cst}) - \mathrm{Dev}(F_{cov})]/[\mathrm{Dev}(F_{cst}) - \mathrm{Dev}(F_t)]$ (Skalski 1996).

To summarize, our initial finite mixture model was:

$\Phi_{age_{(1to2)}.cohort+sex}^{juv}\ \Psi_{sex}^{juv \to G1}\ \Phi_{age_{(3to8)}.sex}^{imm}\ \Phi_{age_{(9to13)},age_{(>13)}.sex}^{immG1}\ \Phi_{age_{(9to13)},age_{(>13)}.sex}^{immG2}\ \Psi_{age.sex}^{immG1 \to adG1}\ \Psi_{age.sex}^{immG2 \to adG2}$ for the immature component and $\Phi_{sex.state}^{adG1}\ \Phi_{sex.state}^{adG2} \Psi_{state}^{G1 \to G1} \Psi_{state}^{G2 \to G2}\ p_{age}^{pre} p_{state}^{ad}$ for the adult component, where the juvenile (juv) survival probability (Φ) was sex and cohort dependent, the immature (imm) survival probability was age and sex dependent, the adult (ad) survival probability was sex and state dependent, the probability of transition (Ψ) from immature to adult through recruitment was age and sex dependent, the probability of transition into the group 1 (G1) given recruitment was sex dependent, the pre-recruitment capture probability (p) was age dependent, and the adult capture probability was state dependent. In this model notation, symbol "." indicates interactive effects, "+" indicates additive effect, "1to2", "3to8" and "9to13" indicate that age classes were grouped and ">13" indicates that age classes were grouped after 13 years

2.4 Breeding performances

Since our model had full state dependent transitions, we did not have direct access to breeding probability and breeding success estimates. Both were calculated from the outputs of the multievent modeling. For a given state, breeding probability is the probability to be in success plus the probability to be in failure. The breeding success is the ratio between the probability to be in success and the probability to reproduce (with success or not). 95% confidence intervals for these derived estimates were obtained with a bootstrap method as described in appendix D2. To investigate breeding performances during adulthood, we did not consider the Successful Breeder state (SB) since most of the individuals in this state take a sabbatical year, i.e. they transition toward the PSB state at the next occasion, nor Post-Failed Breeder state since less than 5% of individuals take a sabbatical year after a failure.

2.5 Model selection and goodness-of-fit

All models were run using program E-SURGE (Choquet, Rouan & Pradel 2009b). Model selection was done using Akaike Information Criteria (AIC, Burnham & Anderson 2002) to test sex and group specific actuarial senescence patterns and sex and cohort effects on group assignment $\psi^{juv \to G2}_{sex+cohort}$. Models with ΔAIC < 2 were not considered meaningfully different (Burnham & Anderson 2002).

There is no test available to assess the goodness-of-fit (GOF) of multi-event models. We thus performed GOF tests using program U-CARE (v.2.3.2, Choquet et al. 2009a) on a simplified dataset, which distinguished solely successful breeders from failed breeders and assigned randomly a reproductive status, i.e. failed or successful, to each individual for which no information was available (Pradel 2005). Results suggested slight overdispersion with a variance inflation factor ($\hat{c}$) of 1.37. Since a substantial part of this overdispersion not captured by the simple multi-state model used for GOF testing was likely captured in our finite mixture model controlling for age, cohort and individual heterogeneity, we assumed that our general model fitted the data correctly.

3 Results

Fitting two classes in the mixture model improved strongly our general homogenous model (Table 1, M1 vs M2: ΔAIC = 1026.3) suggesting important individual heterogeneity in this population. On average, 40% ± 3% of birds belonged to the first group and 60% ± 3% to the second group. However, model selection suggested sex-specific partitioning (Table 1, M2 vs M3: ΔAIC = 39.8), with 53%± 4% of females assigned to the first group compared with 30%± 3% for males. In accordance with the concept of individual quality, individuals from the first group showed consistent higher performances than individuals from the second group.

Table 1: Testing for individual heterogeneity in wandering albatrosses from Crozet Island from 1965 to 2012. M1 (nul) and M2 (cst) test respectively for absence or presence of individual heterogeneity. M3 (sex) tests for sex-specific group assignment. M4 and M5 test for cohort-specific group assignment with respectively additive (+) and interactive effects (.). Results include the number of mathematical parameters (k), the deviance (Dev), Akaike Information Criterion value (AIC) and the difference in AIC value of the model with respect to the best model (ΔAIC). The best supported model is in bold characters.

No.	Model	k	Dev	AIC	ΔAIC
M1	$\psi^{\mathrm{juv}\to \mathrm{G1}}(\mathrm{nul})$	116	95835.8	96067.8	1074.5
M2	$\psi^{\mathrm{juv}\to \mathrm{G1}}(\mathrm{cst})$	167	94707.5	95041.5	48.2
M3	$\psi^{\mathrm{juv}\to \mathrm{G1}}(\mathrm{sex})$	169	94663.7	95001.7	8.4
M4	$\boldsymbol{\psi^{\mathrm{juv}\to \mathrm{G1}}(\mathrm{sex}+\mathrm{coh})}$	**202**	**94589.3**	**94993.3**	**0**
M5	$\psi^{\mathrm{juv}\to \mathrm{G1}}(\mathrm{sex.coh})$	235	94545.0	95015.0	21.7

Table 2: Heterogeneity of immature survival for the wandering albatross population of Crozet. Estimates (±SE) came from the model 4 (Table 1). Survival estimates for >13-year-old females from group 1 are not identifiable because at this age full recruitment has been reached (Figure 2).

Age class	Sex	Estimate		
		Group 1	Group 2	Without heterogeneity (Fay et al. 2015)
9-13 years	Male & female	0.999±0.001	0.960±0.019	0.980±0.008
>13 years	Male	0.940±0.115	0.869±0.039	0.876±0.036
>13 years	Female	/	0.922±0.029	0.768±0.061

Immature individuals from group 1 showed both higher survival probability (Table 2) and higher recruitment rate (Figure 2). Independently of age and sex, recruitment probability was consistently higher in group 1 (Figure E1), leading to full recruitment after 10 years for females and at 14 years for males. In contrast, about 20% of immature individuals from the second group had still not recruited at 15 years old.

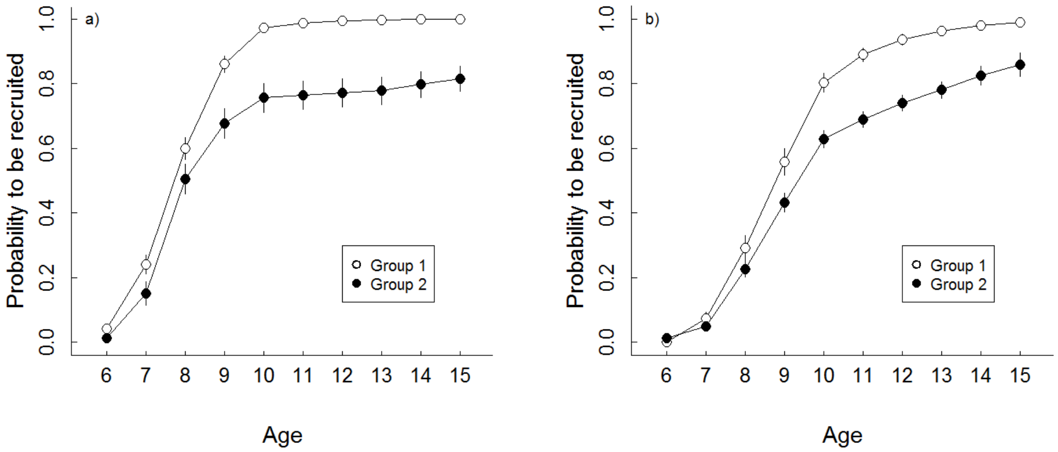

Figure 2: Heterogeneity of cumulated probability to be recruited according to age and sex for (a) females and (b) males for the wandering albatross population of Crozet. Estimates and standard errors are calculated from age specific recruitment and survival probability (Model 4, Table 1) by bootstrapping methods (1000 simulations).

Furthermore, given recruitment, we found that breeding success at first reproduction was higher in the first group (0.50±0.03) compared to the second (0.42±0.03). During adulthood, individuals from group 1 were breeding more often whatever their previous state and had also more success, but only for previous failed breeders, (0.60±0.03 against 0.53±0.04, respectively, Figure 3). The average annual probability to produce a chick, i.e. both breeding probability and success probability given reproduction, weighted by the proportion of individuals in each state was 0.63 in group 1 and 0.38 in group 2. Contrary to reproductive performances, we found less evidence for heterogeneity in adult survival. Until 30 years old, survival probability was equal between groups for both males and females. After this age, although senescence appeared in both sexes with a progressive decrease of survival probability, this aging pattern seemed group-specific for males (but not females). Indeed, while the best supported model, including heterogeneity for male senescence rate, was not meaningfully different from a model without heterogeneity (Table 3, M2 vs M5: ΔAIC = 1.63), we noted that removing heterogeneity for female senescence rate reduced AIC by 4 points, whereas removing heterogeneity for male senescence rate increased AIC by 1.2 point. Furthermore, although we found support for sex-specific senescence rates

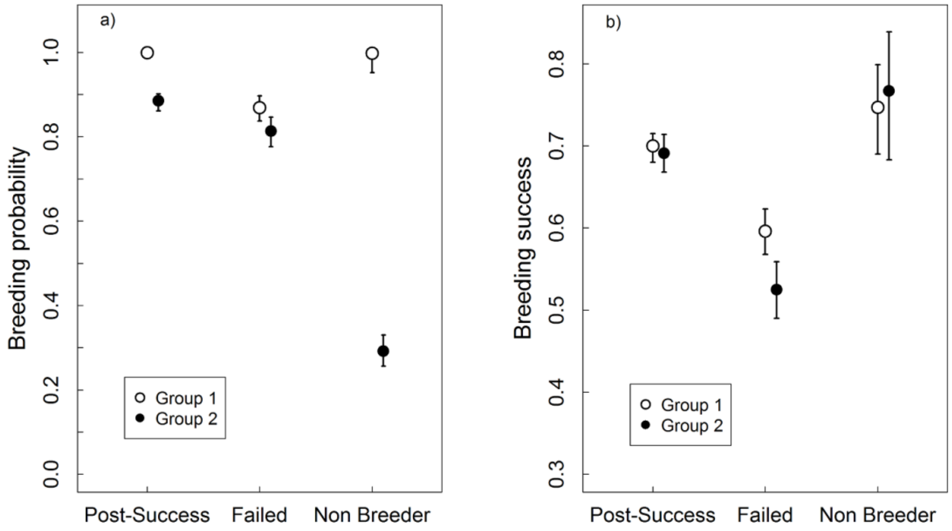

Figure 3: Heterogeneity in breeding probability (a) and breeding success (b) considering the previous breeding state for adult wandering albatrosses from Crozet Island from 1965 to 2012. Estimates were calculated from the outputs of M4 (Table 1) and ±95% confidence intervals were obtained with a bootstrap method.

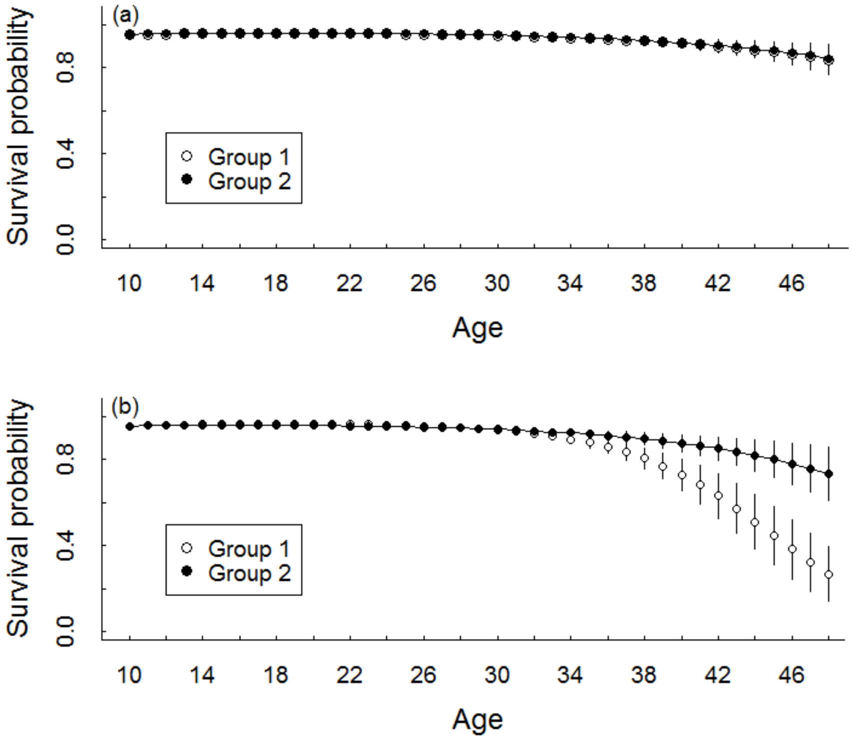

Figure 4: Heterogeneity of age-specific survival probability for breeders and post reproductive breeders (a) females and (b) males for the wandering albatross population of Crozet. Estimates (±SE) came from the model averaging of three best competitive models (M2, M4 and M5, Table 3).

Table 3. Model selection for the effects of sex and heterogeneity on survival senescence rate for wandering albatrosses of Crozet (1965-2012). Fe = Female, Ma = Male, G = heterogeneity group effect, X = Y mean that senescence rate of X is constraint to be equal to senescence rate of Y. For example, (Fe=Ma.G2) + Ma.G1 indicates that senescence rate of females from both heterogeneity groups (1 and 2) is constraint to be equal to the senescence rate of males from group 2, but is different from the senescence rate of males from group 1. k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion and the difference in AIC value of the model with respect to the best model (ΔAIC). The best supported model is in bold characters.

No.	Model	k	Dev	AIC	ΔAIC
M1	Fe.G + Ma.G	172	94672.96	95016.96	4.21
M2	Fe + Ma	168	94678.38	95014.38	1.63
M3	G	168	94684.02	95020.02	7.27
M4	Fe + Ma.G	170	94672.96	95012.96	0.21
M5	**(Fe=Ma.G2) + Ma.G1**	**168**	**94676.75**	**95012.75**	**0**
M6	(Fe=Ma.G1) + Ma.G2	168	94682.37	95018.37	5.62
M7	Fe.G + Ma	170	94678.18	95018.18	5.43
M8	Fe.G1 + (Fe.G2=Ma)	168	94681.06	95017.06	4.31
M9	Fe.G2 + (Fe.G1=Ma)	168	94682.67	95018.67	5.92

(Table 3, M3vs M1: ΔAIC = 3.06), senescence rate of males from group 2 was not distinguishable from female senescence rate (Table 3, M5 vs M4: ΔAIC = -0.21), contrary to senescence rate of males from group 1 (Table 3, M6 vs M4: ΔAIC = 5.41). This suggested heterogeneity for male (but not female) senescence rate. Estimates from model averaging of the three best competitive models (Table 3, M2, M4 and M5) suggested clearly faster decrease of survival for males from group 1. For this group, survival probability fell sharply from 0.96 before 30 years old to less than 0.50 after 45 years old, whereas over the same age range, survival for males from group 2 declined gradually to 0.80 (Figure 4).

Finally, our results support additive cohort-specific probability to belong to one of the two groups (Table 1, M3 vs M4: ΔAIC = 8.4). The probability to transit in group 2 decreased from about 0.80 in the end of the 1960s to 0.25 in early the 1980s, and then increased progressively to 0.60 in the late 1990s (Figure 5). Investigating early-life conditions that could explain these variations, we found a positive effect of population size the year of birth on the probability to belong to group 2 (Table 4, Ftestcst/co/t=3.60, p-value=0.04, Figure E2). This variable explained 18% of cohort variations. Thus individuals born in years of low population density tended to had higher demographic performances throughout their life (except for senescent males).

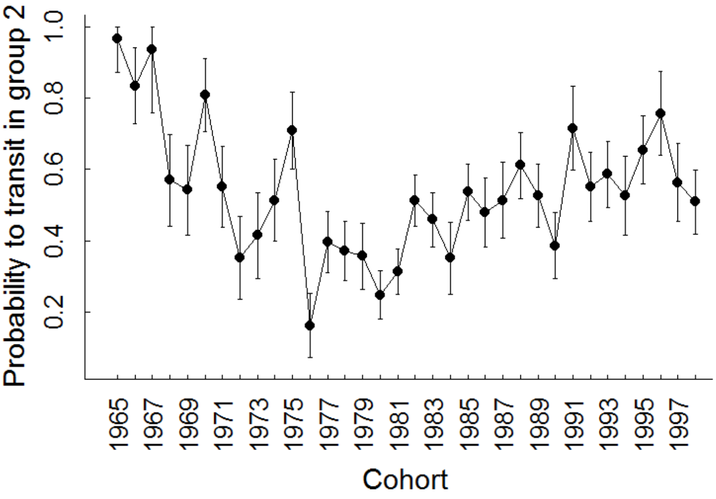

Figure 5: Cohort heterogeneity, cohort specific probability to transit in group 2. Estimates (±SE) were derived from model M4 (Table 1).

Table 4: Testing the effect of early-life environmental conditions on the cohort-specific probability to belong to group 2 (low quality individuals) for the wandering albatross population of Crozet. Results include the deviance (Dev), the statistic Ftestcst/co/t testing the null hypothesis that the focal environmental variable has no effect on transition probability to group 2, the percentage of variation explained by the covariates (r2), and the 95% CI of the slope for linear relationships. All covariates were standardized. Models with statistically significant covariate effects at the level of 5% are in bold characters.

No.	Model	Dev	F	p-value	r^2	Slope [95% CI]
M7	$\boldsymbol{\psi^{juv \to G2}(\mathrm{sex} + N)}$	**94650.0**	**3.60**	**0.04**	**0.18**	**0.33±0.10**
M8	$\psi^{juv \to G2}(\mathrm{sex} + N + N^2)$	94649.5	0.13	0.88		
M9	$\psi^{juv \to G2}(\mathrm{sex} + \mathrm{SSTA})$	94606.0	0.04	0.96		
M10	$\psi^{juv \to G2}(\mathrm{sex} + \mathrm{SSTA} + \mathrm{SSTA}^2)$	94603.3	0.93	0.45		
M11	$\psi^{juv \to G2}(\mathrm{sex} + N + \mathrm{SSTA})$	94650.0	0.01	0.99		
M12	$\psi^{juv \to G2}(\mathrm{sex} + N + \mathrm{SSTA} + \mathrm{SSTA}^2)$	94648.2	0.14	0.93		

4 Discussion

This study highlighted strong heterogeneity in life-history trajectories and the importance of individual quality to explain these variations. In agreement with the predictions from to the individual quality hypothesis, mixture models showed that individuals had consistent performances throughout their life showing positive covariation between various demographic traits. Furthermore, cohort specific variations in demographic traits suggested that individual quality could be determined by the environment experienced in early-life. We found that individuals born in years with high population densities tended to have lower performances during their lifespan, suggesting delayed density dependence effects acting through individual quality.

4.1 Individual heterogeneity and the individual quality hypothesis

As predicted by the individual quality hypothesis, we found positive relationships between different individual fitness components throughout the life cycle. From early-life to adult stage, we found positive relationships between immature survival, recruitment rate, breeding success at recruitment, adult reproductive probability and adult breeding success probability given reproduction. In early-life, consistent among-individual differences are already visible through the positive covariation between immature survival and recruitment as also documented in the Pacific black brant Branta *bernicla nigricans* (Lindberg, Sedinger & Lebreton 2013). In long-lived species survival may decline in oldest immature age-classes (Desprez et al. 2014; Fay et al. 2015), suggesting that individuals delaying recruitment are individuals with lower intrinsic survival probability, i.e. lower quality (Fay et al. 2016). This result is consistent with the idea of individual quality determined in very early-life through fixed intrinsic characteristics.

Young individuals having both higher recruitment rate and higher breeding success at their first reproduction tended to have also higher chick productivity during adulthood. Similarly, higher first-year survival probability was associated to higher adult performances in the Red-billed chough *Pyrrhocorax pyrrhocorax* (Reid et al. 2006), earlier age at first reproduction was associated to higher adult survival and reproductive performances in female reindeer *Rangifer tarandus* (Weladji et al. 2008) and female mute swan *Cygnus olor* (McCleery et al. 2008). Thus, as found in other long-lived species, some individuals outperformed others without apparent cost during most of the adult life (Hamel et al. 2009a).

Demographic parameter estimates suggested that the level of heterogeneity differed among life-history traits. In particular, survival heterogeneity was less important compared to reproductive heterogeneity. We suggest that this pattern could be linked to the canalization of life history traits. The canalization theory suggests that natural selection buffers life-history traits that are the most closely related to individual fitness against both genetic and environmental perturbations (Stearns & Kawecki 1994). In long-lived species, adult survival, which is strongly related to individual fitness, is buffered against temporal variation (Gaillard & Yoccoz 2003). In species with slow life-history strategies, individuals may skip reproduction when experiencing poor environmental conditions (Cubaynes et al. 2011), or, if breeding is under way, decrease breeding investment, shunting the costs to their offspring to assure their proper maintenance (Navarro & González-Solís 2007). Thus, the lower heterogeneity observed in survival compared to breeding parameters could result from the canalization of survival being buffered against temporal variations to the detriment of breeding investment. This suggests that individuals adopt a prudent strategy regardless their phenotypic characteristic (Jenouvrier et al. 2015) and do not support the existence of different individual reproductive strategies in this species. Furthermore, if this interpretation is correct, it follows that short lived species adopting faster life-history strategies should show, relatively to long-lived species, higher heterogeneity in survival and lower heterogeneity for reproductive process. This prediction has never been addressed in the literature and need to be investigated in future studies.

