

UNIVERSITY OF POITIERS
DOCTORAL SCHOOL GAY-LUSSAC
SCIENCES POUR L'ENVIRONNEMENT

P h D T H E S I S

in application for the degree of

Doctor of Philosophy

submitted to the

University of Poitiers

Specialty : **BIOLOGIE DE L'ENVIRONNEMENT,
DES POPULATIONS, ÉCOLOGIE**

Defended by

Matthieu AUTHIER

**Unveiling the At-Sea Ecology
of Southern Elephant Seals
From Indirect Evidence**

Thesis Advisors: Christophe GUINET & Ilham BENTALEB

prepared at Centre d'Études Biologiques de Chizé,
MARINE PREDATOR Team

defended on October 21, 2011

Jury :

<i>Reviewers :</i>	Andrew PARNELL	-	University College Dublin
	Christophe THÉBAUD	-	Université Toulouse III
<i>Advisor :</i>	Christophe GUINET	-	Centre d'Études Biologiques de Chizé
<i>Co-Advisor :</i>	Ilham BENTALEB	-	Université de Montpellier 2
<i>President :</i>	Didier BOUCHON	-	Université de Poitiers

Acknowledgments

Je remercie Vincent Bretagnolle, directeur du Centre d'Études Biologiques de Chizé, de m'avoir accueilli au CEBC et permis d'effectuer ce travail de thèse.

Je remercie l'École Doctorale Gay-Lussac et l'Université de Poitiers pour m'avoir accueilli. Je remercie en particulier Mme Sylvie Perez et Sabrina Biais pour leur disponibilité et pour avoir toujours facilité les démarches administratives.

Je remercie grandement Christophe Guinet pour m'avoir encadré et fait partagé sa passion des mammifères marins. Merci de m'avoir repêché et donner la grande chance de pouvoir re-faire une thèse après mes déboires boréaux. Merci aussi d'avoir supporté mes sautes d'humeur et mes atermoiements.

Je tiens à remercier Ilham Bentaleb pour l'accueil à Montpellier! Merci aussi à Céline Martin et Aurore Ponchon pour m'avoir aidé à braver le micromill.

Je remercie également Olivier Commonwick pour la mise en forme L^AT_EX.

Je remercie également les chercheurs du CEBC en particulier Yves Cherel et Christophe Barbraud pour leurs conseils et leur disponibilité. Merci également à Dominique Besson, sans qui bien des choses auraient été plus compliquées.

Un merci tout particulier à mon petit JB! Une belle rencontre, faite sur cette bonne île d'Amsterdam, qui dure depuis... Peut-être y as tu d'ailleurs revu 'la masse' : ce brave petit V976. En tout cas, tu avais encore une fois raison : South Park pendant la rédaction de thèse, ça aide beaucoup!

Merci aussi à toi Clara, pour toute cette bonne humeur et tout ce talent! Et pour avoir supporté ma maniaquerie (standardise!!!!). Aucun doute que l'on recroisera encore autour d'une bonne grille ou pour parler RRRRrrrr!

Milles mercis à toi Quentin pour m'avoir permis de squatter ton appart pendant tout ce temps à Montpellier. Certes, cela s'est payé en soirée tri de pelotes de chouettes! Rhââ! Et puis surtout merci de m'avoir montré comment manipuler ces grosses bêtes que sont les Éléphants de Mer!

Je ne sais pas non plus comment te remercier Manue pour toutes ces discussions et toutes ces interactions! Merci aussi d'avoir été là pendant les périodes de tempêtes... Satanées matrices!

À Aurélie, Vincent, et Annette. Merci les colloques de votre soutien et bonne humeur. Ah! Annette, le potager va mal : on aura quand même dû traiter un peu! Vincent, il me reste encore des soupes en sachets, mais je ne crois pas les boire un jour, même à ta santé. Aurélie, ton chat fiche des roustes au mien : ça ne va pas du tout!

Merci à Sophie et Maxime, compagnons de galère des dernières heures de rédaction. Elles sont toujours extra ces petites pauses thé. Et Thibaut, je serai encore dispo pour plumer un dindon les soirs où tu t'ennuieras! On ne laissera pas crever la viande!

Merci à la "Guinet's Team" : Anne-Cécile (à la découverte des Éléphants Mer! Pas toujours facile mais on en est revenu!), Morgane (bonnes bestioles que tes otaries), Cédric (alors ça gam?), Paul (sales bêtes que tes orques), Flore (dommage pour le dernier Pot-pot...), Adrien, Guillaume, Marie, et Cécile.

Merci à la Team agropip aussi pour la bonne humeur : Boen, Adrien, Vincent.

Et au fait Amélie, merci encore pour la Love room! On retourne quand tu veux se baigner dans une eau à 10° avec Ibou!

Une pensée bien particulière aux gens que je néglige depuis trop longtemps avec mes histoires de sciences. En premier lieu mes amis VCAT, Jean-Marie, Odile, Anne et Vincent (et Manon!!!).

À Alicia et Mila, I still treasure your friendship, my preciousss! J'espère que Mila se souvient bien de comment on fait la loutre.

À Paul et Claire, merci d'ouvrir encore votre porte parisienne à ce sauvage des Deux-Sèvres.

Anaïs, Thomas et Luka.... j'ai honte de mon silence!

Un immense merci à Lusignan : Tata Claudie et Tonton Jean-Paul; Sébastien (merci de subvenir à la recherche avec ton jardin!), Florence, Antoine, et Adèle; Florian, Pauline et Augustin; Pauline.

Une pensée toute particulière à Joss et Delphin, Cathy et Domi, Xavier, Christine, Noémie, Aïcha : la joyeuse bande du 18 rue Rivals! Merci de ces soirées incroyables!

Enfin, merci à mon petit frère, Stéphane et à mes parents, Gérard et Rolande de supporter mes longues absences et mes longs silences depuis 10 ans... Je n'aurai jamais pu faire tout ce que j'ai pu sans votre éternel soutien.

Et merci à toi Grégory, d'être là aujourd'hui et demain.

Attention conservation notice

We have to remember that what we observe is not nature itself, but nature exposed to our methods of questioning.
W. K. Heisenberg (1958)

He learned many things, and generalized much and often erroneously [...]. He saved himself, however, after the sane and conservative manner of his kind, by labeling his generalizations as "tentative".
Jack London (1909)

'I hear you have strong political views.'
I said: 'Oh no. Extreme views weakly held.'
A.P.J. Taylor (1977)

Another fault is anger. Often a scientist becomes angry, and this is no way to handle things. Amusement, yes, anger, no. Anger is misdirected.
R. Hamming (1986)

Specialization of science also robbed us of much of our passion. We wanted to grasp science whole, but by then the whole was something far too vast and complex to master. Only rarely could we ask the deep questions that had first drawn us to science.
E.P. Wigner

The rage for wanting to conclude is one of the most deadly and most fruitless manias to befall humanity. Each religion and each philosophy has pretended to have God for itself, to measure the infinite, and to know the recipe for happiness.
What arrogance and what nonsense!
G. Flaubert (1863)