Although our results strongly support consistent between-individual demographic rates, a major result of this study is that performance patterns seemed to be reversing in late life. While survival decreased progressively after the age of 30 in both sexes, survival of high quality males, but not high quality females, decreased more strongly compare to low quality individuals. This suggests that the high performances of high quality males, but not females, result in a stronger senescence rate and confirms the sex-specific aging pattern found in this species (Pardo, Barbraud & Weimerskirch 2013). The performances of high quality individuals could be constrained at older age by a tradeoff between survival and reproduction which was not apparent during most of the adult life. Similarly, high quality female ground squirrel *Tamiasciurus hudsonicus* (Descamps et al. 2006) and high quality male Alpine ibex *Capra ibex* (Toïgo, Gaillard & Loison 2013) showing high reproductive rate, suffered lower adult survival than low quality individuals only at the end of life. Individuals having consistently higher demographic performances without apparent short term costs may show long term decreasing performances supporting the existence of a trade-off between early and late life performances (Lemaître et al. 2015). This result suggests also that individual quality could be an important factor to explain between individual variations in senescence rate.

4.2 The origin of individual quality

Studies investigating individual heterogeneity agree that permanent differences among individuals arise from both intrinsic factors (i.e. genetic) and extrinsic factors affecting ontogenetic developmental conditions (i.e. early-life environment, parental effect). However, few empirical studies have addressed this issue directly. Here, focusing on the potential effect of early-life environment, we found that the probability to be associated to one of the two quality groups varied over time. Keeping in mind that the two heterogeneity groups used in our finite mixture model are just a modelling approximation to catch unobservable individual quality which is theoretically a continuous trait, this result suggests that different cohorts, which by definition are born different years, have individuals of different average quality. These temporal variations support the importance of environmental factors for the determination of individual quality since it is the only source of variation expected to generate strong fluctuations over short (yearly) time scales.

Long-lasting cohort effects until adulthood have been documented in various taxon including birds (Reid et al. 2003), mammals (Descamps et al. 2008), squamates (Madsen & Shine 2000) and fishes (Baudron et al. 2014). Individuals experiencing favorable early-life conditions may exhibit higher demographic performance through their life compared to those exposed to poor early-life conditions (Lindström 1999; Metcalfe & Monaghan 2001). Recently, (van Gils et al. 2016) reported morphological variation between cohorts of the red knot *Calidris canutus* that could be considered as variation in individual quality. Individuals born during warm years, corresponding to years with low food availability, showed body shrinkage, especially shorter bills, that decreased their foraging abilities on wintering ground and negatively affected their future survival. Food availability during the ontogenetic period, acting directly or indirectly through parental care, seems to be a key environmental factor determining the quality of a given cohort in birds and mammals (Descamps et al. 2008; Millon et al. 2011), although temperature could also be determinant for ectothermic organisms such as fishes (Baudron et al. 2014). These results suggest that beyond direct effects on demography, environmental variations impairing the quality of an entire cohort, may have important delayed effects on population dynamics (Beckerman et al. 2002; Lindström & Kokko 2002).

4.3 Long-lasting density effect

Results suggest that cohort quality in this albatross population was related to population density the year of birth. Individuals born the years of low population density had a higher probability to be associated to the high quality group, and thus to show high demographic performances throughout their life. This corresponds to a delayed density effect. Relationships between individual quality and population density the year of birth have already been observed in moths. (Wellington 1960) documented that when *Malacosoma pluviale* were overcrowded, emerging larvae were much weaker and sluggish and that this frailty persisted through the larval stage until adult age. Decreasing individual quality seemed an important factor to explain population collapse after an outbreak in the study population. Thereafter, this quality density-dependent mechanism has been suggested to be a driving factor in cycle population dynamics of six species of Lepidoptera (Ginzburg & Taneyhill 1994). In ungulates, high population density the year of birth may impairs the quality of an entire cohort with visible consequences until adulthood (Bonenfant et al. 2009). Cohorts born under high population density were lighter at the adult stage while adult body mass was an important factor for individual fitness in this taxon (Mysterud et al. 2002; Pettorelli et al. 2002). Similarly, Soay sheep *Ovis aries* born under low population density had higher survival probability later in life (Forchhammer et al. 2001). Long-lived species could be particularly prone to such long-term density effects since juveniles, i.e. growing individuals, are expected to be the first individuals affected by increasing population density (Eberhardt 2002). To our knowledge, this study is the first to suggest long-lasting population density effects on cohort performances in birds.

Density effects may induce cohort variations that have double consequences. First, a direct numerical effect (sensu Gaillard et al. 2003) due to decreasing juvenile survival that may induce variation in future recruitment, and second, a long term effect through individual quality that affects individual performance throughout life. However, long-lasting effects are more complex to anticipate that direct numerical effects since negative consequences at the cohort scale did not occur in every case. By contrast, increasing early-life mortality under poor environmental conditions may also remove lower quality individuals form the cohort and thus bringing together individuals with high performances at the adult stage, a process known as viability selection. Based on three ungulate species, (Hamel et al. 2009b) concluded that a substantial part of variation in individual quality between cohorts originates from the early-life environment, but, depending on the species, negative long-term effect or viability selection was predominantly observed. These two non-exclusive mechanisms have even been described simultaneously within the same population acting either one or the other preponderantly according to the sex, for example in the roe deer *Capreolus capreolus* (Garratt et al. 2015). In our study, even if viability selection may have taken place owing to heterogeneity in immature survival, results suggest the preponderance of negative long-term effects of the early-life environment. Indeed, cohorts born under high population density suffered higher juvenile morality (Fay et al. 2015) and, contrary to what is expected by viability selection, tended to have lower performances throughout their adult life.

5 Conclusion

This study showed that the observed heterogeneity in life history trajectory in a wandering albatross population could be related to variation in individual quality, i.e. variation in the intrinsic ability to survive and reproduce. Some individuals consistently outperformed others during most of their life, except at older age since senescence was stronger in individuals with high performances. Variations in individual quality seemed strongly affected by extrinsic factors experienced during the ontogenetic period. Results suggested that population density the year of birth partly explained variations in individual quality leading to population regulation via delayed density effects. This study adds to the emerging view that individual quality, more than a noisy parameter, may be a structuring feature affecting individual life history trajectories and potentially population dynamics.

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Discussion Générale

1. Contributions à la démographie des populations animales

1.1. Démographie des oiseaux marins

1.1.1. Estimation de la survie juvénile

Le stade pré-reproducteur est resté durant de longues années une boite noire pour l'étude des oiseaux marins. En particulier, les estimations précises de survie en début de vie étaient rares dans la littérature scientifique jusqu'à la fin des années 2000. Cette thèse avait pour objectif de contribuer à améliorer nos connaissances en fournissant des estimations de survie pour les premiers stades de vie chez l'albatros hurleur. Grâce au suivi continu sur près de 50 ans de la population de Crozet, nous avons pu estimer ces taux vitaux pour différentes classes d'âge. Nous avons estimé une survie annuelle durant les deux premières années de vie de 0.80, une survie annuelle immature de 0.92 entre la troisième et la huitième année, puis une survie annuelle de 0.98 après 8 ans. On remarque que la survie atteint chez les individus immatures les plus âgés une valeur supérieure à celles précédemment estimées pour les adultes reproducteurs (autour de 0.95). Ceci s'explique par le fait que notre échantillon ne contient pas d'individus vieillissant contrairement à études antérieures. Il représente donc probablement le taux de survie d'individus dans la force de l'âge. Il est important de noter ici que ces seuils sont en partie dus à des contraintes de modélisation et qu'ils ne reflètent pas nécessairement le patron biologique de cette espèce. Par exemple, la survie durant la première année est probablement beaucoup plus faible que celle de la seconde. En effet, durant la période pré-reproductrice, la plupart de la mortalité intervient les premières semaines après l'indépendance (Naef-Daenzer, Widmer & Nuber 2001). David Lack suggérait déjà en 1954 que la survie des jeunes vanneaux huppés n'était plus distinguable de celle des adultes 6 mois seulement après leur indépendance. Ce patron a été confirmé depuis par de nombreuses études plus approfondies chez diverses espèces d'oiseaux longévifs montrant que la survie atteint, la deuxième année de vie, une valeur proche, sinon égale, à celle des adultes (Hénaux, Bregnballe & Lebreton 2007; Millon, Petty & Lambin 2010; Horswill *et al.* 2014; Chantepie *et al.* 2016; Payo-Payo *et al.* 2016). Récemment, une étude sur l'albatros de Laysan *Phoebastria immutabilis* suggère que la survie durant la deuxième année n'est pas distinguable de celle des classes d'âge supérieures (van den Hoff 2011). Ainsi, dans notre cas, si nous égalisons la survie durant la seconde année à la survie des 3-8 ans, on estime alors une survie juvénile, c'est-à-dire durant la première année de vie après l'envol, de 0.70. Cette estimation peut être comparée aux survies juvéniles estimées chez d'autres espèces d'oiseaux marins. Un examen de la littérature permet d'identifier

Table 1 : Estimations de survie durant la première année (juvénile) et/ou durant les deux premières années en mer chez les oiseaux marins. Ont été retenues uniquement les études utilisant la modélisation capture-marquage-recapture. Les individus sont tous bagués peu de temps avant leur envol. Lorsque plusieurs études sont parues pour une même population, j'ai gardé l'estimation la plus fiable au vu des tailles d'échantillon et des méthodes statistiques employées. Une estimation de l'importance de l'émigration permanente sur l'estimation de survie est donnée à titre indicatif selon trois niveaux : négligeable, faible et modéré. Cette évaluation est fait au regard de l'écologie des espèces, du protocole de suivi mis en place et des commentaires des auteurs fournissant ces estimations. Ce tableau n'est pas exhaustif.

Espèce	N	Cohort	Survie juvénile	Survie les 2 premières années	Effet potentiel émigration permanente	Effet sexe	Reference
Procellariiformes							
Albatros de Laysan *Phoebastria immutabilis*	477	14	0.76	0.74	négligeable	na	VanderWerf & Young 2016
Albatros hurleur *Diomedea exulans*	9 685	46	0.70	0.60	négligeable	Oui	Fay *et al.* 2015
Albatros à pieds noirs *Phoebastria nigripes*	13 854	24	0.65	0.63	négligeable	na	Lebreton & Veran 2013
Albatros à sourcils noirs *Thalassarche melanophrys*	4 450	35	0.52	0.45	faible	na	Fay et al.en préparation
Pétrel de la Trinité *Pterodroma arminjoniana*	853	20	0.63	0.61	faible	na	Nicoll *et al.* 2016
Puffin fuligineux *Puffinus griseus*	1175	14	/	0.29	faible	na	Fletcher *et al.* 2013
Puffin fuligineux *Puffinus griseus*	2770	4	/	0.17	faible	na	Fletcher *et al.* 2013
Pétrel de Gould *Pterodroma gouldi*	928	17	/	0.73	faible	na	Jones *et al.* 2011
Pélécaniformes							
Fou de Bassan *Moranus sula*	44 582	43	0.42	0.35	faible	na	Wanless *et al.* 2006
Cormoran huppé *Phalacrocorax aristotelis*	19 168	43	0.51	0.38	faible	na	Frederiksen *et al.* 2008
Grand cormorant *Phalacrocorax carbo*	14 018	10	0.50	0.45	faible	na	Hénaux *et al.* 2007
Charadriiformes							
Guillemot de Troïl *Urial aalge*	1 522	16	/	0.49	modéré	na	Votier *et al.* 2008
Guillemot de Troïl *Urial aalge*	4 935	20	0.56	0.44	faible	na	Harris *et al*. 2007
Macareux moine *Fratercula arctica*	251	2	/	0.83	négligeable	na	Sandvik *et al.* 2008
Macareux moine *Fratercula arctica*	2 050	24	/	0.48	faible	na	Breton *et al.* 2006
Sterne de Dougall *Sterna dougallii*	594	6	0.55	0.45	?	na	Monticelli & Ramos 2012
Sterne de Dougall *Sterna dougallii*	?	10	/	0.38	faible	na	Lebreton *et al.* 2003
Sterne de Dougall *Sterna dougallii*	91	1	/	0.44	?	na	Shealer, Saliva & Pierce 2005
Sterne pierregarin *Sterna hirundo*	3 315	18	/	0.35	faible	Non	Szostek *et al.* 2014
Sterne des baleiniers *Sterna balaenarum*	678	9	/	0.35	modéré	na	Braby *et al.* 2011
Goéland railleur *Chroicocephalus genei*	3 479	12	0.77	0.64	modéré	na	Acker *et al.* en préparation
Goéland d'Audouin *Larus audouinii*	24 038	25	0.60	0.55	faible	na	Payo-Payo *et al.* 2016

Table 1 suite : Estimations de survie durant la première année (juvénile) et/ou durant les deux premières années en mer chez les oiseaux marins

Sphenisciformes							
Manchot pygmée *Eudyptula minor*	23 686	36	0.17 **a**	0.12 **a**	modéré	na	Sidhu *et al.* 2007
Manchot pygmée *Eudyptula minor*	12 824	20	0.20	0.17	modéré	na	Sidhu *et al.* 2012
Manchot pygmée *Eudyptula minor*	3 970	17	0.42**a**	0.34 **a**	modéré	na	Agnew *et al.* 2016
Manchot Adélie *Pygoscelis adeliae*	2 734	12	0.53	0.48	modéré	na	Emmerson & Southwell 2011
Manchot Adélie *Pygoscelis adeliae*	600	9	0.34	0.29	modéré	na	Ballerini *et al.* 2009
Gorfou macaroni *Eudypes chrysolophus*	1070	10	0.33	0.29	modéré	na	Horswill *et al.* 2014
Gorfou sauteur *Eudyptes chrysocome*	114	2	0.81	0.79	négligeable	Non	Dehnhard *et al.* 2014
Gorfou sauteur *Eudyptes chrysocome*	514	7	0.27 **a**	0.22 **a**	modéré	na	Guinard *et al.* 1998
Manchot empereur *Aptenodytes forsteri*	873 **b**	18 **b**	0.41	0.36	faible	na	Abadi *et al.* 2016
Manchot royal *Aptenodytes patagonicus*	2375	7	>0.70	>0.70	faible	Oui	Saraux *et al.* 2011b

Phaethontiformes							
Phaéton à brins rouges *Phaethon rubricauda*	31 527	10	0.77	0.66	?	na	Schreiber *et al.* 2004)

a : marquage alaire connu pour diminuer la survie des adultes.

b : Modèle de population intégré. Taille d'échantillon pour les adultes marqués, les jeunes n'étant pas identifiés individuellement. La survie juvénile est estimée indirectement au vu de la dynamique de l'ensemble de la population.

une trentaine d'articles fournissant des estimations de survie en début de vie chez les oiseaux marins.On remarque que ces études sont récentes, une seule référence est antérieure aux années 2000, et 63% (20/32) des références sont postérieures à 2010. Les survies durant la première année de vie sont estimées chez les procellariiformes entre 0.63 chez Pétrel de la Trinité *Pterodroma arminjoniana* et 0.76 chez l'albatros de Laysan. L'estimation de 0.70 pour l'albatros hurleur apparait, en comparaison, tout à fait cohérente. Si l'on s'intéresse à la période des deux premières années de vie, on remarque que les procellariiformes présentent des taux de survie très variables compris entre 0.17 et 0.74, avec tout de même une majorité des estimations autour de 0.60. A titre de comparaison, les taux de survie apparents sur les deux premières années sont estimés autour de 0.40 chez deux espèces de cormorans et trois espèces de sternes, autour de 0.50 chez trois espèces d'alcidés, entre 0.20 et 0.50 chez cinq espèces de manchots. Ainsi les procellariiformes, et les albatros en particulier, semblent montrer en début de vie les taux de survie les plus élevés parmi les oiseaux marins. Cette particularité est à mettre en relation avec les stratégies d'histoire de vie extrêmement lentes observées chez l'ensemble des espèces de ce taxon. On remarque par exemple que l'ensemble des procellariiformes ne pondent qu'un seul œuf.

La théorie prédit que la survie en tout début de vie devrait être sexe-spécifique chez les espèces montrant un fort dimorphisme sexuel. Le sexe le plus massif devrait montrer une survie plus faible du fait de ses besoins énergétiques plus importants. En effet, cette particularité l'expose davantage aux risques de mortalité par inanition (Clutton-Brock, Albon & Guinness 1985). Conformément à cette théorie, nous avons trouvé que la survie durant les deux premières années est sexe-spécifique chez le grand albatros. La survie des mâles, morphologiquement plus grands, est plus faible que celle des femelles durant la période critique du début de vie. De manière cohérente, chez le fou de Grant *Sula grantii*, où le dimorphisme sexuel est inversé, des résultats suggèrent que la survie des jeunes femelles est inférieure à celle des mâles. Cette relation entre le dimorphisme sexuel est la survie en début de vie est bien établie chez les mammifères (Clutton-Brock *et al.* 1985), mais reste peu testée chez les oiseaux en général et les oiseaux marins en particulier (Maness & Anderson 2013). Dans les études rassemblées dans le tableau 1, seulement 13% (4/33) sont à même de tester l'effet du sexe sur la survie en début de vie. Cela s'explique principalement par la difficulté à identifier le sexe des jeunes individus chez les oiseaux avant que les techniques de sexage moléculaires ne soient misent au point. Cependant, même lorsque que le sexe des individus a pu être déterminé, une difficulté supplémentaire consiste à distinguer la mortalité de l'émigration permanente qui est habituellement biaisée en faveur des femelles chez les oiseaux (Greenwood 1980). Ainsi la survie apparente légèrement supérieure chez les jeunes manchots royaux mâles, légèrement plus grands que les femelles, pourrait être due à une dispersion plus importante des femelles (Saraux *et al.* 2011b). La même limite empêche de conclure sur la survie des jeunes sternes pierregarin *Sterna hirundo* qui semble indépendante du sexe (Szostek *et al.* 2014). Pour ce qui concerne la dernière étude prenant en compte l'effet du sexe sans montrer d'effet sur la survie, avec seulement 114 individus pour les deux sexes confondus (Dehnhard *et al.* 2014), la puissance statistique peut-être questionnée. Ainsi l'estimation de survie sexe-spécifique en tout début de vie que nous documentons est unique chez les oiseaux marins.

La théorie de la canalisation suggère que les traits qui ont le plus d'impact sur le taux d'accroissement de la population sont protégés contre les variations environnementales (Gaillard & Yoccoz 2003). Chez les espèces longévives, le taux d'accroissement des populations dépend plus fortement de la survie des adultes que de celle des jeunes individus (Heppell, Caswell & Crowder 2000; Sæther & Bakke 2000). Ainsi, il est généralement prédit que la survie en début de vie est non seulement plus faible mais également plus variable que celle des adultes (Gaillard *et al.* 2000; Levitis 2011). Nous avons pu confirmer cette prédiction chez l'albatros hurleur en montrant que le taux de survie augmente et se stabilise progressivement avec l'âge. Les études documentant des estimations de survie en tout début de vie font également apparaitre cette variabilité. En effet, les estimations de survie au sein d'une même espèce peuvent varier substantiellement en fonction des populations. On relève ainsi des estimations divergentes de plus de 10% chez deux populations de puffins fuligineux *Puffinus griseus* et de plus de 20% entre deux populations de manchot Adélie *Pygoscelis adeliae* et de manchots pygmées *Eudyptula minor*. De plus, on constate que lorsque les estimations de survie sont basées sur un petit nombre de cohortes, elles peuvent atteindre des valeurs extrêmes, parfois très élevées, s'approchant alors des taux de survie adulte. Les deux études qui rapportent les taux de survies les plus élevées sur les deux premières années de vie cumulée, 83% pour une population de macareux moine *Fratercula arctica* et 79% pour une population de gorfou sauteur *Eudyptes chrysocome*, sont toutes deux basées sur 2 cohortes. Ces taux, au caractère exceptionnel, reflètent probablement des conditions environnementales particulièrement favorables. En effet, des études basées sur d'autres populations des mêmes espèces, disposant d'échantillons à la fois plus importants et répartis sur un plus grand nombre de cohortes, fournissent des valeurs plus faibles et donc plus cohérentes au vu des estimations documentées chez des espèces proches. Si l'on prend par exemple les 5 cohortes au taux de survie les plus forts au sein du suivi de la population d'albatros hurleur de Crozet, on trouve une survie sur les deux premières années de vie cumulée de plus de 80%. Ces cohortes ont pris leur envol au milieu des années 1980, lorsque la population a atteint sa taille minimale. Cette époque correspond probablement à une période où la compétition intraspécifique était de fait réduite, favorisant la survie des jeunes individus. En effet, nous avons pu montrer (Chapitre 2) que la survie des jeunes albatros est négativement associée à la taille de la population. Ainsi, nous concluons que pour avoir des estimations de survie juvénile fiables, il semble nécessaire de prendre en compte de nombreuses cohortes. Ceci pourrait être particulièrement important si la densité de population varie dans le temps. En effet, comme nous allons voir dans la partie suivante, la survie des jeunes oiseaux marins pourraient être plus fréquemment densité-dépendante que ce qui était pensé précédemment.

1.1.2. La densité dépendance

La densité dépendance est un mécanisme central pour comprendre la régulation des populations en milieu naturel (Lack 1954; Sinclair 1989). Historiquement, ce concept a été documenté chez des mammifères terrestres dès les années 1940. Des études ont signalé que les performances de reproduction et de survie observées chez des populations d'ongulés variaient conjointement à la taille de la population (Rasmussen 1941; Morton & Cheatum 1946). Depuis, ce mécanisme de régulation et ses effets sur de nombreux taux vitaux tels que la croissance, l'âge de première reproduction et la dispersion, ont été décrit chez un grand nombre d'espèces de mammifères (Fowler

1987; Matthysen 2005; Bonenfant *et al.* 2009). La régulation des population par densité dépendance a également été bien documentée chez les insectes (Stiling 1988), les poissons (Lorenzen 2008; Andersen *et al.* 2016) et les oiseaux (Lack 1954; Newton 1998; Sæther, Engen & Matthysen 2002). En ce qui concerne plus spécifiquement les oiseaux marins, les premières observations suggérant un mécanisme de régulation par densité dépendance sont associées aux taux de croissance des colonies qui diminuent lorsque leur taille augmente (Coulson 1983, Figure 1).