Contents

1	Introduction	1
1.1	Foraging Ecology	2
1.2	Studying Wild Populations	2
1.2.1	Biologging Approach	4
1.2.2	Indirect Evidence of Foraging: Stable Isotopes	5
1.3	Coping with Indirect Evidence	7
1.3.1	The Ecologist’s Telescope	7
1.3.2	The Statistician as an Interpret	8
1.4	Objectives of the thesis	10
1.4.1	Biological Cycle of the Southern Elephant Seal	11
1.4.2	Short Description of the Addressed Questions	13
2	Southern Elephant Seal Biology	15
2.1	Estimating Population Size	16
2.1.1	Breeding Female Census	16
2.1.2	Asynchronous Breeding	16
2.2	Hierarchical Modelling	17
2.2.1	Haul-Out Process	17
2.2.2	Variance Partitioning	19
2.2.3	Peak Presence and Synchrony	20
2.3	Corrected Censuses	24
2.3.1	Phenomenological shift	25
2.3.2	Population Trend	26
3	Foraging Strategies	29
3.1	Foraging Locations	29
3.2	Integrating Stable Isotopes and Satellite Telemetry	33
3.2.1	Track Data Analysis	33
3.2.2	Temporal Resolution	33
3.2.3	Southern Ocean Isoscapes	37
3.3	Maternal Strategies	43
3.3.1	Fitness Proxy	43
3.3.2	Data Collection	44
3.3.3	Blood Stable Isotopes	44
3.3.4	Inferring Foraging Strategy	46
3.3.5	Environmental Conditions	53
3.4	Concluding Remarks	57

4	Foraging and Life History	59
4.1	Ontogeny of Foraging	60
4.1.1	Cross-Sectional Data	60
4.1.2	Trophic Level of Southern Elephant Seals	65
4.2	The Importance of Study Design	66
4.3	Ontogenetic Shifts	67
4.3.1	Isotopic Data Collection	67
4.3.2	Change-point Models	69
4.3.3	Hierarchical Formulation	71
4.3.4	Results	72
4.4	Ecological Correlates of Longevity	79
4.4.1	Longevity in the Wild	79
4.4.2	Joint Longitudinal/Survival Models	80
4.4.3	Results	83
4.4.4	Life-History Consequences of Early Life	85
5	Concluding Discussion	89
5.1	Indirect evidence	90
5.2	Mixture Models and Stable Isotopes	91
5.3	Some Limits of Indirect Evidence	94
5.4	Where to Next?	97
A	Bayesian Statistics	99
B	Methods for Chapter 2	103
B.1	Priors	103
B.2	Alternatives to the Inverse Wishart Prior	103
C	Methods for Chapter 3	111
C.1	Laboratory Analyses	111
C.2	Statistical Analyses	111
C.2.1	Temporal Resolution	111
C.2.2	Southern Ocean Isoscapes	112
C.2.3	Inferring Foraging Strategy	113
C.2.4	Mixture Model Selection	113
C.2.5	Robust Link Function: the Robit	114
D	Methods for Chapter 4	117
D.1	Laboratory Analyses	117
D.1.1	Blood Data	117
D.1.2	Tooth Data	118
D.2	Cross Sectional Data	120
D.3	Hierarchical Change-Point Model	120
D.3.1	Priors	120
D.3.2	Model Selection and Fit	121

D.4 Joint Longitudinal-Survival Model	125
D.4.1 Priors	125
D.4.2 Model Checking	125
D.4.3 Stochastic Search Variable Selection	126
Bibliography	131

Introduction

Contents

1.1 Foraging Ecology	2
1.2 Studying Wild Populations	2
1.2.1 Biologging Approach	4
1.2.2 Indirect Evidence of Foraging: Stable Isotopes	5
1.3 Coping with Indirect Evidence	7
1.3.1 The Ecologist's Telescope	7
1.3.2 The Statistician as an Interpret	8
1.4 Objectives of the thesis	10
1.4.1 Biological Cycle of the Southern Elephant Seal	11
1.4.2 Short Description of the Addressed Questions	13

1.1 Foraging Ecology

Foraging is the ability of organisms to acquire and secure resources whose later expenditure will determine their biological fitness. Patterns of expenditure translate into life-history patterns through the process of allocation (Boggs, 1992; Stearns, 1989). Allocation is a within-individual process while foraging is a between-individual one (Figure 1.1). If resources are limited, individual organisms will face allocation trade-offs: for example allocation of time and energy to reproduction may depress growth and survival (Pianka, 1976; Stearns, 1989). Foraging is thus critical as it will determine whether individual organisms will face such allocation trade-offs, either because key resources are limited in the environment or because individuals vary in their ability to extract resources (van Noordwijk and de Jong, 1986). The former limits stem from competition while the latter stem from differences in individual quality hereafter understood as a static trait that positively correlates with fitness (Cam et al., 2002; Bergeron et al., 2011). Because of the intricate links between foraging and life-history patterns, a detailed knowledge of how organisms cope with extracting resources from their environment is needed to further understand the population consequences of these life-history patterns (Cole, 1954). Such an understanding is a difficult endeavour: it is a multilevel problem (Robinson, 2009; Cooch et al., 2002). Data both at the between-individual and within-individual levels are needed for a complete elucidation as emphasized on Figure 1.1 which depicts feedback loops between these two levels.

1.2 Studying Wild Populations

In the wild, environmental resources usually fluctuate both in space and time (Boggs, 1992). This heterogeneity structures the ecological theatre in which organisms evolve. Foraging may thus be apprehended as an optimization problem: given the constraints set by the environment in a broad sense (abiotic and biotic), how can organisms forage efficiently? Efficiency may be equated with a rate of resources extracted per time unit spent foraging, and a causal link between biological fitness (the ability of organisms to survive and contribute viable offsprings to the next generation) and foraging ability is then typically assumed. This second assumption is often made in order to bypass the notoriously difficult problem of estimating a biological fitness (Link et al., 2002; Metcalf and Parvard, 2006). Fitness is here understood as the currency of natural selection; that is as an individual latent (and maybe multi-dimensional) trait that measure the propagation rate of genotypes into subsequent generations (Link et al., 2002). This retrospective definition of fitness makes it difficult¹, to estimate the biological fitness of organisms that are still-living, haven't reproduce yet *etc.*

¹although not impossible (Link et al., 2002; Link and Barker, 2009)