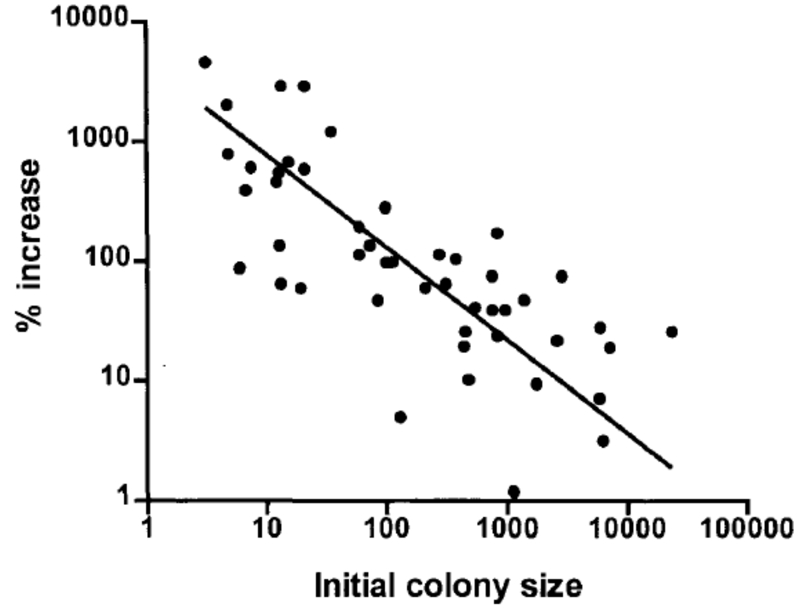

Figure 1 : Relation entre les tailles des colonies et leur taux d'accroissement entre 1959 et 1969 chez des populations de mouette tridactyle *Rissa tridactyla* au Royaume Uni et en Irlande. D'après (Coulson 1983).

Cependant, à la différence des autres taxons, les mécanismes démographiques sous-jacents sont longtemps restés inconnus. Lack suggérait que les populations sont d'abord limitées par la compétition interindividuelle pour la recherche alimentaire en particulier durant la période hivernale (Lack 1968). Ashmole, quant à lui, insistait sur la déplétion possible des ressources alimentaires autour des colonies de reproduction qui limiterait le succès de reproduction de celles-ci et contrôlerait rétroactivement leur taille (Ashmole 1963). Il fallut attendre les années 1980 pour que des études empiriques viennent étayer ces assertions. L'hypothèse du halo d'Ashmole fut confortée par plusieurs observations suggérant que les ressources alimentaires autour des colonies sont effectivement déplétées lorsque la population augmente en entrainant, en retour, une diminution des performances de reproduction. On observe ainsi que la taille des colonies de quatre espèces d'oiseaux marins se reproduisant au Royaume-Uni et en Irlande est négativement associée à la présence d'autres colonies à proximité (Furness & Birkhead 1984). Ce résultat montre que la taille d'une colonie ne limite pas seulement son propre développement (Figure 1) mais également la taille des colonies avoisinantes. Cela suggère que les colonies proches sont en compétition pour une ressource alimentaire commune entrainant un mécanisme de densité dépendance à plus grande échelle. Par la suite, des études empiriques ont montré que la densité des proies diminuait au cours de la période de reproduction à proximité des colonies (Birt *et al.* 1987) et que la qualité des proies capturées se dégradait lorsque les tailles de colonies augmentent (Forero *et al.* 2002). La diminution des ressources alimentaires à proximité des colonies affecte l'efficacité de recherche alimentaire des individus reproducteurs. Par exemple, le succès de pêche décroit lorsque la taille de la colonie augmente chez une population de manchot Adélie (Lescroël *et al.* 2010) et le temps moyen d'un voyage en mer pour un individu reproducteur augmente avec la taille des colonies chez le fou de Bassan *Morus bassanus* (Lewis *et al.* 2001). Ces contraintes affectent les performances de reproduction en diminuant la taille des pontes, la croissance des poussins et le succès de reproduction (Hunt, Eppley & Schneider 1986). Ces études corroborent parfaitement le mécanisme de régulation proposé par Ashmole qui est par ailleurs aujourd'hui largement accepté (Gaston, Ydenberg & Smith 2007). Cependant, ce mécanisme ne constitue pas le seul processus densité dépendant qui régule la taille des populations d'oiseaux marins. En effet, avec le développement des méthodes d'analyses de type capture-marquage-recapture, il est devenu possible d'estimer des taux de survie et d'essayer d'établir des liens entre leur variation et les tailles de populations. Les preuves de survie densité dépendante chez les oiseaux marins ne sont donc apparues que secondairement. Ainsi, la survie des individus adultes est négativement reliée à la taille de la population chez une population de grand cormoran *Phalacrocorax carbo* (Frederiksen & Bregnballe 2000), de mouette tridactyle *Rissa tridactyla* (Coulson 2001a), de pétrel bleu *Halobaena caerulea* (Barbraud & Weimerskirch 2003), et de macareux moine *Fratercula arctica* (Breton *et al.* 2006). Barbraud et Weimerskirch montrent en particulier que la plus grande partie de la mortalité intervient sur les aires d'hivernage comme le suggérait Lack (1954, 1968).

Cette thèse sur l'albatros hurleur documente pour la première fois chez les oiseaux marins une survie densité dépendante chez de jeunes individus. Ce résultat est d'autant plus intéressant que des études antérieures chez cette même espèce suggèrent que la survie des adultes varie, au contraire, indépendamment de la taille de la population (Rolland 2009)Rolland *et al.* 2009). Cela souligne la forte sensibilité des jeunes individus à l'augmentation de la densité de population comme cela a pu être documenté chez d'autres espèces d'oiseaux (Gamelon *et al.* 2016) et de mammifères (Coulson

2001b; McAdam & Boutin 2003; Bonenfant *et al.* 2009). Payo-Payo *et al.* (2016) ont également reporté très récemment des variations de survies juvéniles densités dépendantes chez le goéland d'Audouin *Ichthyaetus andouinii*. Ces résultats tendent à désapprouver l'intuition d'Ashmole (1963) qui écrivait: « I think it is unlikely that in many species the mortality among juveniles after they have dispersed over the most favourable feeding areas, is to a significant extent density-dependent ». Ces relations entre la survie en début de vie et la taille de la population peuvent cependant être expliquées par deux mécanismes différents. En effet, l'augmentation de la taille des populations peut entrainer une intensification de la compétition intraspécifique pour acquérir des ressources alimentaires en mer. Cette compétition entre les classes d'âge se ferait au détriment des plus jeunes individus moins compétitifs. D'autre part, comme nous l'avons vu dans la revue bibliographique ci-dessus, la compétition entre les individus reproducteurs affecte leurs performances de recherche alimentaire. En réponse à ces contraintes, les oiseaux marins tendent à diminuer leur investissement reproducteur afin d'assurer la maintenance de leur soma (Mauck & Grubb 1995; Navarro & González-Solís 2007; Jenouvrier, Peron & Weimerskirch 2015), conformément aux stratégies d'histoire de vie lentes de ces espèces. On observe ainsi que la condition corporelle des jeunes à l'envol diminue lorsque la taille des colonies augmentent (Gaston, Chapdelaine & Noble 1983; Hunt *et al.* 1986). La condition à l'indépendance étant un facteur clé pour la survie en début de vie (Magrath 1991; Maness & Anderson 2013), la survie densité dépendante pourrait être, chez les jeunes oiseaux marins, le résultat d'effet parentaux qui s'exprimeraient sur le long terme. Ces deux mécanismes, compétition directe et effet parentaux, ne sont pas exclusifs, les deux pouvant intervenir simultanément et interagir. Aujourd'hui, bien que les deux processus de densité dépendance proposés par Ashmole et Lack aient été documentés, il apparait encore difficile de déterminer leur importance relative pour la régulation des tailles de populations d'oiseaux marins.

Au cours de cette thèse, le mécanisme de densité dépendance a également pu être suggéré pour expliquer les variations d'âge de première reproduction. L'âge de primiparité intervient à des âges plus précoces lorsque la taille de la population décroit. Ce résultat a été largement documenté chez plusieurs espèces d'oiseaux marins (Tavecchia *et al.* 2007; Votier *et al.* 2008) et plus généralement chez les oiseaux (Reid *et al.* 2003; Ferrer, Otalora & GarcÍa-Ruiz 2004; Cooper *et al.* 2009), les mammifères (Fowler 1987; Gaillard *et al.* 2000; Wauters *et al.* 2004) et les poissons (Lorenzen 2008). Les mécanismes sous-jacents impliquent la compétition pour l'accès à un site de reproduction, en particulier chez les espèces longévives (Sæther *et al.* 2002), et la compétition pour l'accès à la ressource alimentaire qui induit, toutes choses égales par ailleurs, une diminution de la croissance et de la condition des jeunes individus lorsque la densité de population augmente. L'engagement dans la reproduction étant étroitement lié à la croissance et à la condition corporelle (Weimerskirch 1999; Martin & Festa-Bianchet 2012), les individus retardent leur entrée dans la population reproductrice lorsque les conditions environnementale sont peu favorables (Dobson & Oli 2001; Millon *et al.* 2010; Oro *et al.* 2010). Ces mécanismes ont été discutés en profondeur dans les chapitres 2 et 4, je ne reviens pas d'avantage ici sur ces points.

1.2. Les performances des juvéniles

1.2.1. Sensibilité à l'environnement

Dans cette thèse, nous avons décrit des relations fonctionnelles entre les taux vitaux des jeunes albatros hurleurs et leur environnement. Ces relations mettent en évidence des mécanismes de régulation à la fois densités dépendants et densités indépendants en lien avec la stochasticité environnementale. Nous avons également pu montrer l'importance de l'âge dans la sensibilité aux variations environnementales. D'une manière générale, les travaux de cette thèse se distinguent nettement des études antérieures menées sur la composante adulte de la population d'albatros hurleur de Crozet par les multiples relations établies entre les conditions environnementales et les taux vitaux. En effet, les variations interannuelles de succès de reproduction ou de survie ne semblent pas être affectées par les conditions environnementales chez les adultes (Rolland, Weimerskirch & Barbraud 2010). Ce contraste souligne l'importance de la prise en compte de l'âge pour la compréhension des processus démographiques en général et des relations fonctionnelles entre les taux vitaux et l'environnement en particulier (Barbraud & Weimerskirch 2005; Pardo *et al.* 2013a; Oro *et al.* 2014; Chantepie *et al.* 2016). Les jeunes classes d'âge représentent une source importante de variabilité pour la dynamique des populations en particulier chez les espèces longévives (Sæther *et al.* 2013). Par exemple les variations de taille des populations de pétrels géants *Macronectes giganteus* et de pétrel de Hall *M. halli* sont associées aux localités d'hivernages des jeunes individus (van den Hoff 2011), et le taux d'accroissement d'une population d'otaries à fourrure antarctique *Arctocephalus gazella* est déterminé rétrospectivement par les variations de survie juvénile (Schwarz *et al.* 2013). Plusieurs hypothèses ont été évoquées pour expliquer cette infériorité des performances démographiques des jeunes individus, l'hypothèse de la contrainte, l'hypothèse de la retenue et l'hypothèse de la sélection (voir l'introduction générale pour plus de détails). Le développement récent des technologies de biologging a permis d'étudier le comportement des jeunes animaux en milieu naturel après leur indépendance. Ces études ont révélé l'importance du mécanisme de la contrainte en particulier pour ce qui concerne la survie en début de vie. Par exemple, chez de jeunes oiseaux plongeurs, les performances de recherche alimentaire, plus faibles que chez les adultes, sont associées aux chances de survie des individus (Daunt *et al.* 2007; Orgeret, Weimerskirch & Bost 2016). Bien qu'ils disposent des mêmes caractéristiques morphologiques que les adultes, les jeunes vautours fauves *Gyps fulvus* montrent des performances de vol plus faibles vraisemblablement par manque d'expérience (Harel, Horvitz & Nathan 2016). Les performances de vol sont également plus faibles en début de vie chez le fou brun *Sula leucogaster* (Yoda, Kohno & Naito 2004) et chez l'albatros hurleur *Diomedea exulans* (Weimerskirch, Akesson & Pinaud 2006). Chez ce dernier, on estime que les performances proches de celles des adultes sont atteintes à partir du troisième mois (Riotte-Lambert & Weimerskirch 2013). Chez des espèces migratrices, les capacités d'orientation et de vol des jeunes oiseaux sont réduites relativement aux performances des adultes et peuvent être associées à des risques accrus de mortalité (Mueller *et al.* 2013; Sergio *et al.* 2014; Rotics *et al.* 2016). Toutes ces études montrent que les performances des individus en début de vie sont fortement contraintes par leur immaturité et leur manque d'expérience. Ces contraintes expliquent probablement en grande partie leur sensibilité aux variations environnementales.

1.2.2. Les effets parentaux

Les traits démographiques des jeunes albatros hurleurs ne sont pas uniquement affectés par les conditions environnementales qu'ils rencontrent après leur envol, ils subissent également les variations environnementales qui précèdent leur indépendance. Nos études montrent en effet que les conditions climatiques avant l'envol peuvent être associées aux risques de mortalité des jeunes oiseaux après leur indépendance, alors qu'ils se situent à des milliers de kilomètres de leur lieu de naissance (Weimerskirch *et al.* 2006). Ces effets de l'environnement à long terme sont probablement répercutés chez les jeunes individus via les soins parentaux. En effet, chez les espèces longévives comme l'albatros hurleur, la théorie des stratégies d'histoire de vie prédit que l'investissement dans la reproduction diminue lorsque les conditions rencontrées par les individus reproducteurs se détériorent, afin d'assurer leur propre survie. De fait, chez ces espèces la survie est fortement protégée, canalisée, contre les variations environnementales. Ainsi de nombreuses études chez des oiseaux et des mammifères longévifs décrivent une diminution de l'investissement parental lorsque les conditions environnementales se dégradent (Martin & Festa-Bianchet 2012; Thomson *et al.* 2014; Jenouvrier *et al.* 2015). Cette réponse adaptative conduit à l'altération de la condition des jeunes individus et ainsi à une diminution de leur aptitude phénotypique à court, moyen ou long terme (Gorman & Nager 2004; Monaghan 2014). Ce mécanisme est un exemple d'effets parentaux qui se définissent comme l'influence des parents sur leurs descendants indépendamment du patrimoine génétique qui leur ont transmis (Mousseau & Fox 1998; Wolf *et al.* 1998).

Les effets parentaux ne conduisent cependant pas systématiquement à une diminution de l'aptitude phénotypique des jeunes individus. En effet, dans certains cas, les parents peuvent influencer le phénotype de leurs progénitures en fonction des conditions environnementales afin de maximiser leurs chances de survie et de reproduction (Marshall & Uller 2007). Par exemple les effets maternels modulent la durée de diapause chez les insectes (Mousseau & Dingle 1991) ainsi que le temps de dormance des graines chez de nombreuses plantes (Roach & Wulff 1987). Une étude sur une espèce de grillon (*Gryllus pennsylvanicus*) a montré expérimentalement que les mères étaient capables de modifier le comportement de leur descendance via des effets maternels en réponse à la présence de prédateurs dans leur environnement (Storm & Lima 2010). Les jeunes individus issus de femelles gravides ayant été exposées à la présence d'un prédateur développent des comportements d'antiprédation plus efficaces. Ces individus montrent en effet une plus grande propension à l'immobilité lorsqu'ils sont soumis à leur prédateur ce qui augmente leur chance de survie. Ce type d'effets parentaux, qui font intervenir des mécanismes épigénétiques (Uller 2008), permettent une réponse rapide face aux changements environnementaux et semblent être répandus chez les vertébrés puisque des processus similaires ont été décrits chez des poissons (Taborsky 2006), des oiseaux (Mariette et al. 2016) et des mammifères (Champagne 2008).

Les effets parentaux ne résultent cependant pas tous de mécanismes adaptatifs et certains effets transgénérationnels ne sont bénéfiques ni aux parents, ni aux jeunes individus (Marshall & Uller 2007). Un certain nombre de caractéristiques parentales comme leur taille ou leur expérience pourront affecter les phénotypes de leurs descendants indépendamment du génome transmis. Toutes choses égales par ailleurs, l'aptitude phénotypique de la progéniture tant à augmenter avec la taille et l'expérience de la mère (Coulson & Porter 1985; Marquis *et al.* 2008; Lee *et al.* 2013). Plus généralement, l'âge parental est un facteur important pour le devenir des jeunes individus (Parsons 1964).

1.2.3. L'âge parental

L'effet de l'âge parental sur les performances des individus est un sujet de recherche particulièrement ancien en écologie évolutive (Bell 1918). Dès le début du vingtième siècle, de nombreux chercheurs rapportent que la longévité des individus diminue avec l'âge de leur mère (Lansing 1947). Ce résultat connu sous le nom de l'effet de Lansing a été décrit chez de nombreux taxons incluant des plantes, des rotifères, des nématodes, des insectes, et les vertébrés (Priest, Mackowiak & Promislow 2002). Plus récemment, les effets de l'âge parental sur l'aptitude phénotypique ont été investigués chez des populations sauvages. En effet, étant aujourd'hui admis que la sénescence est un phénomène ubiquiste en milieu naturel (Nussey *et al.* 2013), on peut se demander dans quelle mesure les traits d'histoire de vie des individus sont affectés par l'âge de leurs parents. Des études sur des oiseaux et des mammifères ont montré que la survie en début de vie et le nombre de descendants qu'un individu engendre au cours de sa vie peuvent être associés à l'âge de ses parents. Cependant, la relation entre l'âge parental et les performances de la descendance varient fortement en fonction des espèces, l'aptitude phénotypique des individus étant associée positivement, négativement ou quadratiquement à l'âge des parents (Chapitre 3).

Dans ce contexte, nous avons étudié l'effet de l'âge des parents sur les performances de survie et de reproduction en début de vie chez l'albatros hurleur. Pour ce travail nous avons considéré non seulement l'âge maternel mais également l'âge paternel. Bien que les effets paternels soient aujourd'hui reconnus (Crean & Bonduriansky 2014), nous n'avons trouvé aucune étude chez les mammifères investiguant l'effet de l'âge du père sur le devenir de sa progéniture après l'indépendance en milieu naturel, et seulement trois études chez les oiseaux (Reid *et al.* 2010; Torres, Drummond & Velando 2011; Schroeder *et al.* 2015). Notre étude montre que les probabilités de survie au cours des deux premières années de vie sont négativement affectées par l'âge du père sans évidence d'un effet de l'âge maternel. Une fois que ce différentiel de survie a été pris en compte, nous n'avons pas détecté d'effet de l'âge des parents sur la probabilité et l'âge de première reproduction. La prédominance de l'effet paternel sur la survie en début de vie constitue un résultat unique au regard de la littérature actuelle. Ce résultat est à mettre en relation avec l'investissement important du mâle dans l'élevage de sa progéniture et les caractéristiques écologiques de cette espèce. Les mâles, plus massifs et plus compétitifs que les femelles, occupent les zones océaniques les plus productives et sont donc à même de fournir une plus grande quantité de nourriture au jeune, environ le double en masse relativement aux apports de la mère (Weimerskirch, Barbraud & Lys 2000). Le bon développement du poussin dépend donc en grande partie des soins paternels. Or, on sait également que chez cette espèce la sénescence est plus marquée chez les mâles (Pardo, Barbraud & Weimerskirch 2013b) et est associée à une diminution de capacité de recherche alimentaire (Lecomte *et al.* 2010). Ainsi les individus élevés par un père âgé connaissent, indépendamment de l'âge de leur mère, des conditions d'élevage peu favorables. Ce résultat est cohérent avec la relation entre les conditions climatiques avant l'envol et la survie après l'indépendance que j'ai évoqué dans le premier paragraphe de cette partie. En effet cette relation est vérifiée uniquement lorsque l'on considère les conditions environnementales sur l'aire de nourrissage des mâles pendant la période d'élevage du poussin. Ce résultat confirme que la contribution du père dans le nourrissage est très importante pour le devenir du jeune chez l'albatros hurleur. Ce résultat constitue un apport original de cette thèse sur la connaissance de cette espèce et plus largement sur les effets parentaux.

Les effets paternels tels que nous les avons décrits chez notre modèle d'étude pourraient être relativement fréquents chez les oiseaux. En effet, chez la plupart des espèces de ce taxon les deux sexes participent à l'élevage des jeunes et les mâles sont couramment plus massifs que les femelles (Szekely et al. 2007) montrant une contribution fréquemment plus importante que celle des femelles dans l'apport de nourriture (Owens and Hartley 1998). En outre, la théorie de la sénescence prédit que l'intensité du vieillissement est plus importante chez les mâles (voir introduction) et ce d'autant plus que le dimorphisme sexuel et marqué. Dans ce contexte, il est prévisible que le résultat que nous documentons puisse être répliqué chez d'autres espèces d'oiseaux.

2. Traits d'histoire de vie et qualité individuelle

2.1. La qualité individuelle chez l'albatros hurleur

Au cours de cette thèse, nous avons pu montrer l'existence de la qualité individuelle au sein de la population d'albatros hurleurs de Crozet. Nos résultats suggèrent en effet que les individus diffèrent intrinsèquement dans leur capacité à survivre et se reproduire de manière durable dans le temps. Les variations de qualité des individus semblent exister dès le début de vie. En particulier, les individus pré-reproducteurs les plus âgés montrent une diminution des chances de reproduction et de survie après l'âge respectif de 10 et 13 ans. Ces patrons suggèrent que les individus qui se reproduisent pour la première fois à des âges avancés disposent de capacités intrinsèques plus faibles. Des résultats similaires ont été décrit chez deux espèces de phoques, le phoque de Weddell *Leptonychotes weddellii* (Hadley *et al.* 2006) et l'éléphant de mer du sud *Mirounga leonina* (Desprez *et al.* 2014), ainsi que chez une autre espèce d'oiseau marin, la mouette tridactyle *Rissa tridactyla* (Aubry, Cam & Monnat 2009). Bien que ces patrons associés aux dernières classes d'âges immatures restent peu documentés dans la littérature, il est probable que les mêmes processus aient lieu chez un grand nombre d'espèces longévives. Ces premiers résultats suggérant une relation entre l'âge de première reproduction et la qualité d'un individu ont été confirmés par la suite à l'aide de deux études intégratives mettant en relation les traits démographiques du début de vie avec les taux vitaux adultes. Ces travaux montrent que l'âge de première reproduction d'un individu peut être un prédicteur de ses performances futures au cours de sa vie adulte. En effet, les individus dont la primiparité intervient aux âges les plus avancés se reproduisent moins fréquemment durant leur vie adulte et avec un succès plus faible. D'une manière générale, la qualité individuelle apparait comme un facteur structurant des trajectoires d'histoire de vie, les performances démographiques d'un individu étant positivement associées les unes aux autres au cours de sa vie comme cela a été documenté chez de nombreuses espèces (Clutton-Brock 1984; Cam *et al.* 2002; McCleery *et al.* 2008; Zhang *et al.* 2015). Cependant il semble y avoir une exception à cette règle. Nos résultats suggèrent effectivement qu'en toute fin de vie les chances de survie des individus mâles de meilleure qualité sont inférieures à celles des individus de moins bonne qualité. Ce renversement de situation peut être mis en relation avec le coût de reproduction supposé important chez les mâles, en lien avec leur fort investissement dans l'élevage du jeune et leur vieillissement plus rapide relativement aux femelles. Ainsi les mâles de meilleure qualité seraient paradoxalement plus exposés à la sénescence en raison de leur fréquence de reproduction plus élevée. Ce résultat supporte la théorie du soma jetable par ailleurs aujourd'hui documentée chez de nombreuses espèces d'oiseaux, de mammifères et de reptiles (Lemaître *et al.* 2015). Les performances des individus de bonne qualité semblent, dans ce cas précis, rattrapées par les contraintes issues des compromis d'allocation d'énergie. De manière similaire, chez l'écureuil roux américain *Tamiasciurus hudsonicusi*, les femelles de bonne qualité se reproduisent plus tôt et ont plus de succès durant leur vie adulte mais subissent, en contrepartie, une mortalité plus importante du fait des coûts de reproduction (Descamps *et al.* 2006). De même, les bouquetins des alpes mâles *Ibex ibex* de meilleure qualité souffrent de taux de mortalité plus importants en toute fin de vie (Toïgo, Gaillard & Loison 2013).

2.2. Conséquences de la qualité individuelle

2.2.1. Patrons démographiques âge-dépendants et dynamique de population

La qualité individuelle a de nombreuses conséquences notamment sur notre perception des patrons démographiques. La présence d'individus aux aptitudes de survie différentes entraine un mécanisme de sélection provoquant une modification de la composition de la population à travers le temps (Vaupel & Yashin 1985). Dans nos travaux nous montrons par exemple que le succès lors de la première reproduction tend à décroitre avec l'âge des individus. Ce patron a été mis en relation avec la qualité des individus et ne décrit donc pas l'évolution biologique de ce trait avec l'âge. Si tous les individus étaient homogènes du point de vue de leur qualité, on aurait probablement observé une augmentation du succès de reproduction à la primarité avec l'âge (Forslund & Pärt 1995). Ce résultat suggère que l'apparition progressive des individus de plus faible qualité biaise notre perception du patron biologique entre le succès lors de la première reproduction et l'âge à laquelle elle intervient. Si nous ne contrôlons pas l'effet de la qualité individuelle, le patron perçu tend à sous-estimer la relation positive entre l'âge de première reproduction et les chances que cet évènement aboutisse à un succès. Au-delà du processus de sélection qui biaise les patrons observés à l'échelle de la population, la qualité individuelle complexifie également la détection des compromis évolutifs (Van Noordwijk & de Jong 1986; Wilson *et al.* 2014). Le coût de reproduction peut par exemple être atténué ou dissimulé si l'on ne prend pas en compte la qualité des individus (Linden & Møller 1989; Hamel *et al.* 2009a; Chambert *et al.* 2013). Il en va de même pour les processus individuels associés à la sénescence dont l'importance est généralement sous-évaluée si la qualité individuelle n'est pas prise en compte (Nussey *et al.* 2008; Péron *et al.* 2010).

Les conséquences démographiques de la qualité ne se limitent pas aux performances des individus, elles concernent également les propriétés démographiques émergeantes à l'échelle de la population (Bolnick *et al.* 2011; Vindenes & Langangen 2015). Des études théoriques ont montré que les variations d'aptitude de survie et de reproduction entre individus affectent le taux de croissance, la taille à l'équilibre ainsi que la stabilité des populations (Bjørnstad & Hansen 1994). Lorsque que les performances de survie sont associées aux performances de reproduction, l'hétérogénéité individuelle tend à augmenter le taux d'accroissement des populations (Kendall *et al.* 2011) ainsi que la taille des populations à leur équilibre (Stover, Kendall & Fox 2012) relativement à la situation ou tous les individus sont homogènes. De même, les variations individuelles sont généralement associées à une plus grande stabilité de la population et de ce fait entraineraient une diminution du risque d'extinction (Fox & Kendall 2002; Fox 2005; Acker *et al.* 2014; Noonburg *et al.* 2015). Cependant, l'ensemble de ces résultats dépendent des hypothèses faites dans les modèles théoriques notamment ceux concernant l'hérédité de la qualité individuelle (Robert, Sarrazin & Couvet 2003; Vindenes, Engen & S\a ether 2008). Par exemple, sous certaines conditions, la présence de variations démographiques individuelles pourrait déstabiliser la dynamique d'une population (Lindström & Kokko 2002). Ces études montrent que les conséquences des variations de qualité individuelle sur les dynamiques des populations est un champ de recherche en cours de développement. Sa progression est cependant limitée par notre compréhension de l'expression de la qualité des individus en milieu naturel incluant l'ensemble des conséquences pour leurs performances et son hérédité. Bien qu'un nombre croissant d'études s'intéressent aux variations individuelles au sein d'une population, des mécanismes fondamentaux comme la sélection de viabilité restent mal connus. Ce processus décrit l'augmentation de la qualité moyenne d'une cohorte au cours du temps du fait de la disparition progressive des individus les moins aptes. Chez les cerfs élaphes mâles *Cervus elaphus* et les chevreuils femelles *Capreolus capreolus*, on a observé qu'au sein d'une cohorte l'augmentation de la mortalité en début de vie est associée à une meilleure survie à l'âge adulte, ce qui suggère un mécanisme de sélection de viabilité (Rose, Clutton-Brock & Guinness 1998; Garratt *et al.* 2015). Bien que ce type de processus puisse être déterminant pour comprendre les conséquences de la qualité individuelle sur la dynamique d'une population, peu d'études ont à ce jour investigué empiriquement les mécanismes de sélection au sein des cohortes. On peut noter ici que l'importance de ce processus de sélection pourrait dépendre du rythme de vie des espèces. En effet l'hétérogénéité de survie pourrait être plus importante chez les espèces à stratégie de vie rapide en accord avec la théorie de la canalisation (discussion Chapitre 5, Péron *et al.* 2016).

2.2.2. Dynamiques éco-évolutives

Comme nous l'avons vu dans l'introduction, les conditions environnementales durant le développement semblent particulièrement importantes pour expliquer la qualité d'un individu (Lindström 1999; Monaghan 2008; Cam & Aubry 2011). Les travaux menés au cours de cette thèse suggèrent également que les conditions natales pourraient jouer un rôle prépondérant pour déterminer les capacités des individus à survivre et se reproduire sur le long-terme. Ces résultats sont cohérents vis à vis des prédictions théoriques. En effet, il est attendu que l'héritabilité des caractères fortement associés à la valeur sélective des individus soit faible. Les fortes pressions de sélection que ces traits subissent devraient éroder la diversité génétique qui leur est associée (Fisher 1930; Stearns & Kawecki 1994). Ainsi la part des facteurs génétiques impliqués dans les variations des taux vitaux directement associés à la valeur sélective tel que la survie devrait être faible. Des études empiriques menées en milieu naturel ont confirmé cette prédiction (Mousseau & Roff 1987; McCleery *et al.* 2004; Teplitsky *et al.* 2009). L'héritabilité du taux de survie et de la longévité a par exemple été estimée respectivement à 2 et 0% chez une population de mésange bleue *Cyanistes caeruleus* (Papaïx *et al.* 2010) et de moineau domestique *Passer domesticus* (Schroeder *et al.* 2012). De même, l'héritabilité du taux de reproduction, bien que non nulle, est faible chez une population de phoque de Weddell *Leptonychotes weddellii* (Chambert, Rotella & Garrott 2014). Il apparait donc qu'une grande partie (de 30 à 50% chez les grands herbivores) des variations individuelles de capacité de survie et de reproduction observées dans les populations sauvages soient induites par des effets non génétiques mais par les conditions environnementales natales (Hamel *et al.* 2009b). Dans ce contexte, l'existence de la qualité individuelle modifie en profondeur les dynamiques éco-évolutives. En effet, les effets à long terme de l'environnement impliquent qu'une partie des performances des individus est déterminée indépendamment de facteurs génétiques. Dans ces conditions, il s'ensuit que la qualité individuelle diminue la force de la sélection naturelle, ou plus exactement l'intensité des boucles de rétroaction évolutives, en augmentant l'importance de la dérive génétique. Dans le cas où la qualité est en grande partie le fait des conditions environnementales natales, l'association supposée étroite entre la valeur sélective et l'aptitude phénotypique des individus n'est plus vérifiée (encadré 1 de l'introduction générale). La qualité individuelle serait donc un paramètre important pour comprendre l'évolution des populations en milieu naturel.

2.3. Adaptation à la qualité individuelle

2.3.1. Le choix du partenaire sexuel

Le choix du partenaire a été reconnu comme une force évolutive majeure dès la formulation de la théorie de l'évolution par sélection naturelle (Darwin 1859). En effet, au cours de la vie d'un individu, les choix des partenaires de reproduction peuvent fortement influencer le nombre de descendants qu'il engrangera. La sélection sexuelle a conduit de nombreuses espèces à développer des attributs permettant aux individus de signaler « honnêtement » leurs aptitudes reflétant la valeur sélective de leur patrimoine génétique (Andersson 1994). Le caractère « honnête » des signaux est assuré par le coût qu'ils représentent, c'est la théorie du handicap (Zahavi 1975). Seuls les individus en bonne condition sont capables de produire ces signaux attestant de fait de leurs aptitudes à survivre et se reproduire. Ainsi ces attributs évoluent en même temps que les goûts et l'attirance envers ces signaux chez le sexe opposé. La sélection sexuelle est un mécanisme fondamental car elle permet aux individus de maximiser leur performance en choisissant des partenaires à forte valeur sélective. Cependant, il semble que ces signaux puissent évoluer au sein d'une population en dehors des informations qu'ils apportent sur la qualité génétique des individus. Pour développer cette idée, plaçons-nous dans une population théorique ou tous les individus présentent le même patrimoine génétique en dehors des gènes associés aux choix du partenaire. On imagine ici que les facteurs génétiques associés aux choix du partenaire n'interviennent dans aucun autre trait biologique. Dans ces conditions, l'évolution de signaux par sélection sexuelle paraît impossible car tous les individus présentent en moyenne la même valeur sélective. Quel que soit le choix d'un individu, la valeur sélective de sa descendance sera la même. Cependant, si l'on considère l'existence de la qualité individuelle comme nous l'avons abordé dans cette thèse, le choix de son partenaire devient de nouveau déterminant.

En effet, les performances d'un individu sont affectées par la qualité de son partenaire qui, nous l'avons vu, peut varier même en absence de variabilité génétique. Les conséquences du choix du partenaire ont été particulièrement étudiées chez les oiseaux. Chez ce taxon, le choix du partenaire est aussi important pour les mâles que pour les femelles car le plus souvent les deux partenaires élèvent leur progéniture conjointement. Ainsi les caractères secondaires ont évolué par sélection sexuelle chez les deux sexes (Kraaijeveld, Kraaijeveld-Smit & Komdeur 2007). En plus des choix mutuels, les individus indépendamment de leur sexe, allouent leur énergie dans la reproduction en fonction des caractéristiques phénotypiques de leur partenaire (Sheldon 2000; Pilastro, Griggio & Matessi 2003; Cornwallis & Birkhead 2007). On a observé chez les oiseaux que les capacités des parents à prodiguer des soins à leur progéniture variaient en fonction des individus et ce de manière répétable dans le temps (Schwagmeyer & Mock 2003; Saraux *et al.* 2011a). Choisir le bon partenaire semble donc primordial. La qualité du partenaire détermine en grande partie les conditions dans lesquels se développent les jeunes individus et affecte donc leur qualité phénotype (Metcalfe & Monaghan 2001; Naguib & Gil 2005; Naguib, Nemitz & Gil 2006). De plus, pour un individu donné, la qualité du partenaire impacte également son propre phénotype. Des études expérimentales sur le diamant mandarin *Taeniopygia guttata* ont démontré que la qualité d'un individu pouvait affecter le phénotype de son partenaire de manière durable. Lorsqu'un oiseau est associé à un partenaire de faible qualité, l'étude montre que ses performances individuelles diminuent sur le long-terme, en particulier pour ce qui concerne la longévité (Monaghan *et al.* 2012). Les auteurs suggèrent que ce résultat n'est pas dû à une augmentation de l'investissement reproductif, et donc à un coût de la reproduction, mais plutôt à l'augmentation du stress avec une dégradation de la protection sociale (*social buffering* en anglais, (Hennessy, Kaiser & Sachser 2009). Ainsi, la qualité d'un individu, indépendamment de ses caractéristiques génétiques, est probablement un critère important pour le choix du partenaire de reproduction.

Si l'on revient à notre population théorique, on peut donc supposer que les capacités à identifier la qualité individuelle de ses partenaires évoluent même en absence initiale de variation génétique en dehors des gènes influençant le choix du partenaire. En effet les individus capables de discriminer les individus au regard de leur qualité auront en moyenne un plus grand nombre de descendants à la fois directement au cours de leur vie et indirectement via leur descendance du fait des effets parentaux. Chez les passereaux, le chant semble être un indicateur de la qualité des individus. Les femelles diamants mandarins sont capables, à la seule écoute des chants, de discriminer des mâles adultes ayant connu des conditions stressantes lors de leur développement (Spencer *et al.* 2005). L'implication de la qualité individuelle dans le choix de partenaire ne se limite pas à cela. Il s'avère en effet que la qualité d'un individu modifie ses propres préférences envers ses partenaires de reproduction. Les femelles diamants mandarins ayant connu des conditions stressantes en début de vie montrent une plus grande attractivité pour les mâles de qualité inférieure (Holveck & Riebel 2010). Ces résultats suggèrent que les préférences des individus sont modifiées par leur phénotype. Les auteurs stipulent que ces modifications comportementales sont adaptatives épargnant aux individus les moins attractifs les coûts associés à la compétition pour l'acquisition d'un partenaire de qualité élevée. Ces résultats montrent que la prise en compte de la qualité individuelle non génétiquement déterminée modifie notre compréhension des systèmes d'appariement. Dans la partie suivante nous allons voir que la qualité d'un individu ne modifie pas seulement ses choix de partenaire mais pourrait aboutir à l'évolution de stratégies d'histoire de vie différentes en fonction des caractéristiques individuelles.

2.3.2. Qualité individuelle et stratégie individuelle

Comme nous l'avons vu dans l'introduction générale (voir 1.3.4.), différentes stratégies individuelles sont susceptibles de se maintenir si elles ont en moyenne la même valeur sélective. La prise en compte de la qualité individuelle amène cependant à réviser ce postulat. Si les individus diffèrent dans leur capacité intrinsèque à survivre et se reproduire alors il est possible que différentes stratégies se maintiennent même si elles n'ont pas en moyenne la même valeur sélective. En effet, il suffit que chaque stratégie permette à un individu, *compte tenu de sa qualité*, de maximiser ses performances pour que celle-ci se maintienne. Dans certain cas, les individus sont contraint à tirer le meilleur parti possible d'une mauvaise situation (Dawkins 1982; Dominey 1984). A titre d'exemple, les stratégies de reproduction de type « combattant » et « parasite » décrites dans l'introduction peuvent être réinterprétées en prenant en compte l'existence des différences de qualité individuelle. Si un individu est de faible qualité, il peut être de taille plus petite que la moyenne pour un âge donné. Ainsi cet individu maximisera ses performances en adoptant la stratégie de reproduction de type « parasite » car une grande taille est une condition indispensable pour être compétitif au sein des individus de type « combattant ». On observe que ces stratégies de reproduction sont souvent condition dépendantes suggérant que la stratégie « parasite » rassemble des individus ayant, en moyenne, une qualité inférieure à celles des individus de la stratégie « combattant ». Ainsi il est théoriquement possible que les performances de la stratégie « parasite » soient inférieures à celle de la stratégie « combattant ». Ces stratégies étant évolutivement stables si elles permettent aux individus de mauvaise qualité de maximiser leurs performances. Ici il faut garder à l'esprit que les coûts associés à cette plasticité sont également à prendre en compte (DeWitt 1998).

D'une manière plus générale, l'existence de qualité individuelle pourrait favoriser l'émergence de stratégie d'histoire de vie individuelle. Théoriquement, il est attendu que l'investissement dans la reproduction soit fonction de la valeur reproductive résiduelle (Fisher 1930). Lorsqu'un individu a peu de chance de se reproduire à l'avenir, il est avantageux pour lui d'investir beaucoup d'énergie dans la reproduction actuelle. Par exemple, lorsque des épinoches *Gasterosteus aculeatus* sont soumises à la présence d'un prédateur, elles accélèrent leur rythme de vie en investissant plus d'énergie dans la reproduction (Candolin 1998). Chez les oiseaux, lorsque la valeur reproductive résiduelle de mésanges charbonnières *Parus major* est expérimentalement diminuée par la manipulation de la taille de la ponte, les individus ajustent leur comportement en conséquence en étant plus prompts à prendre des risques en toutes situations (Nicolaus *et al.* 2012). Les capacités intrinsèques d'un individu à survivre et se reproduire déterminent en partie sa valeur reproductive. Si l'on compare un ensemble d'individus du même âge, plus la qualité d'un individu est faible, moins sa valeur reproductive est importante. Cela signifie qu'en fonction de leurs capacités intrinsèques, les individus ne font pas tous face au même compromis d'allocation. Dans ce contexte, des individus du même âge de qualité hétérogène pourraient maximiser leurs performances en adoptant des stratégies différentes créant ainsi une divergence des traits d'histoire de vie au sein d'une même population (Clark 1994). En particulier, un individu de faible qualité devrait adopter une stratégie de vie plus rapide, en investissant son énergie en priorité vers la reproduction au détriment de sa survie, car les gains potentiels sont plus importants relativement à un individu de qualité supérieure. Ce mécanisme a été proposé sous le nom de *réponse adaptative prédictive interne* (*Internal predictive adaptive response*(Nettle, Frankenhuis & Rickard 2013). Un certain nombre d'études empiriques ont rapporté des résultats soutenant l'existence de ce mécanisme adaptatif. Chez l'homme, des travaux suggèrent que les femmes qui ont connu des conditions de vie stressantes durant leur développement ont leur première grossesse à un âge plus précoce (Nettle, Coall & Dickins 2011). De même, les jeunes rattes ayant connu un stress nutritif durant leur ontogénie montrent une maturité sexuelle plus précoce en accord avec une accélération du rythme de vie (Sloboda *et al.* 2009). Très récemment, une étude menée en milieu naturel suggère que les rennes *Rangifer tarandus* femelles s'engagent dans la reproduction à un seuil de condition corporelle plus faible, autrement dit elles prennent plus de risques, lorsque qu'elles ont connus des conditions de développement peu favorable lors de leur développement ontogénique in-utéro (Douhard *et al.* 2016). Il n'y a pas d'étude comparable chez les oiseaux en milieu naturel étudiant la réponse démographique des individus suite à des conditions de développement stressantes, mais l'on peut tout de même signaler une étude sur le faucon crécerelle de l'île Maurice *Falco punctatus* qui suggère une accélération de son rythme de vie lorsque les individus se sont développés dans un environnement fortement anthropisé, moins favorable à l'espèce (Cartwright *et al.* 2014). Toutes ces études supportent l'idée que les individus résolvent leurs compromis d'allocation différemment en fonction de leur qualité et adoptent des stratégies de vie individualisées.

Ces stratégies individuelles peuvent être rapprochées du développement récent de la théorie du syndrome du rythme de vie (*pace of life syndrome*). Cette théorie étend la théorie des stratégies d'histoire de vie, historiquement limitée au domaine de la démographie, au domaine de l'écologie comportementale et à la physiologie (Reale *et al.* 2010). Elle propose qu'au cours de l'évolution des stratégies d'histoire de vie, ce ne sont pas seulement les traits démographiques qui se sont modifiés mais également les traits comportementaux (Wolf & Weissing 2012) et physiologiques (Ricklefs & Wikelski 2002). Chez une espèce au rythme de vie rapide, la sélection naturelle favoriserait un métabolisme élevé ainsi que les traits comportementaux permettant un investissement reproductif important à court terme au détriment de la survie, par exemple en favorisant les comportements à risques pour augmenter le succès de recherche alimentaire ou les comportements de défense de sa progéniture en dépit de sa propre survie. Cette théorie s'étend naturellement de l'échelle des espèces jusqu'à l'échelle des individus où les traits démographiques, le comportement et la physiologie paraissent également structurés (Reale *et al.* 2010). Dans ce contexte, si des stratégies démographiques ont évolué en lien avec les capacités intrinsèques des individus, comme nous l'avons suggéré dans la partie précédente, il pourrait en être de même de la physiologie ainsi que du comportement (Wolf *et al.* 2007). Cette réflexion nous conduit à proposer que les traits de personnalité récemment mis en évidence chez l'ensemble des animaux (Stamps & Groothuis 2010) ont évolué en interaction avec les variations de qualité individuelle. Si tel est le cas, nous pouvons prédire que les individus de mauvaise qualité adoptent plus facilement des comportements à risque et qu'ils montrent également plus d'agressivité en relation avec leur stratégie d'histoire de vie potentiellement plus rapide. Bien que la relation entre la personnalité et le rythme de vie ait été établie chez diverses espèces (Smith & Blumstein 2007), la connexion entre les syndromes comportementaux et les caractéristiques intrinsèques des individus, c'est-à-dire la qualité individuelle, reste non testée à ce jour. L'étude de la personnalité chez les populations animales est très récente et la connaissance à ce sujet reste limitée. Par exemple l'effet de l'âge et notamment de la sénescence commence juste à être étudié (Class & Brommer 2016). Il faut donc attendre que ce champ de recherche se développe d'avantage pour pouvoir interpréter les variations comportementales avec plus de recul et tenter d'établir des liens solides avec des stratégies démographiques et les aptitudes de chaque individu.

3. Perspectives

La théorie des stratégies d'histoire de vie vise à expliquer les variations des traits démographiques que l'on observe chez l'ensemble des êtres vivants. Historiquement, cette théorie s'est principalement intéressée aux variations observées à l'échelle des espèces et peu aux variations interindividuelles. Il a souvent été suggéré que les contraintes phylogénétiques et allométriques étaient déterminantes pour expliquer les stratégies d'histoire de vie des espèces suggérant implicitement que les variations à l'échelle des individus étaient réduites (Stearns 1983; Gaillard *et al.* 2005). Cependant si l'on donne de l'importance aux facteurs écologiques pour expliquer l'évolution et la diversification des stratégies d'histoire de vie à l'échelle des espèces, il devient naturel d'envisager également une variabilité de stratégies entre les individus. Dans ce cas, on peut facilement établir un parallèle entre la variabilité des stratégies d'histoire de vie entre les espèces et le mécanisme adaptatif que nous avons décrit à l'échelle individuelle. Si les risques de mortalité extrinsèques sont supposés être un facteur déterminant pour expliquer la position d'une espèce sur le continuum rapide-lent, il pourrait également jouer un rôle dans la stratégie de vie observé à l'échelle de l'individu (Pepper & Nettle 2014). Cela suggère que l'on retrouve le gradient rapide-lent des stratégies d'histoire de vie décrit à l'échelle des espèces au sein d'une même population (Cameron *et al.* 2008; Reid *et al.* 2010). Un nombre croissant de théories considèrent les variations individuelles observées au sein d'une même population et les recherches empiriques menées ces 15 dernières années tendent à considérer d'avantage la singularité des individus. Comme nous l'avons vu, il est incontestable que la notion de qualité individuelle joue ici un rôle important en ayant de nombreuses conséquences tant d'un point de vue écologique qu'évolutif. Cette prise en compte des propriétés individuelles pose la question des répercutions sur les niveaux d'organisation supérieurs. Par exemple, nous savons que l'environnement natal affecte fortement la qualité d'un individu et donc ses performances de survie et de reproduction sur le long-terme. On peut alors se demander comment les processus démographiques à large échelle interagissent avec l'hétérogénéité des habitats. La répartition spatiale des individus n'étant généralement pas aléatoire au regard de leur qualité, on peut supposer que les habitats les moins favorables, composés d'individus nés localement et d'immigrants venant en partie de zones plus favorables, abritent une plus grande hétérogénéité interindividuelle. Ainsi on peut se questionner sur les conséquences de la qualité individuelle sur les dynamiques démographiques spatialisées tels que les systèmes de dynamique de populations sources-puits.

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Appendix A

Appendix A1: Sex assignment

We used the life histories of 9685 individuals ringed as chicks and resighted between 1965 and 2013. Individuals were sexed in the field based on sexual size and plumage dimorphism, courting and mating behaviours. Since 1999 genetic assignments were available and were systematically used from 2003 (Weimerskirch, Lallemand & Martin 2005). Sex was known for 4913 birds (2431 females and 2482 males), including 2554 from observation (1264 females and 1290 males), and 2359 from genetic (1167 females and 1192 males). Of the remaining unsexed birds, 96.5 % were never seen after fledging on Possession Island, and can be considered as dead before recruitment (Charmantier et al. 2011). As all individuals needed to be included in the model in order to avoid overestimating survival, we inferred the sex of the unsexed birds using a binomial random distribution as in Pardo, Barbraud & Weimerskirch (2013). Knowing that our study population showed an equilibrium sex ratio at fledging (n=3126, p-value=0.99) and that the sex ratio of recaptured birds was also unbiased (n=3085, p-value=0.43), we deduced that the large majority of these birds never seen at the colony were individuals of both sexes in equal proportion. Thus, we were confident that this sex-inference procedure did not introduce spurious patterns since almost all individuals had the same life history (i.e. seen as chick and never recaptured) with a deductible sex-ratio of 1. To valid our process, we repeated the random sex assignment 10 times to check the stability of the sex specific survival parameters.

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Appendix A2: Parameterization of the general model

Pre-recruitment state and biological constraints

The initial state was constrained to the pre-recruitment state because all birds were banded as chick. Then, from the first year of life to the fifth, transition probability to the pre-recruitment stage was fixed to 1 because no recruitment occurred before 6 year-old. To model the pre-recruitment period we defined two main stages: the *juvenile* stage, which was an unobservable state, corresponding to the first 2 years of life spent continuously at sea (i.e. no individual of 1 or 2 year-old were observed at the colony), and the *immature* stage corresponding to non-recruited birds older than 2 years that started to visit the colony and could be potentially observed. Juvenile survival was set to be cohort dependent due to its expected high sensitivity to natal and current environmental conditions (Gaillard et al. 2000). The immature stage was decomposed in two age classes: a 3-8 years age-class and a >8 years age-class. We estimated average survival for individuals from age 3 to 8 due to few recapture events in early-life (only 50 recaptures for individuals of 3 year-old) and because early return at the natal colony may reflect differences in individual quality and bias the survival estimates of the first age-classes. With the age class 3-8 years, we considered individuals just before the peak of recruitment (Gauthier, Milot & Weimerskirch 2012) so as to obtain a robust and representative immature survival estimate. Thus, age-specific survival was tested only into the age class >8 years. Our overall model comprised a year effect for immature survival. Finally both juvenile and immature survivals were assumed sex-dependent. Recapture probability of the immature stage was modelled as age dependent to fit the progressive return of individuals at the breeding colony before recruitment. From 6 years of age birds may recruit and move toward the mature states SB and FB depending both on sex and age (Gauthier, Milot & Weimerskirch 2012). We constrained recruitment rate to be constant after age 15 owing to few recruits after this age (Weimerskirch & Jouventin 1987). Our overall model included a time effect for recruitment since recruitment process may have been affected by variations in population size across the study period (Weimerskirch & Jouventin 1987).

Adult stage modelling and biological constraints

For mature birds, following the results of Barbraud and Weimerskirch (2012), survival was assumed sex-dependent. Based on Pardo, Barbraud & Weimerskirch (2014), we distinguished different survival probabilities for breeders and post reproductive breeders on one side and recruited non-breeders on the other side. Since wandering albatrosses are monogamous and both sexes exhibit a quasi-biennial breeding, transitions between mature states were constrained to be similar between sexes. Recapture probabilities were assumed state dependent due to lower detection probability for observable non-breeders and failed breeders compared to successful breeders.

Finally our initial model was:

$$\Phi^{pre}_{a_{(1to2)}.sex.cohort,a_{(3to8,9+)}.sex.time}\Phi^{ad}_{sex.state}\quad\Psi^{pre\rightarrow ad}_{a.sex.time}\Psi^{ad\rightarrow ad}_{cst}\ p^{pre}_{a}\ p^{ad}_{state}$$

where the pre-recruitment (pre) survival probability (Φ) was age (a), sex, cohort and time dependent, the adult (ad) survival probability was sex and state dependent, the probability of transition (Ψ) from pre-recruitment to adult was age, sex and time dependent, the probability of remaining is the adult stage was constant (cst), the pre-recruitment capture probability (p) was age dependent, and the adult capture probability was state dependent. In this model notation, symbols "." indicate interactive effects, "1to2" and "3to8" indicate indicate that age classes were grouped and "9+" indicates that age classes were separated from 9 to 16.

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Appendix A3: Environmental covariates

Our selected covariates included a large-scale climate index, the Southern Annular Mode (SAM) defined as the difference in the normalized monthly zonal mean sea level pressure between 40°S and 65°S (Gong & Wang 1999). SAM is the leading mode of atmospheric circulation variability in the Southern Hemisphere affecting wind condition in the Southern Ocean (Gong & Wang 1998; Marshall 2003). Previous studies showed that changes in wind regime over the Southern Ocean have influenced the foraging ecology and life-history traits of adult wandering albatrosses (Weimerskirch et al. 2012). SAM may affect albatrosses both directly through increasing wind speeds and thus travel time efficiency (Weimerskirch et al. 2012), and indirectly though increasing Ekman transport accentuating upwelling intensity and consequently the primary productivity (Thompson et al. 2011). We assessed the impact of average yearly SAM on age-specific pre-recruitment survival and recruitment rates. We used average yearly SAM since we estimated annual demographic parameters. SAM data were selected from the online database of the British Antarctic Survey (http://www.nerc-bas.ac.uk/icd/gjma/sam.html).

We used the Sea Surface Temperature Anomaly (SSTA), a local climate variable which is a proxy of the oceanographic conditions that may determine the development and productivity of the whole trophic web. SSTA were related to demographic parameters for many seabird species in the Southern Ocean and elsewhere, probably through indirect mechanisms such as the abundance of food resources (e.g. Sandvik et al. 2005; Frederiksen, Mavor & Wanless 2007; Votier et al. 2008; Barbraud et al. 2012). The recently acquired knowledge about the at-sea distribution of all stages in wandering albatrosses allowed us to extract average yearly SSTA values over the spatial areas used during the entire year for each age stage previously defined (Delord et al. 2013, Weimerskirch et al. 2014). As for SAM we assessed the impact of average yearly SSTA on age-specific pre-recruitment survival and recruitment rates. SSTA data were available from the IRI Data Library http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/ .CMB/.GLOBAL/.ReynSmithOIv2/.monthly/.ssta/.

Seabirds are particularly vulnerable to longline fishing since they are attracted by bait accessible on the surface and hooked when trying to catch them (Brothers, Cooper & Lokkeborg 1999). Longline fisheries are known to have important impacts on seabirds in particular through additional mortality (Gales et al. 1998), including the Crozet wandering albatross (Weimerskirch, Brothers & Jouventin 1997). Albatrosses interact with fishing vessels and young individuals could have different attractiveness than adults, and thus be impacted differently (Barbraud et al. 2012). To assess the potential effect of longline fisheries activities on early life survival, a direct estimate of accidental bycatch rate was not available both for the whole distribution area and for the period of investigation. Thus, following earlier studies (Véran et al. 2007; Rolland, Barbraud & Weimerskirch 2008; Rolland, Weimerskirch & Barbraud 2010) we used the fishing effort expressed as numbers of hooks assuming that bycatch rate was proportional to fishing effort. We assessed the impact of the annual total number of hooks set on age-specific pre-recruitment survival only since we only expected effects on survival. Fishing effort data were extracted from the Indian Ocean Tuna Commission (IOTC; http://www.iotc.org/data/capacity-building-data) and were expressed as numbers of hooks set over the spatial area used by individuals during the pre-recruitment stage.

To test for an effect of density dependence on pre-recruitment survival and recruitment we used the number of breeding pairs observed annually at Possession Island as a covariate. Detecting and assessing the strength of density dependence can be challenging and results may be strongly biased when uncertainty in population size is large and not accounted for (Lebreton & Gimenez 2013). However, methods for detecting density dependence in life history traits are generally conservative and tend to underestimate the strength of density dependence (Lebreton & Gimenez 2013). In addition, counts of breeding pairs of wandering albatrosses on Possession Island are very precise (≤ 5%, C. Barbraud unpublished data) given the very high detectability of individuals on their nest.

To test for the effect of candidate covariates we used logistic models as:

$\mathrm{logit}(\varphi^{n}) = \beta_0+\beta_1 * x_n$

where φ is the survival probability, β_0 is an intercept parameter, β_1 is a slope parameter, and x_n is the covariate x the year n.

We then performed an analysis of deviance test with a Fisher-Snedecor distribution (ANODEV; Grosbois et al. 2008) by comparing the amount of deviance between the model assuming full time dependence (t), the model including the covariate (co), and the one assuming no time variation (cst) through the ratio $Ftest_{\mathrm{cst/co/t}} = \frac{\left(\frac{Dev(F_{cst}) - Dev(F_{co})}{I-1}\right)}{\hat{c}}$, where $\hat{c} = \frac{Dev(F_{co}) - Dev(F_t)}{n-I}$ with *n* the number of survival estimates obtained from model F_t and *I* the number of parameters required to describe the relationship between the demographic parameter and the focal covariate. The percentage of variation that was explained by a covariate (r^2) was estimated as: $r^2 = [(Dev(F_{cst}) - Dev(F_{cov})]/[Dev(F_{cst}) - Dev(F_t)]$ (Skalski 1996).

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Appendix A4: Estimation of temporal variation

To make inference about differences in temporal variability, it is important to separate process variance from sampling variance which is inherent to the estimation of unknown population parameters (Gould & Nichols 1998). True temporal variability, $\hat{T}^2$, can be calculated as:

$$\hat{T}^2 = \hat{S}^2 - \frac{1}{n}\sum_{1}^{\mathrm{n}} \hat{E}[\mathrm{Var}(\hat{\varphi}_i \mid \mathrm{F})] + \frac{2}{n(n-1)}\sum_{i<j} \hat{E}\,[\mathrm{Cov}(\hat{\varphi}_i, \hat{\varphi}_j \mid \mathrm{F})]$$

with $\hat{S}^2$ the total variance of the estimated survival rates between the years 1 to *n*, $\mathrm{Var}(\hat{\varphi}_i \mid \mathrm{F})$ the sampling variance of the survival estimate of the year i, and $\mathrm{Cov}(\hat{\varphi}_i, \hat{\varphi}_j \mid \mathrm{F})$ the sampling covariance between survival rate estimate *i* and *j*. We used the following simplified formula:

$$\hat{T}^2 \approx \hat{S}^2 - \frac{1}{n}\sum_{1}^{\mathrm{n}} \hat{E}[\mathrm{Var}(\hat{\varphi}_i \mid \mathrm{F})]$$

This approximation was acceptable since sampling covariance between survival rates are commonly low and both positive and negative, and total sampling covariance is negligible compared to total variance (Gould & Nichols 1998). Because survival is a probability, its maximum possible variance is a function of its mean value. To make comparisons among age-class groups, we scaled the process variance by the maximum possible variance for the corresponding survival value which was $s \times (1 - s)$ where s is the mean survival rate (Gaillard & Yoccoz 2003). We called this variance *relative process variance*.

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Appendix A5: Goodness-of-fit and model selection

There is no test available to assess the goodness-of-fit (GOF) of multi-event models. Hence, we performed GOF tests using program U-CARE (v.2.3.2, Choquet et al., 2009a) on a simplified dataset where we suppressed the first capture event to focus on adults (Lebreton et al. 2003) and which distinguished solely successful breeders and failed breeders and assigning randomly a reproductive status, i.e. failed or successful, to each individual for which no information was available. Model building, model selection and parameter estimates were obtained using program E-SURGE (v.1.8.5, Choquet, Rouan & Pradel 2009b). Model selection was performed using Akaike’s Information Criterion (AIC; Burnham & Anderson 2002). A variance inflation factor ($\hat{c}$) was taken into account following GOF tests by correcting AIC for extra-binomial variation. The ability of two models to describe the data was assumed to be not different if the difference in their QAIC was < 2.

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Table A1: Results from the GOF tests performed on the adult component of the dataset with known states.

	Females			Males		
Test	$\chi2$	df	P	$\chi2$	df	P
WBWA	192.3	136	0.001	251.8	194	0.003
3G.SR	156.5	98	<0.001	244.9	100	<0.001
3G.Sm	571.7	471	0.001	688.6	547	<0.001
M.ITEC	262.6	110	<0.001	359.8	161	<0.001
M.LTEC	82.9	44	<0.001	78.4	57	0.032

GOF tests indicated that some assumptions of the JMV model were not supported. First, test M.ITEC indicated the presence of trap-dependence (Pradel et al. 2005). This was clearly due to the quasi-biennial breeding strategy of wandering albatrosses, which is known to create trap-shyness in GOF tests (individuals seen breeding in year t are less likely to be seen in year t+1 due to their sabbatical year). However, given that our general model structure included unobservable states to explicitly take into account quasi-biennial breeding, we ignored the M.ITEC component in the GOF test of the general model. Second, although we removed the first capture corresponding to the fledging stage, test 3G.SR indicated the presence of transience. This was partly due to young individuals visiting the colony for the first time and never seen again. Finally, test WBWA indicated that individuals tended to remain in the same state from one occasion to the other. We thus estimated the GOF of the general model by summing the components WBWA, 3G.SR, 3G.Sm and M.LTEC of the GOF tests and used a variance inflation factor. Note that since the general model included age effects on survival, our model selection is conservative since these age effects partly accounted for transience.

Table A2: Pre-recruitment survival and recruitment modelling as a function of age (*a*), sex, cohort (*c*) and time (*t*) of the wandering albatross population of Crozet Island from 1965 to 2012. Results of model selection include: number of mathematical parameters (k), the relative deviance corrected by the overdispersion factor (QDev) and Akaike Information Criterion value corrected by the overdispersion factor (QAIC). Symbols ".", and "+" indicate interactive and additive effects respectively, ":" and "_" indicate that age classes are grouped and separated respectively. All models were full rank. The best models are marked in bold characters.

No.	Pre-recruitment survival	k	QDEV	QAIC
12	a(1:2).[c+sex]+a(3:8).[t+sex]+a(9:13)+a(>13).[t+sex]	184	80194.30	80562.30
11	a(1:2).[c+sex]+a(3:8).[t+sex]+a(9:13).t+a(>13).sex	189	80201.62	80579.62
10	**a(1:2).[c+sex]+a(3:8).[t+sex]+a(9:13)+a(>13).sex**	**156**	**80214.33**	**80526.33**
9	a(1:2).[c+sex]+a(3:8).t.sex+a(9:13)+a(>13).sex	194	80207.62	80595.62
8	a(1:2).[c+sex]+a(3:8).[c+sex]+a(9:13)+a(>13).sex	156	80276.68	80588.68
7	a(1:2).[c+sex]+a(3:8).c.sex+a(9:13)+a(>13).sex	194	80234.65	80622.65
6	a(1:2).[c+sex]+a(3:8,>13).sex+a(9:13)	118	80292.36	80528.36
5	a(1:2).c.sex+a(3:8,>13).sex+a(9:13)	156	80250.60	80562.60
4	a(1:2,3:8,>13).sex+a(9:13)	80	80520.92	80680.92
3	a(1:2,3:8,9:13,>13).sex	81	80520.28	80682.28
2	a(1:2,3:8,9:13,>13)	77	80531.13	80685.13
1	cst	74	80650.46	80798.46

No.	Recruitment	k	QDEV	QAIC
19	**[a(6,7,8,9,10,>10).ma+a(6,7,8,9:10,>10).fe]+t**	**149**	**80129.22**	**80427.22**
18	[a(6,7,8,9,10,>10).ma]+t+[a(6,7,8,9:10,>10).fe]+t	181	80108.21	80470.21
17	[a(6,7,8,9,10,>10).ma].t+[a(6,7,8,9:10,>10).fe].t	459	79775.60	80693.60
16	a(6,7,8,9,10,>10).ma+a(6,7,8,9:10,>10).fe	118	80292.36	80528.36
15	a.sex	129	80284.05	80542.05
14	a	118	80466.54	80702.54
13	cst	107	81854.25	82068.25

Figure A1: Distribution area from which SSTA and fishing effort values were extracted for (a) juvenile (1-2years), (b) immature (>2years), (c) parents of both sexes and (d) parents distinguishing male range (solid square) from female range (dashed square).

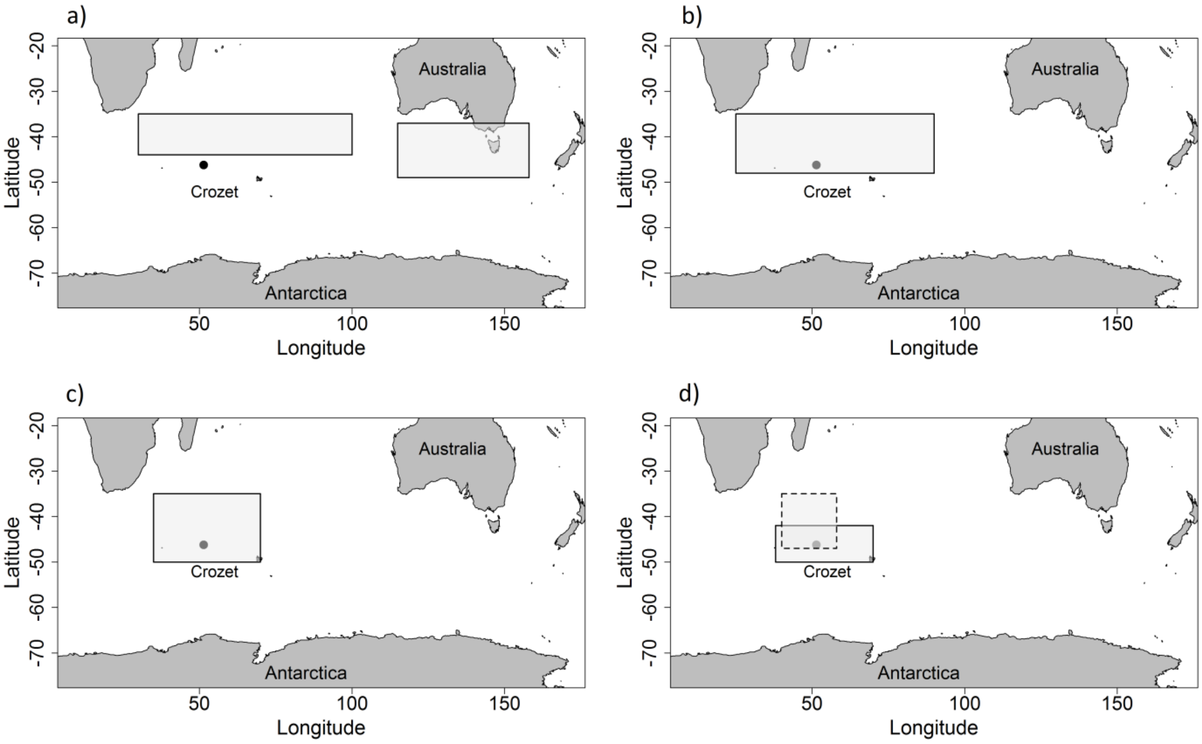


Figure A2: Graph summarizing selected environmental covariate: sea surface temperature anomaly (SSTA), southern annular mode (SAM), Breeding success of the colony (BS), Breeding population size (N) and Fishing effort (Fisheries), and the early life demographic parameters potentially affected: survival (φ) and recruitment probabilities (ψ). We tested for both long term effects of natal environmental conditions during chick rearing (i.e. April-November) and environmental conditions encountered by individuals after fledging on these early life demographic parameters.

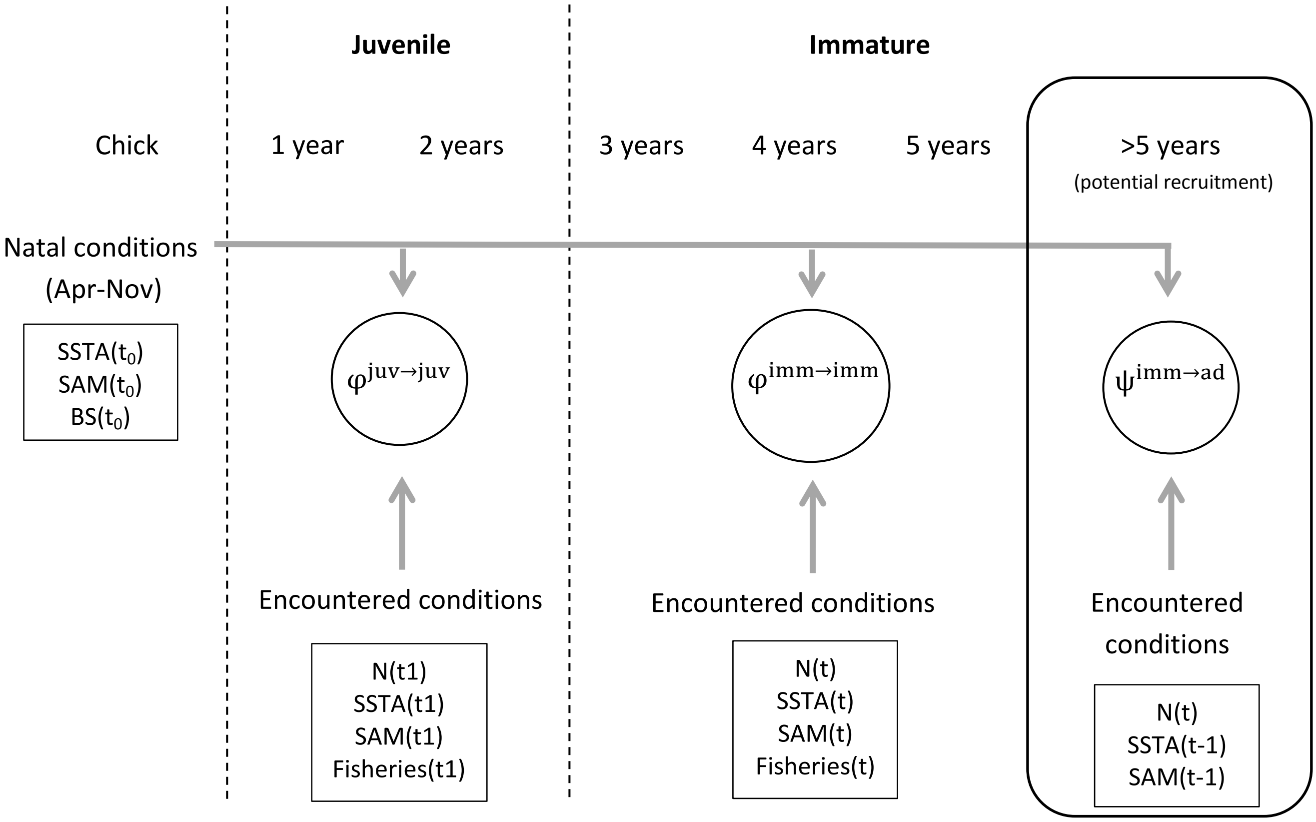
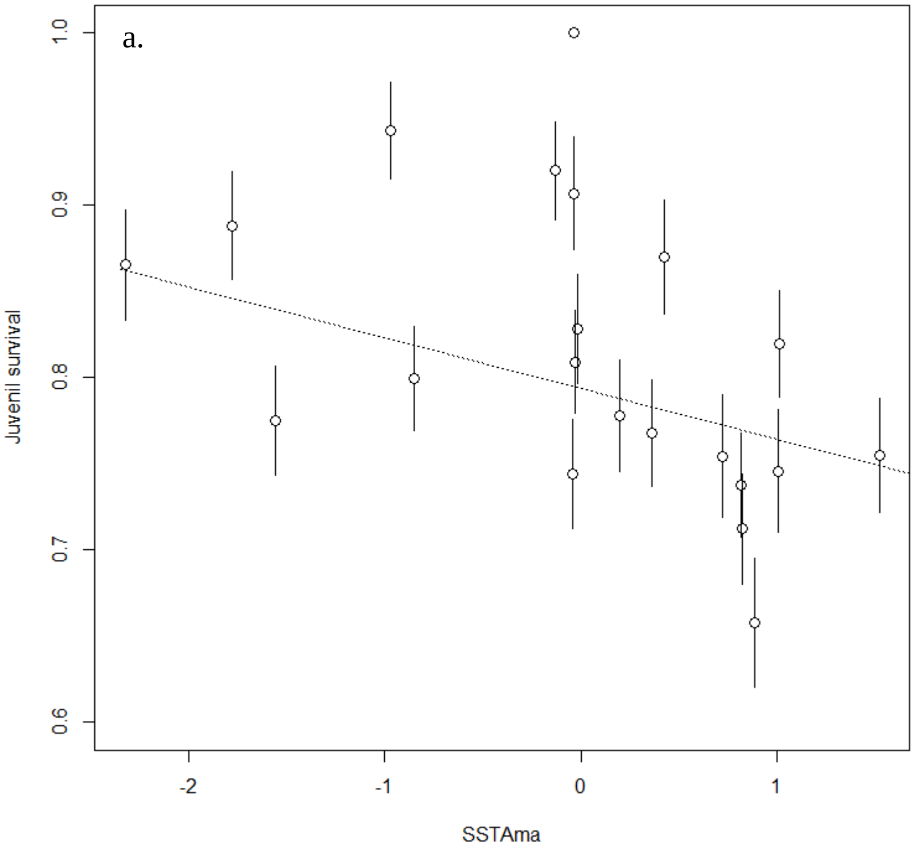
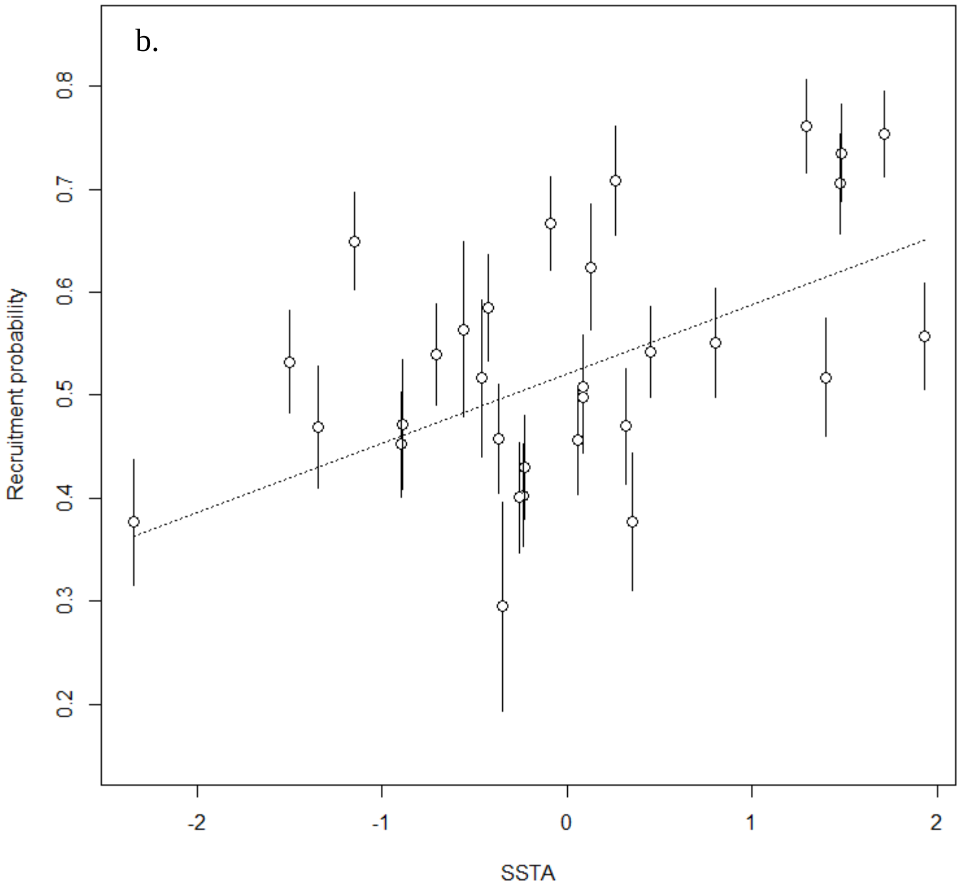


Figure A3: Relationships between early life survival and recruitment probabilities in the wandering albatross population of Crozet and environmental covariates. **a** 1-2 year-old juvenile survival from time-dependent model (filled circles ±SE, Table 1 Model 10) and 1-2 year-old juvenile survival modelled as a function of standardized SSTA on the male foraging ground during chick rearing (dotted line, Table 2 Model 7, P_{Anodev}=0.01). For illustration the relationship is shown for females. **b** recruitment probability from time-dependent model (filled circles ±SE, Table 1 Model 19) and recruitment probability modelled as a function of standardized SSTA (dotted line, Table 2 Model 28, P_{Anodev}<0.001), **c** recruitment probability modelled as a function of standardized SAM (dotted line, Table 2 Model 29, P_{Anodev}<0.001). For illustration the relationships are shown for 9-10 year-old females.




b.
Recruitment probability
0.2
0.3
0.4
0.5
0.6
0.7
0.8
-2
-1
0
1
2
SSTA

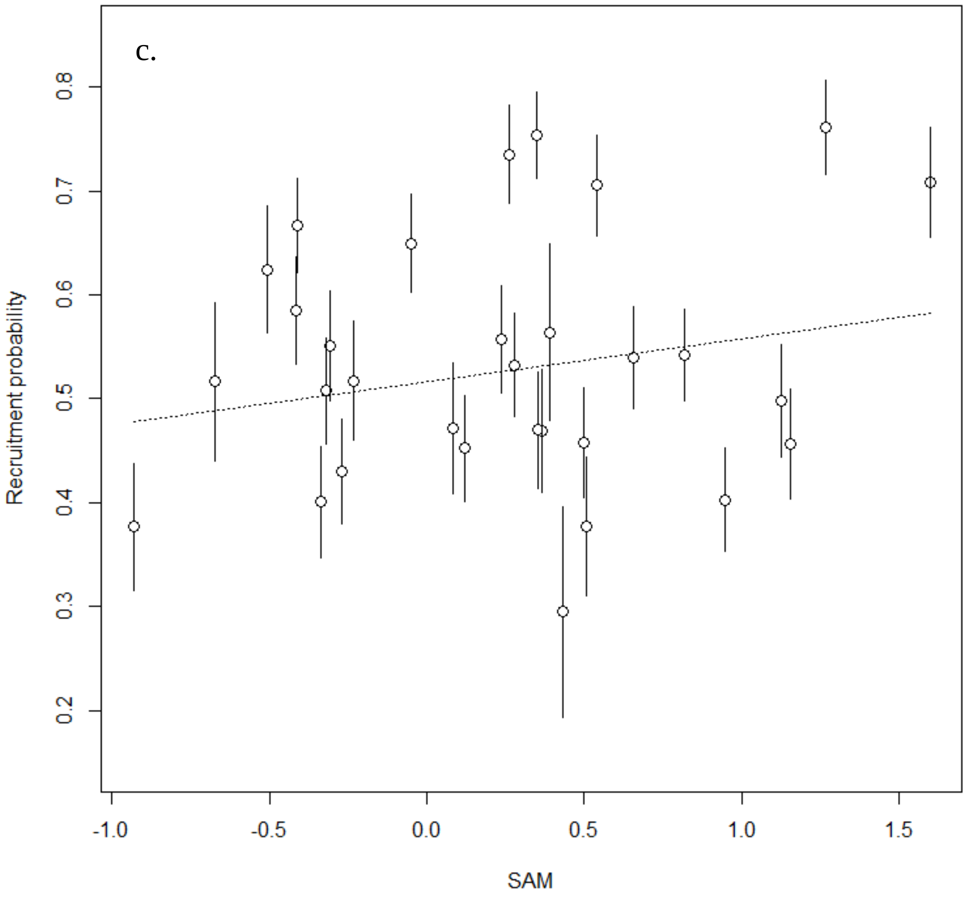
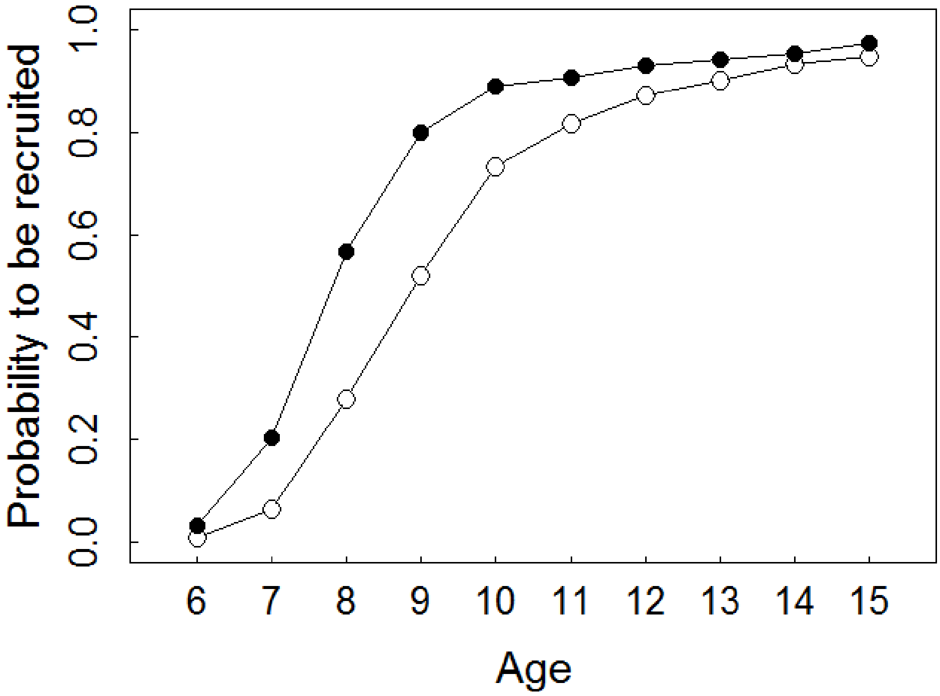

c.
Recruitment probability
0.2
0.3
0.4
0.5
0.6
0.7
0.8
-1.0
-0.5
0.0
0.5
1.0
1.5
SAM

Figure A4: Estimated cumulated probability to be recruited according to age and sex for the wandering albatross population of Crozet. Open and filled dots stand for males and females respectively. Estimates are calculated from age specific recruitment probability by bootstrapping methods (1000 simulations). Standard errors estimate are of the same magnitude that dot size.



Appendix B

Appendix B1: Parametrization of the general model and biological constraints

Several biological constraints were applied to improve parameter identifiability. The initial state was constrained to the pre-recruitment state because all birds were banded as chick. Then, from the first year of life to the fifth, transition probability to the pre-recruitment stage was fixed to 1 because no recruitment occurred before 6 year-old. To model the pre-recruitment period we defined two main stages: the juvenile stage, which was an unobservable state, corresponding to the first 2 years of life spent continuously at sea (i.e. no individual of 1 or 2 year-old were observed at the colony), and the immature stage corresponding to non-recruited birds older than 2 years that started to visit the colony and could be potentially observed. Based on previous results provided by Fay et al. (2015), the immature stage was decomposed in three age classes: 3-8 years, 8-13 years and >13 years. Juvenile survival was set to be cohort dependent and both juvenile and immature survival rates were assumed to be sex-dependent. Recapture probability of the immature stage was modelled as age dependent to fit the progressive return of individuals at the breeding colony before recruitment. From 6 years of age birds may recruit and move toward the mature states SB and FB depending both on sex and age. Recruitment rate was constrained to be constant after age 10 (Fay et al. 2015). For mature birds, survival was assumed to be sex-dependent (Barbraud and Weimerskirch 2012). Based on Pardo, Barbraud & Weimerskirch (2014), we distinguished different survival probabilities for breeders and post reproductive breeders on one side and recruited non-breeders on the other side. Note that we were not able to model actuarial senescence as in Prado et al. (2013) due to a very small sample size of old individuals with known aged parents. Transitions were set to be state dependent. Since wandering albatrosses are monogamous and both sexes exhibit a quasi-biennial breeding, transitions were constrained to be similar between sexes. Recapture probabilities were assumed to be state dependent due to lower detection probability for observable non-breeders and failed breeders compared to successful breeders. Finally, our general model was:

$$\Phi^{pre}_{a_{(1to2)}.sex.cohort,a_{(3to8,9to13,13+)}.sex}\Phi^{ad}_{sex.state}\Psi^{pre\rightarrow ad}_{a.sex}\Psi^{ad\rightarrow ad}_{cst}\ p^{pre}_{a}p^{ad}_{state}$$

where the pre-recruitment (pre) survival probability (Φ) was age-class (a), sex and cohort dependent, the adult (ad) survival probability was sex and state dependent, the probability of transition (Ψ) from pre-recruitment to adult was age and sex dependent, the probability of remaining in the adult stage was constant (cst), the pre-recruitment capture probability (p) was age dependent, and the adult capture probability was state dependent. In this model notation, symbols "." indicate interactive effects, "1to2", "3to8" and "9to13" indicate that age classes were grouped and ">13" indicates that age classes were grouped after 13 years.

Appendix C

Table C1: Threshold model selection for the effect of paternal age (a) on early life survival (φ), for wandering albatrosses at Possession Island, 1983-2013 (n = 4538 chicks). k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion. a ≤ n = function of paternal age with a threshold at n year. Threshold models were implemented fitting the logistic model: logit(Φ) = β0 + β1 * $a_{i \leq n}$ + β2 * $a_{i>n}$, where Φ is a demographic parameter, β0 is an intercept parameter, β1 and β2 are the slope parameters, and ai is the age of the parent at birth of individual i. Thus, we fitted two linear models with one intercept. β1 is the slope describing the relation for juvenile survival and paternal age between 6 to n years old and β2 for juvenile survival and paternal age between n+1 to 41 year-old. The best supported model is in bold characters.

No.	Model	k	DEV	AIC	Slope1 ± s.e.	Slope2 ± s.e.
Survival						
M1	**φ(a)**	**69**	**28587.6**	**28725.6**	**-0.17±0.05**	/
M2	φ(a ≤ 10)	70	28586.8	28726.8	-0.09 ± 0.10	-0.20 ± 0.06
M3	φ(a ≤ 15)	70	28586.7	28726.8	-0.07 ± 0.11	-0.24 ± 0.09
M4	φ(a ≤ 20)	70	28587.2	28727.2	-0.11 ± 0.10	-0.21 ± 0.09
M5	φ(a ≤ 25)	70	28587.6	28727.6	-0.16 ± 0.07	-0.18 ± 0.09
M6	φ(a ≤ 30)	70	28587.6	28727.6	-0.15 ± 0.06	-0.24 ± 0.13

Table C2: Detail results of GOF tests.

	Chicks from known paternal age					
	Females			Males		
Test	$\chi 2$	df	P	$\chi 2$	df	P
WBWA	39.933	52	0.889	70.993	63	0.229
3G.SR	42.221	55	0.897	53.498	51	0.379
3G.Sm	134.582	180	0.995	143.865	197	0.998
M.ITEC	65.410	31	<0.001	102.275	39	<0.001
M.LTEC	18.636	16	0.288	42.961	18	0.001

	Chicks from known maternal age					
	Females			Males		
Test	$\chi 2$	df	P	$\chi 2$	df	P
WBWA	41.849	53	0.865	75.177	63	0.14
3G.SR	31.912	52	0.987	64.463	50	0.082
3G.Sm	135.355	187	0.998	153.241	190	0.977
M.ITEC	73.933	32	<0.001	91.791	42	<0.001
M.LTEC	21.172	17	0.219	24.639	16	0.076

GOF tests indicated that one assumption of the JMV model was not supported. Indeed, the test M.ITEC indicated the presence of trap-dependence. This effect was due to the quasi-biennial breeding strategy of wandering albatrosses. Individuals which are breeders a given year have a greater chance to take a sabbatical year spent continuously at sea the next year and such to be missed at colony. Unlike breeders, individuals which are on sabbatical year a given year have a greater chance to attempt to breed the next year and then to be observed at the colony. This behavior creates trap-shyness in GOF tests. However, given that our general model structure included unobservable states to explicitly take into account quasi-biennial breeding, we ignored the M.ITEC component in the GOF test of the general model.

Table C3: Testing for the effects of paternal age (a) on early life survival (φ) considering individual random effect (h) and paternal identity as a random effect (PI) for wandering albatrosses from Possession Island, 1977-2013 (n = 4538 chicks). Results include the number of parameters (k), the deviance (Dev), the Likelihood Ratio Test (LRT), and the p value (p). Best supported models are in bold characters.

No.	Model	k	Dev	*LRT*	*p*
	Parental identity random effect				
M1	$\varphi(\mathrm{cst})$	68	28597.4		
M2	$\varphi(\mathrm{cst} + \mathrm{PI})$	69	28597.1	0.3	0.584
M3	$\varphi(\mathrm{a} + \mathrm{PI})$	70	28587.6	9.5	0.002
	Individual random effect				
M1	$\varphi(\mathrm{cst})$	68	28597.4		
M4	$\varphi(\mathrm{cst} + \mathrm{h})$	69	28589.0	8.4	0.004
M5	$\varphi(\mathrm{a} + \mathrm{h})$	70	28584.1	4.9	0.027

Table C4: Testing for the effects of age difference between the parents (dif) on early life survival (φ), recruitment rate (ψ^{rate}) and early recruitment probability (ψ^{early}) for wandering albatrosses, Possession Island, 1983-2013 (n = 3454 chicks). Models with significant covariate effects are marked in bold characters. k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion. cst = constant, dif = age difference between the parents, a.sex = interaction between age difference between the parents and sex of the juvenile. Best supported models are in bold characters.

No.	Model	k	DEV	AIC	Slope ± s.e.
Survival					
M1	$\varphi(\mathrm{cst})$	68	20963.6	21099.6	
M2	$\boldsymbol{\varphi}(\mathbf{dif})$	**69**	**20958.6**	**21096.6**	**-0.11 ± 0.06**
M3	$\varphi(\mathrm{dif.sex})$	70	20958.5	21098.5	
M4	$\varphi(\mathrm{dif}+\mathrm{dif}^2)$	70	20958.6	21098.6	
Recruitment					
M9	$\boldsymbol{\psi}^{\mathbf{rate}}(\mathbf{cst})$	**68**	**20963.6**	**21099.6**	
M10	$\psi^{\mathrm{rate}}(\mathrm{dif})$	69	20961.8	21099.7	
M11	$\psi^{\mathrm{rate}}(\mathrm{dif.sex})$	70	20959.8	21099.8	
M12	$\psi^{\mathrm{rate}}(\mathrm{dif}+\mathrm{dif}^2)$	70	20958.6	21098.6	
Early recruitment					
M17	$\boldsymbol{\psi}^{\mathbf{early}}(\mathbf{cst})$	**69**	**20962.2**	**21100.2**	
M18	$\psi^{\mathrm{early}}(\mathrm{dif})$	70	20961.9	21101.9	
M19	$\psi^{\mathrm{early}}(\mathrm{dif.sex})$	71	20960.3	21102.3	
M20	$\psi^{\mathrm{early}}(\mathrm{dif}+\mathrm{dif}^2)$	71	20960.7	21102.7	

Table C5: Testing for the effects of the average age of both parents (a) on early life survival (φ), recruitment rate (ψ^{rate}) and early recruitment probability (ψ^{early}) for wandering albatrosses, Possession Island, 1983-2013 (n = 3454 chicks). k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion. cst = constant, $\bar{a}$ = average parental age, $\bar{a}$.sex = interaction between average parental age and sex of the juvenile. Best supported models are in bold characters.

No.	Model	k	DEV	AIC
Survival				
M1	$\boldsymbol{\varphi}(\mathbf{cst})$	**68**	**20972.1**	**21108.1**
M2	$\varphi(\bar{a})$	69	20970.8	21108.8
M3	$\varphi(\bar{a}.\mathrm{sex})$	70	20970.5	21110.5
M4	$\varphi(\bar{a} + \bar{a}^2)$	70	20970.1	21110.1
Recruitment				
M9	$\boldsymbol{\psi}^{\mathbf{rate}}(\mathbf{cst})$	**68**	**20972.1**	**21108.1**
M10	$\psi^{\mathrm{rate}}(\bar{a})$	69	20971.1	21109.1
M11	$\psi^{\mathrm{rate}}(\bar{a}.\mathrm{sex})$	70	20970.8	21110.8
M12	$\psi^{\mathrm{rate}}(\bar{a} + \bar{a}^2)$	70	20970.1	21110.1
Early recruitment				
M17	$\boldsymbol{\psi}^{\mathbf{early}}(\mathbf{cst})$	**69**	**20971.0**	**21109.0**
M18	$\psi^{\mathrm{early}}(\bar{a})$	70	20970.9	21110.9
M19	$\psi^{\mathrm{early}}(\bar{a}.\mathrm{sex})$	71	20970.8	21112.8
M20	$\psi^{\mathrm{early}}(\bar{a} + \bar{a}^2)$	71	20970.6	21112.6

Table C6: Testing for the simultaneous paternal (a_p) and maternal age effects on early life survival (φ) for wandering albatrosses, Possession Island, 1977-2013 (n = 5378 chicks). k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion. cst = constant, a_p = paternal age, a_m maternal age, "+"= additive effect. The best supported model is in bold characters.

No.	Model	k	DEV	AIC
M1	$\varphi(\mathrm{cst})$	68	35505.5	35641.5
M2	$\boldsymbol{\varphi(\mathrm{a}_p)}$	**69**	**35495.8**	**35633.8**
M3	$\varphi(\mathrm{a}_p + \mathrm{a}_m)$	70	35494.1	35634.1

Table C7: Testing for predominant paternal age effect on early life survival (φ) using interaction between parental age and the sex of the parent for wandering albatrosses, Possession Island, 1977-2013 (n = 5378 chicks). For chick from tow known-aged parents, we chose randomly paternal or maternal age. k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion. cst = constant, a = parental age, sex = sex of the parent, "." = interaction effect. The best supported model is in bold characters.

No.	Model	k	DEV	AIC
M1	φ(cst)	68	35505.5	35641.5
M2	**φ(a)**	**69**	**35500.0**	**35638.0**
M3	φ(a. sex)	70	35596.8	35636.8

Table C8: Investigating the relative importance of within-subject effects and between-subject effects on the relationships between parental age and early life survival (φ), recruitment rate (ψ^{rate}) and early recruitment probability (ψ^{early}) for wandering albatrosses, Possession Island, 1983-2013 (n = 5378 chicks). Following van de Pol and Wright (2009), we estimated the within-subject effects (β_W) and the between-subject effect (β_B). Within-subject effect is estimated though the relationships between the early-life demographic traits and a new parental age variable, Δa. To compute this variable for each chick, we subtracted the mean age of reproduction of the parent from the age of the parent at which the chick was raised, i.e. for a chick raised at occasion i by a parent j, $\Delta a_{ij} = a_{ij} - \bar{a}_j$. This procedure, called within-subject centering, eliminates any between-subject variation. Simultaneously, to estimate between-subject variation, we assessed the relationships between the early-life demographic traits and the average reproductive age of their parent ($\bar{a}_j$). k = number of parameters, Dev = deviance, AIC = Akaike Information Criterion. cst = constant, β_W = the within-subject effects and β_B = the between-subject effect. The best supported model is in bold characters.

No.	Model	k	DEV	AIC	β_W [95%CI]	β_B [95%CI]
Survival						
	Paternal age					
M1	$\varphi(cst)$	68	28595.4	28731.4		
M2	**$\varphi(\Delta a + \bar{a})$**	**70**	**28573.5**	**28713.5**	**-0.26 [-0.37;-0.15]**	**+0.01 [-0.08;+0.10]**
	Maternal age					
M3	**$\varphi(cst)$**	**68**	**27845.2**	**27981.2**		
M4	$\varphi(\Delta a + \bar{a})$	70	27840.6	27982.6	-0.10 [-0.22;+0.02]	+0.03 [-0.07;+0.14]
Recruitment						
	Paternal age					
M5	**$\psi^{rate}(cst)$**	**68**	**28595.4**	**28731.4**		
M6	$\psi^{rate}(\Delta a + \bar{a})$	70	28595.4	28737.4	-0.05 [-0.16;+0.06]	+0.03 [-0.06;+0.13]
	Maternal age					
M7	**$\psi^{rate}(cst)$**	**68**	**27845.2**	**27981.2**		
M8	$\psi^{rate}(\Delta a + \bar{a})$	70	27839.5	27981.5	-0.03 [-0.14;+0.07]	+0.09 [-0.01;+0.19]
Early recruitment						
	Paternal age					
M9	**$\psi^{early}(cst)$**	**69**	**28597.2**	**28735.2**		
M10	$\psi^{early}(\Delta a + \bar{a})$	71	28594.5	28736.5	-0.06 [-0.23;+0.10]	+0.03 [-0.12;+0.19]
	Maternal age					
M11	**$\psi^{early}(cst)$**	**69**	**27847.7**	**27985.7**		
M12	$\psi^{early}(\Delta a + \bar{a})$	71	27846.2	27990.2	-0.01 [-0.18;+0.17]	-0.03 [-0.20;+0.14]

Figure C1: Life cycle graph representing transitions between observable (white) or unobservable states (grey). All birds are ringed as chicks, thus individuals start in the Pre-Recruitment state (PrR). After fledging, all birds remain at least two years continuously at sea (i.e. juvenile stage). Pre-Recruitment state becomes observable from 3 years-old when birds start to return at the colony and are now considered as immature. From 6 years-old, birds can pass into the breeding group of the population though recruitment represented by dashed arrows. Then mature birds irrespectively of age can transit between mature states: successful breeder (SB), failed breeder (FB), recruited non breeder (NB), post successful breeder (PSB) and post failed breeder (PFB).

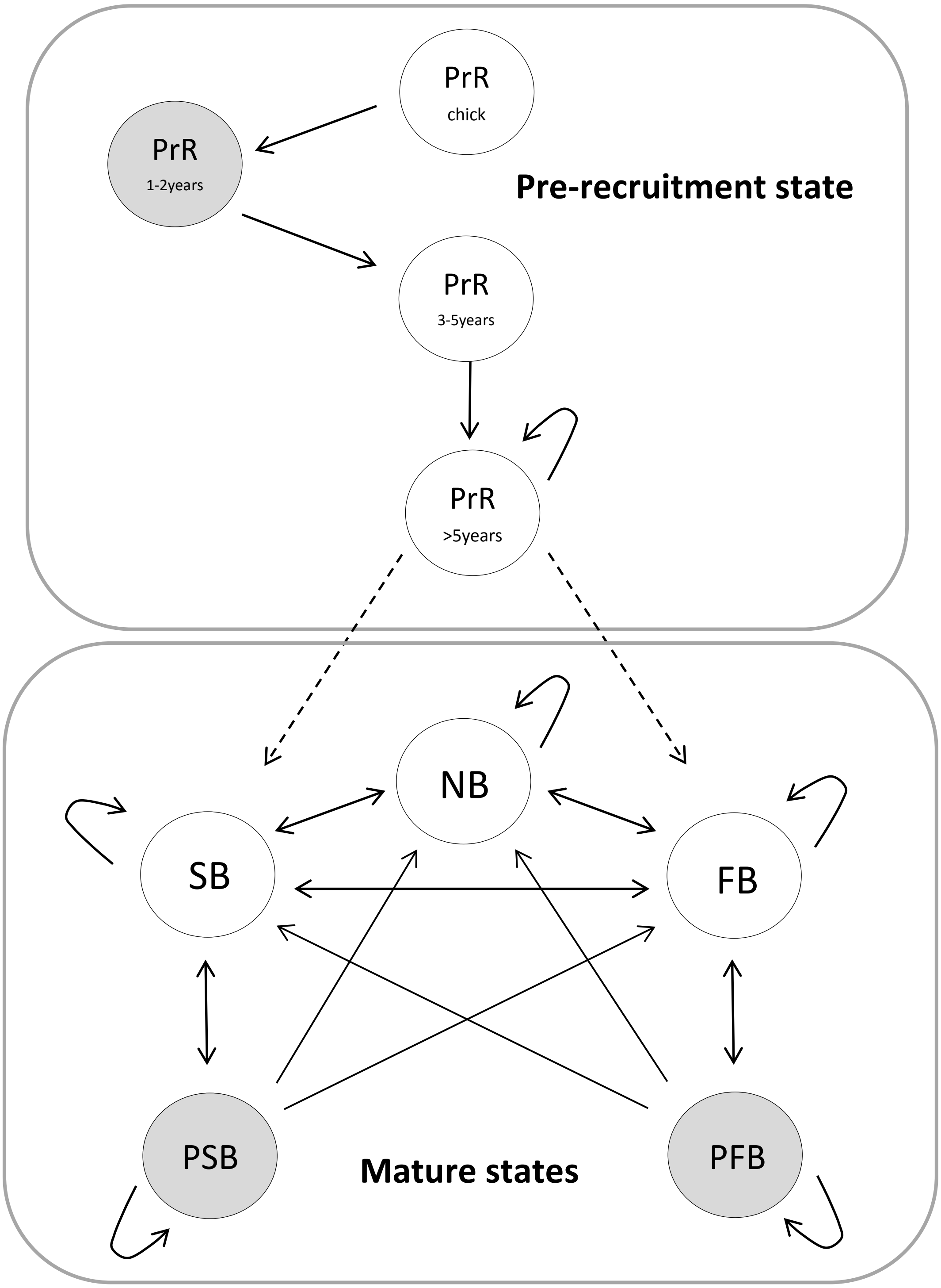
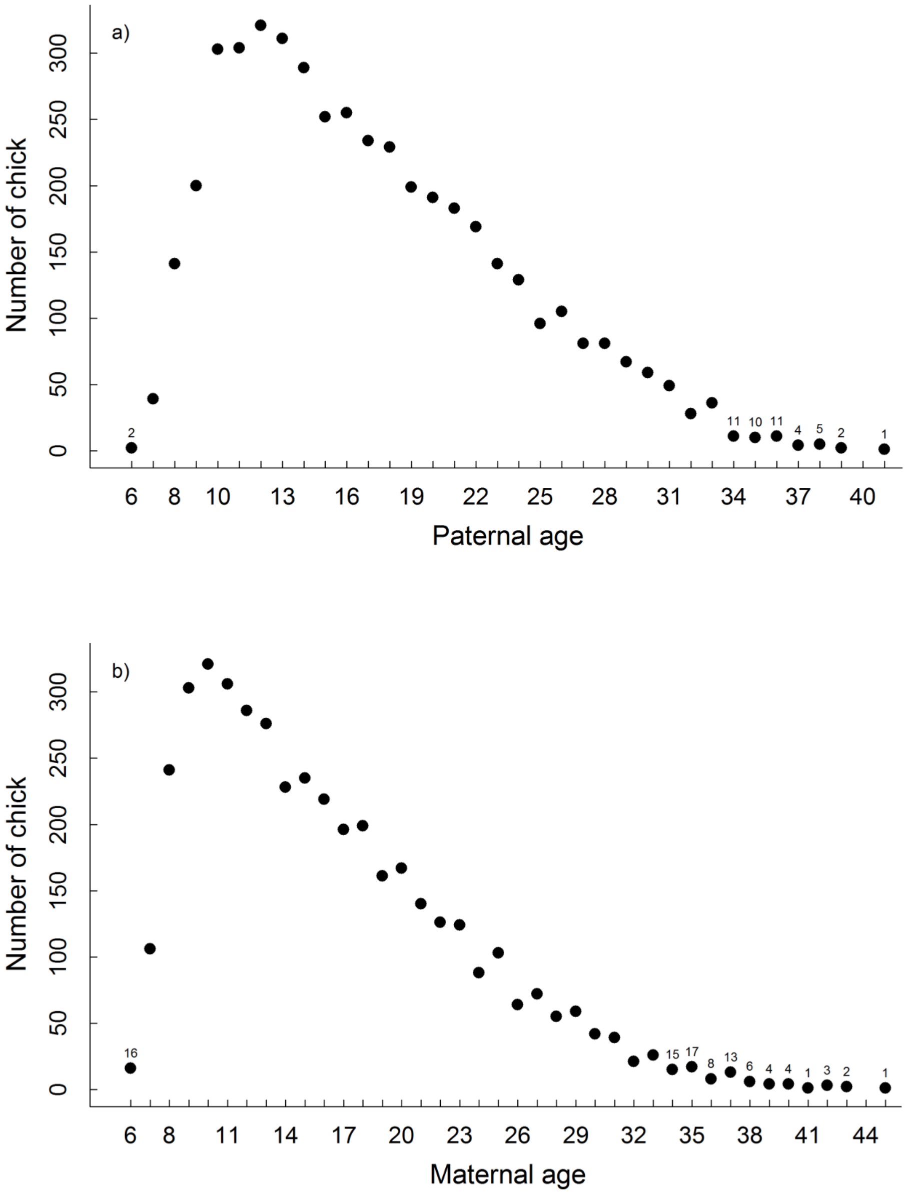


Figure C2: Number of chicks from fathers (a) and mothers (b) of known age. Numbers indicate sample size when it was below 20 individuals for a given parental age.



Appendix D

Appendix D1: Transition matrices and GEMACO scripts implemented in E-Surge.

I. Model used to estimate breeding success at recruitment

The general model consisted in 7 states, the Pre-Recruitment state (PR) to consider individuals during the period of immaturity, the recruited Non Breeder state (NB) to consider individuals that have recruited into the population (i.e. bred at least once) but were observed as non-breeders at the colony, the Successful breeder state (S) to consider individuals that raised a chick to fledging, the Failed breeder state (F) to consider individuals that raised a chick that died before fledging, the Post Successful breeder state (PS) to consider individual that took a sabbatical years after a success, the Post Failed breeder state (PF) to consider individuals that took a sabbatical year after a failure, and the state dead (D). Note that we used other states in matrices to pool previous states or estimate specific parameters. These states were the Recruitment state (R) to consider individuals during their first reproduction, the Not Observed state (NO) to consider the individuals that were not seen at a given year, the Recapture Non Breeder state (RNB) to consider individuals that were recaptured at the colony as non-breeder, the Recapture Successful breeder state (RS) to consider individuals that were recaptured and raised a chick to fledging, and the Recapture Failed breeder state (RF) to consider individuals that were recaptured and raised a chick that died before fledging. Finally, we used 5 events, i.e. five types of observation in the field, 0 = “not observed”, 1 = “seen as non-breeder”, 2 = “seen as a failed breeder”, 3 = “seen as a successful breeder”, 4 = “seen as a breeder but successful status not ascertained”.

1.1. Matrices

Initial state: At the Initial state, all individuals are in the Pre-recruitment stage since only birds ringed as chicks were considered.

$$\begin{array}{cccccc} \text{PR} & \text{NB} & \text{S} & \text{F} & \text{PS} & \text{PF} \\ (* & - & - & - & - & -) \end{array}$$

Transition 1: Diagonal matrix for survival probabilities

$$\begin{array}{c|ccccccc}
 & \mathrm{PR} & \mathrm{NB} & \mathrm{S} & \mathrm{F} & \mathrm{PS} & \mathrm{PF} & \mathrm{D} \\
\mathrm{PR} & \varphi & - & - & - & - & - & * \\
\mathrm{NB} & - & \varphi & - & - & - & - & * \\
\mathrm{S} & - & - & \varphi & - & - & - & * \\
\mathrm{F} & - & - & - & \varphi & - & - & * \\
\mathrm{PS} & - & - & - & - & \varphi & - & * \\
\mathrm{PF} & - & - & - & - & - & \varphi & * \\
\mathrm{D} & - & - & - & - & - & - & *
\end{array}$$

Transition 2: Estimation of recruitment probability

$$\begin{array}{c|cccccccc}
 & \mathrm{PR} & \mathrm{NB} & \mathrm{R} & \mathrm{S} & \mathrm{F} & \mathrm{PS} & \mathrm{PF} & \mathrm{D} \\
\mathrm{PR} & * & - & \varphi & - & - & - & - & - \\
\mathrm{NB} & - & * & - & - & - & - & - & - \\
\mathrm{S} & - & - & * & - & - & - & - & - \\
\mathrm{F} & - & - & - & * & - & - & - & - \\
\mathrm{PS} & - & - & - & - & * & - & - & - \\
\mathrm{PF} & - & - & - & - & - & - & * & - \\
\mathrm{D} & - & - & - & - & - & - & - & *
\end{array}$$

Transition 3: Breeding success probability at recruitment and transition probabilities between adult states

$$\begin{array}{c|ccccccc}
 & \mathrm{PR} & \mathrm{NB} & \mathrm{S} & \mathrm{F} & \mathrm{PS} & \mathrm{PF} & \mathrm{D} \\
\mathrm{PR} & * & - & - & - & - & - & - \\
\mathrm{NB} & - & * & \varphi & \varphi & - & - & - \\
\mathrm{R} & - & - & \varphi & * & - & - & - \\
\mathrm{S} & - & \varphi & * & \varphi & \varphi & - & - \\
\mathrm{F} & - & \varphi & \varphi & * & - & \varphi & - \\
\mathrm{PS} & - & \varphi & \varphi & \varphi & * & - & - \\
\mathrm{PF} & - & \varphi & \varphi & \varphi & - & * & - \\
\mathrm{D} & - & - & - & - & - & - & *
\end{array}$$

Recapture: Detection probability at the colony. Post Successful and Post Failed breeder states (PS and PF respectively) are not observable since individuals in these states stay at sea during a sabbatical year.

$$\begin{array}{c|cccc}
 & \mathrm{NO} & \mathrm{RNB} & \mathrm{RS} & \mathrm{RF} \\
\hline
\mathrm{PR} & * & \varphi & - & - \\
\mathrm{NB} & * & \varphi & - & - \\
\mathrm{S} & * & - & \varphi & - \\
\mathrm{F} & * & - & - & \varphi \\
\mathrm{PS} & * & - & - & - \\
\mathrm{PF} & * & - & - & - \\
\mathrm{D} & * & - & - & -
\end{array}$$

Event: To deal with state uncertainty for individuals classified as breeders without indication on the success or failure at the end of the year, we estimated the probability of observing an individual as a breeder and its successful status not ascertained (4), conditional on recapture in the Successful or Failed breeder state (RS and RF).

$$\begin{array}{c|ccccc}
 & 0 & 1 & 2 & 3 & 4 \\
\hline
\mathrm{NO} & * & - & - & - & - \\
\mathrm{RNB} & - & * & - & - & - \\
\mathrm{RS} & - & - & - & * & \varphi \\
\mathrm{RF} & - & * & \varphi & - & \varphi
\end{array}$$

1.2. GEMACO scripts

Initial state:

i

Transition 1:

a(1:2).f(1).[c(1_38,39:48)+g]+a(3:8,14:15).f(1).g+a(9:13).f(1)+a(7:15).f(2;5).g(2)+a(7:14,15).f(2;5).g(1)+a(6:8,9:15).f(3:4;6:7)

Transition 2:

a(1:5)+a(6_10,11:15).g

Transition 3: At this step we model the breeding success probability at recruitment. The 7 models presented in table D1 were run with the following GEMACO sentences:

M1: a(6:15).f(3)+a(6:15).f(2,4_8).to

M2: a(6_15).f(3)+ a(6:15).f(2,4_8).to

M3: a(6,7:15).f(3)+ a(6:15).f(2,4_8).to

M4: a(6,7,8:15).f(3)+ a(6:15).f(2,4_8).to

M5: a(6).f(3)+[a(7:15)+a(7_15)*x(1)].f(3)+ a(6:15).f(2,4_8).to

M6: a(6).f(3)+[a(7:15)+a(7_15)*x(1) +a(7_15)*x(2)].f(3)+ a(6:15).f(2,4_8).to

M7: a(6).f(3)+[a(7:15)+a(7_15)*x(1)].f(3)+ a(6:15).f(2,4_8).to

Recapture:

a(1,2)+a(6_9,10:15).f(1).t(1:21)+a(6_11,12:15).f(1).t(22:49)+[a(3_5)+a(6:15).f(3_4)].t(1:21,22:49)+a(6:15).f(2).t(1:21,22:49).g

Event:

a(1:5)+a(6:15).f.to

II. Finite mixture model

The general finite mixture model is based on the model used to estimate breeding success at recruitment but mature states have being duplicated in two groups. Thus, the finite mixture model consisted in 12 states, the Pre-Recruitment state (PR) to consider individuals during the period of immaturity, the recruited Non Breeder states (NB1 and NB2) to consider individuals that have recruited into the population (i.e. bred at least once) but were observed as non-breeders at the colony, the Successful breeder state (S1 and S2) to consider individuals that raised a chick to fledging, the Failed breeder state (F1 and F2) to consider individuals that raised a chick that died before fledging, the Post Successful breeder state (PS1 and PS2) to consider individuals that took a sabbatical years after a success, the Post Failed breeder state

(PF1 and PF2) to consider individuals that took a sabbatical year after a failure, and the state dead (D). Note that we used others states in matrices to pool previous states or estimate specific parameters. These states were the Recruitment state (R) to consider individuals during their first reproduction, the Group 1 allocation state (G1) to consider individuals that transited toward group 1 conditional on recruitment, the Group 2 allocation state (G2) to consider individuals that transited toward group 2 conditional on recruitment, the Not Observed state (NO) to consider the individual that were not seen at a given year, the Recapture Non Breeder state (RNB) to consider individuals that were recaptured at the colony as non-breeders, the Recapture Successful breeder state (RS) to consider individuals that were recaptured and raised a chick to fledging, and the Recapture Failed breeder state (RF) to consider individuals that were recaptured and raised a chick that died before fledging. Finally, we used 5 events, i.e. five types of observation in the field, 0 = “not observed”, 1 = “seen as non-breeder”, 2 = “seen as a failed breeder”, 3 = “seen as a successful breeder”, 4 = “seen as a breeder but successful status not ascertained”.

2.1. Matrices

Initial state: At the Initial state, all individuals are in the Pre-recruitment stage since only birds ringed as chicks were considered.

$$
\begin{array}{ccccccccccc}
\mathrm{PR} & \mathrm{NB1} & \mathrm{S1} & \mathrm{F1} & \mathrm{PS1} & \mathrm{PF1} & \mathrm{NB2} & \mathrm{S2} & \mathrm{F2} & \mathrm{PS2} & \mathrm{PF2} \\
\left(* \right. & - & - & - & - & - & - & - & - & - & \left. - \right)
\end{array}
$$

Transition 1: Diagonal matrix for survival probabilities

$$
\begin{array}{c}
\\
\mathrm{PR} \\ \mathrm{NB1} \\ \mathrm{S1} \\ \mathrm{F1} \\ \mathrm{PS1} \\ \mathrm{PF1} \\ \mathrm{NB2} \\ \mathrm{S2} \\ \mathrm{F2} \\ \mathrm{PS2} \\ \mathrm{PF2} \\ \mathrm{D}
\end{array}
\begin{array}{c}
\begin{array}{cccccccccccc}
\mathrm{PR} & \mathrm{NB1} & \mathrm{S1} & \mathrm{F1} & \mathrm{PS1} & \mathrm{PF1} & \mathrm{NB2} & \mathrm{S2} & \mathrm{F2} & \mathrm{PS2} & \mathrm{PF2} & \mathrm{D}
\end{array} \\
\begin{pmatrix}
\varphi & - & - & - & - & - & - & - & - & - & - & * \\
- & \varphi & - & - & - & - & - & - & - & - & - & * \\
- & - & \varphi & - & - & - & - & - & - & - & - & * \\
- & - & - & \varphi & - & - & - & - & - & - & - & * \\
- & - & - & - & \varphi & - & - & - & - & - & - & * \\
- & - & - & - & - & \varphi & - & - & - & - & - & * \\
- & - & - & - & - & - & \varphi & - & - & - & - & * \\
- & - & - & - & - & - & - & \varphi & - & - & - & * \\
- & - & - & - & - & - & - & - & \varphi & - & - & * \\
- & - & - & - & - & - & - & - & - & \varphi & - & * \\
- & - & - & - & - & - & - & - & - & - & \varphi & * \\
- & - & - & - & - & - & - & - & - & - & - & *
\end{pmatrix}
\end{array}
$$

Transition 2: Recruitment probability

$$\begin{array}{c|ccccccccccccc}
 & \mathrm{PR} & \mathrm{R} & \mathrm{NB1} & \mathrm{S1} & \mathrm{F1} & \mathrm{PS1} & \mathrm{PF1} & \mathrm{NB2} & \mathrm{S2} & \mathrm{F2} & \mathrm{PS2} & \mathrm{PF2} & \mathrm{D} \\
\hline
\mathrm{PR} & * & \varphi & - & - & - & - & - & - & - & - & - & - & - \\
\mathrm{NB1} & - & - & * & - & - & - & - & - & - & - & - & - & * \\
\mathrm{S1} & - & - & - & * & - & - & - & - & - & - & - & - & * \\
\mathrm{F1} & - & - & - & - & * & - & - & - & - & - & - & - & * \\
\mathrm{PS1} & - & - & - & - & - & * & - & - & - & - & - & - & * \\
\mathrm{PF1} & - & - & - & - & - & - & * & - & - & - & - & - & * \\
\mathrm{NB2} & - & - & - & - & - & - & - & * & - & - & - & - & * \\
\mathrm{S2} & - & - & - & - & - & - & - & - & * & - & - & - & * \\
\mathrm{F2} & - & - & - & - & - & - & - & - & - & * & - & - & * \\
\mathrm{PS2} & - & - & - & - & - & - & - & - & - & - & * & - & * \\
\mathrm{PF2} & - & - & - & - & - & - & - & - & - & - & - & * & * \\
\mathrm{D} & - & - & - & - & - & - & - & - & - & - & - & - & *
\end{array}$$

Transition 3: Probability to transit toward group 1 conditional on recruitment

$$\begin{array}{c|cccccccccccccc}
 & \mathrm{PR} & \mathrm{G1} & \mathrm{G2} & \mathrm{NB1} & \mathrm{S1} & \mathrm{F1} & \mathrm{PS1} & \mathrm{PF1} & \mathrm{NB2} & \mathrm{S2} & \mathrm{F2} & \mathrm{PS2} & \mathrm{PF2} & \mathrm{D} \\
\hline
\mathrm{PR} & * & - & - & - & - & - & - & - & - & - & - & - & - & - \\
\mathrm{R} & - & \varphi & * & - & - & - & - & - & - & - & - & - & - & - \\
\mathrm{NB1} & - & - & - & * & - & - & - & - & - & - & - & - & - & - \\
\mathrm{S1} & - & - & - & - & * & - & - & - & - & - & - & - & - & - \\
\mathrm{F1} & - & - & - & - & - & * & - & - & - & - & - & - & - & - \\
\mathrm{PS1} & - & - & - & - & - & - & * & - & - & - & - & - & - & - \\
\mathrm{PF1} & - & - & - & - & - & - & - & * & - & - & - & - & - & - \\
\mathrm{NB2} & - & - & - & - & - & - & - & - & * & - & - & - & - & - \\
\mathrm{S2} & - & - & - & - & - & - & - & - & - & * & - & - & - & - \\
\mathrm{F2} & - & - & - & - & - & - & - & - & - & - & * & - & - & - \\
\mathrm{PS2} & - & - & - & - & - & - & - & - & - & - & - & * & - & - \\
\mathrm{PF2} & - & - & - & - & - & - & - & - & - & - & - & - & * & - \\
\mathrm{D} & - & - & - & - & - & - & - & - & - & - & - & - & - & *
\end{array}$$

Transition 4: Breeding success probability at recruitment and transition probabilities between adult states within each group

$$\begin{array}{c|cccccccccccc}
 & \mathrm{PR} & \mathrm{NB1} & \mathrm{S1} & \mathrm{F1} & \mathrm{PS1} & \mathrm{PF1} & \mathrm{NB2} & \mathrm{S2} & \mathrm{F2} & \mathrm{PS2} & \mathrm{PF2} & \mathrm{D} \\
\hline
\mathrm{PR} & * & - & - & - & - & - & - & - & - & - & - & - \\
\mathrm{G1} & - & - & \varphi & * & - & - & - & - & - & - & - & - \\
\mathrm{G2} & - & - & - & - & - & - & - & \varphi & * & - & - & - \\
\mathrm{NB1} & - & * & \varphi & \varphi & - & - & - & - & - & - & - & - \\
\mathrm{S1} & - & \varphi & * & \varphi & \varphi & - & - & - & - & - & - & - \\
\mathrm{F1} & - & \varphi & \varphi & * & - & \varphi & - & - & - & - & - & - \\
\mathrm{PS1} & - & \varphi & \varphi & \varphi & * & - & - & - & - & - & - & - \\
\mathrm{PF1} & - & \varphi & \varphi & \varphi & - & * & - & - & - & - & - & - \\
\mathrm{NB2} & - & - & - & - & - & - & * & \varphi & \varphi & - & - & - \\
\mathrm{S2} & - & - & - & - & - & - & \varphi & * & \varphi & \varphi & - & - \\
\mathrm{F2} & - & - & - & - & - & - & \varphi & \varphi & * & - & \varphi & - \\
\mathrm{PS2} & - & - & - & - & - & - & \varphi & \varphi & \varphi & * & - & - \\
\mathrm{PF2} & - & - & - & - & - & - & \varphi & \varphi & \varphi & - & * & - \\
\mathrm{D} & - & - & - & - & - & - & - & - & - & - & - & *
\end{array}$$

Recapture: Detection probability at the colony. Post Successful and Post Failed breeder states (PS and PF respectively) are not observable for both groups since individuals in these states stay at sea during a sabbatical year.

$$\begin{array}{c|cccc}
 & \mathrm{NO} & \mathrm{RNB} & \mathrm{RS} & \mathrm{RF} \\
\hline
\mathrm{PR} & * & \varphi & - & - \\
\mathrm{NB1} & * & \varphi & - & - \\
\mathrm{S1} & * & - & \varphi & - \\
\mathrm{F1} & * & - & - & \varphi \\
\mathrm{PS1} & * & - & - & - \\
\mathrm{PF1} & * & - & - & - \\
\mathrm{NB2} & * & \varphi & - & - \\
\mathrm{S2} & * & - & \varphi & - \\
\mathrm{F2} & * & - & - & \varphi \\
\mathrm{PS2} & * & - & - & - \\
\mathrm{PF2} & * & - & - & - \\
\mathrm{D} & * & - & - & -
\end{array}$$

Event: To deal with state uncertainty for individuals classified as breeders without indication on the success or failure at the end of the year, we estimate the probability of observing an individual as a breeder and successful status not ascertained (4), conditional on recapture in the Successful or Failed breeder state (RS and RF).

$$\begin{array}{c|ccccc} & 0 & 1 & 2 & 3 & 4 \\ \hline \text{NO} & * & - & - & - & - \\ \text{RNB} & - & * & - & - & - \\ \text{RS} & - & - & - & * & \varphi \\ \text{RF} & - & * & \varphi & - & \varphi \end{array}$$

2.2. GEMACO sentences

Initial state:

i

Transition 1:

a(1:2).f(1).[c(1_38,39:48)+g]+a(3:8,14:15).f(1).g+a(9:13).f(1)+a(7:14,15).f(2,7).g(1)+a(7:15). f(2,11).g(2)+a(6:15).f(3:6,8:11)

Transition 2:

a(1:5)+a(6_10,11:15).g

Transition 3: The 6 model presented in table 1 were run with the following GEMACO sentences:

M1: a(1:5)+a(6:15)

M2: a(1:5)+a(6:15)

M3: a(1:5)+a(6:15).g

M4: a(1:5)+a(6_15)

M5: a(1:5)+[a(6:15)+a(6_15)*x(1)]

M6: a(1:5)+[a(6:15)+a(6_15)*x(1)+a(6_15)*x(2)]

Transition 4:

f(2,3).to.a(6,7:15)+f(4_13).to

Recapture:

a(1,2)+a(6_9,10:15).f(1).t(1:21)+a(6_11,12:15).f(1).t(22:49)+[a(3_5)+a(6:15).f(3;8,5;9)].t(1:21,22:49)+a(6:15).f(2;7).t(1:21,22:49).g

Event :

a(1:5)+a(6:15).f.to

Appendix D2: Bootstrapping method

To estimate breeding probability and breeding success, we needed to combine different estimates of the multi-event model. To obtain 95% confidence intervals of these derived estimates, we used a bootstrapping method based on a multivariate normal distribution. For example, the breeding success is the ratio between the probability to be in success (SB) and the probability to reproduce which is the probability to be in success (SB) plus the probability to be in failure (FB). To estimate the breeding success probability at time t+1 of recruited non breeders (NB) at time t, we used a multivariate normal distribution of two variables corresponding to the average of the two following transitions:

- The probability to be a successful breeder at t+1 ($\psi_{NB}^{NB \rightarrow SB}$)
- The probability to be in failure at t+1 ($\psi_{NB}^{NB \rightarrow FB}$)

In our model, estimates were not independent. Using the corresponding variance covariance matrix for these two estimates, we sampled a value of each transition and then computed the derived estimate as:

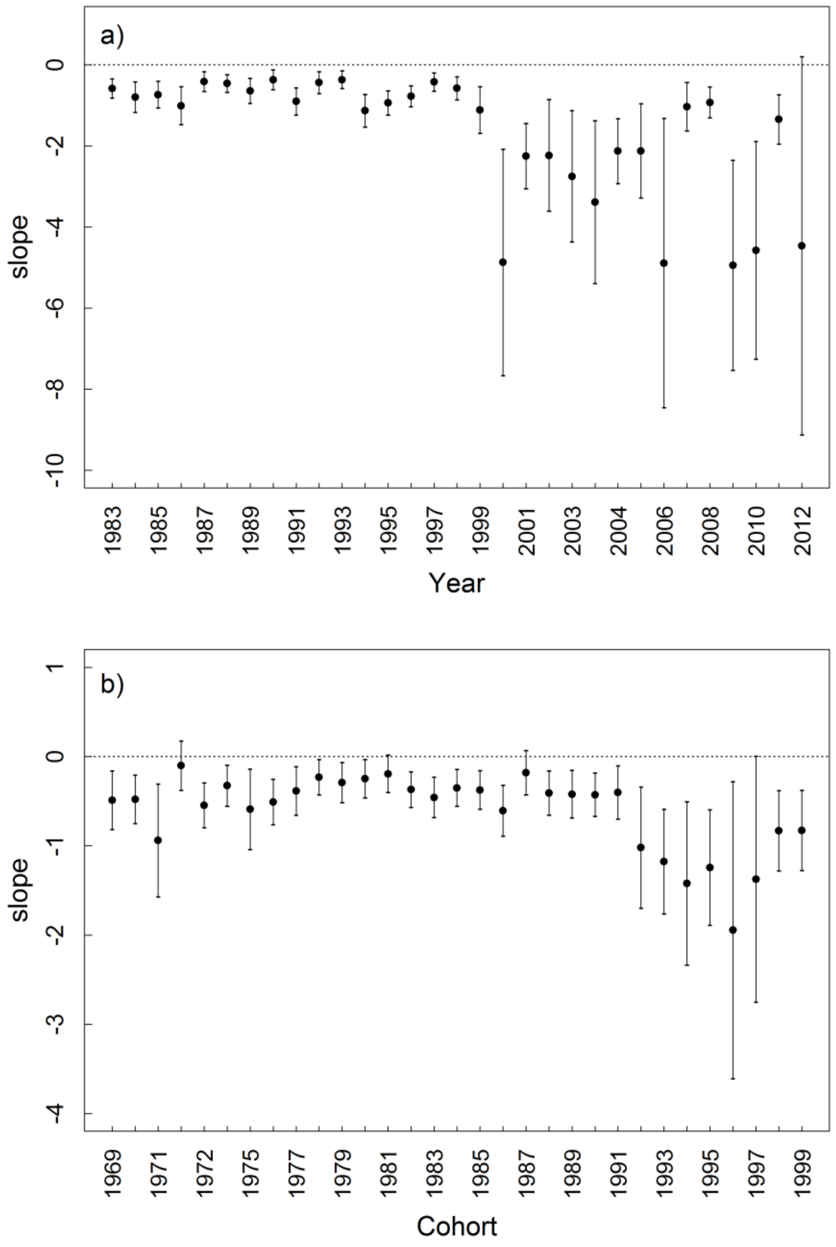
$$\text{Breeding success probability} = \frac{(\psi_{NB}^{NB \rightarrow SB})}{(\psi_{NB}^{NB \rightarrow SB} + \psi_{NB}^{NB \rightarrow FB})}$$

This process is repeated 100000 times and the 95% confidence intervals of the derived parameter were estimated with the quantiles 0.05 and 0.95 of the resulting distribution.

Table D1: Breeding success at the first reproduction as a function of age at recruitment. Symbols ":" and "_" indicate that age classes are grouped and separated respectively. Results include the number of mathematical parameters (k), the relative deviance corrected by the overdispersion factor (QDev), Akaike Information Criterion value corrected by the overdispersion factor (QAIC) and the QAIC weight.

No.	Model	k	QDev	QAIC	Weight QAIC
SM1	$\psi^{\mathrm{R \to SB}}(\mathrm{a}_{6:15})$	118	79709.06	79945.06	0.0490
SM2	$\psi^{\mathrm{R \to SB}}(\mathrm{a}_{6\_15})$	127	79697.04	79951.04	0.0025
SM3	$\psi^{\mathrm{R \to SB}}(\mathrm{a}_{6} + \mathrm{a}_{7:15})$	119	79703.91	79941.91	0.2366
SM4	$\psi^{\mathrm{R \to SB}}(\mathrm{a}_{6\_7} + \mathrm{a}_{8:15})$	120	79703.86	79943.86	0.0894
SM5	$\psi^{\mathrm{R \to SB}}(\mathrm{a}_{6} + a_{7:15}^{linear})$	120	79702.00	79942.00	0.2257
SM6	$\psi^{\mathrm{R \to SB}}(\mathrm{a}_{6} + a_{7:15}^{quatratic})$	121	79701.44	79943.44	0.1102
SM7	$\psi^{\mathrm{R \to SB}}(\mathrm{a}_{6} + a_{7:15}^{inverse\ log})$	120	79701.21	79941.21	0.3356

Figure D1: Slope (±SE) of the relationships between the transition probability to group 1 and recruitment age according to time (a) and cohorts (b). Consistent negative relationships between transition probability into the group 1 and recruitment age across years and cohorts suggest that the negative relationship between recruitment age and adult performances was independent of environmental conditions. The higher slope uncertainty for recent years and cohorts is explained by the difficulty to estimate group assignment for individuals with short observation time after recruitment.



Appendix E

Figure E1: Heterogeneity of age-specific probability of recruitment for (a) females and (b) males of the wandering albatross population of Crozet. Estimates (±SE) came from model 4 (Table 1).

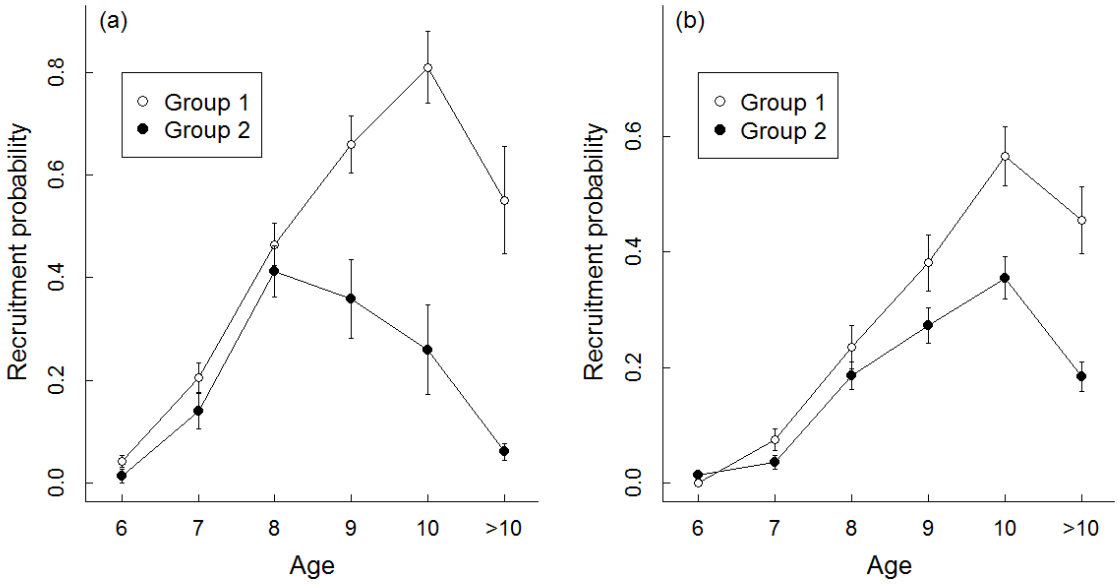


Figure E2: Relationship between the cohort-specific probabilities to belong to group 2 and population density the year of birth for the wandering albatrosses population of Crozet. Estimates of cohort-specific transition (open circles ±SE) were obtained from the additive cohort dependent model (Table 1, M4). Cohort-specific transition probability in group 2 was modelled as a function of population density (dotted line, Table 4, Model 1, PAnodev=0.04).