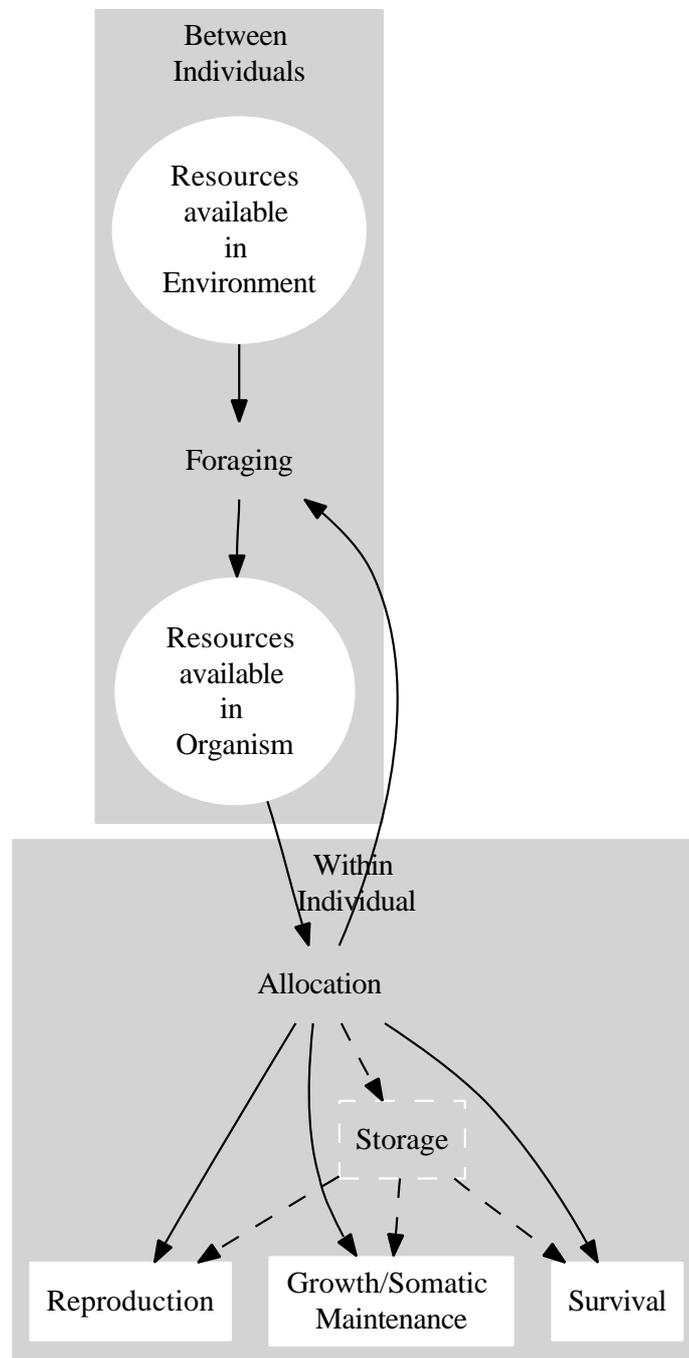


Figure 1.1: Levels of analysis and the interplay between foraging and allocation (modified from [Boggs \(1992\)](#)). In the case of organisms with a dormancy period or a capital breeding strategy, resources may be acquired and stored for later use.

Optimal foraging theory (MacArthur and Pianka, 1966) uses an optimization criterion to assess the merits of different energy extraction strategies (see Doniol-Valcroze et al. (2011) for a thorough study exemplifying the strength of this approach.). Stepping aside from philosophical considerations about optimization in biology (for example Gould and Lewontin (1979); Sakar (2005); Depew (2010)), the practical biologist still face challenges in directly measuring foraging of wild animals.

1.2.1 Biologging Approach

Such challenges have been somewhat relaxed over the last two decades with the advent of miniaturized archival tags (see for example, Péron et al. (2010)) and what has been aptly dubbed the “biologging revolution” (Ropert-Coudert and Wilson, 2005). Using telemetry data and trajectory analysis, foraging behaviour is inferred from movement patterns (Jonsen et al., 2007; Patterson et al., 2008) but the nature of resources that the animals are harvesting usually remains unknown (but see for example Davis et al. (1999)). Enormous progress in miniaturization is rendering possible to even peek into cryptic life-stages of animals such as eels (Aarestrup et al., 2009) or turtles (Hart and Fujisaki, 2010). Hebblewhite and Haydon (2010) critically reviewed the impressive successes of biologging, stressing the shortcomings and challenges still plaguing this revolution. Adopting a deliberate provocative tone, Hebblewhite and Haydon (2010) urged biologists to distinguish between what is impressive and what is important as they get ‘buried under a growing mountain of data comprising millions of locations’. While location data skyrocket, the number of animal that can be equipped with telemetric tags remains usually small from a statistical point of view.

This in turn creates challenges in generalizing patterns observed from a sample to a (typically much) larger population. If indeed conservation decisions are to be taken from the conclusions of biologging studies (Thiebot, 2011), generalization beyond the observed (small) sample is the goal. For example, in one of the most impressive biologging studies, Wakefield et al. (2011) analyzed the foraging behaviour of Black-Browed Albatrosses (*Thalassarche melanophrys*). Inference there is for the worldwide population level (estimated at $\approx 600,000$ pairs), and conclusions are based from a sample of 163 individuals tracked over a 10 year period. Statistical considerations cannot easily be swept aside.

1.2.2 Indirect Evidence of Foraging: Stable Isotopes

Standing in a costwise contrast to bioglogging is the inexpensive technique of measuring the ratio of naturally occurring stable isotopic elements (such as carbon, nitrogen, sulfur, hydrogen, oxygen, etc...) in various biological samples. Since the seminal works of DeNiro and Epstein (1978, 1981) and Fry et al. (1978), the use of stable isotopes to infer and revealed ecological connections between organisms has soared (West et al., 2006). These early studies demonstrated how the stable isotopic composition of consumers is a reflection of the stable isotopic composition of their diet. Knowledge of the diet then renders possible to predict the isotopic composition of consumers (Norman et al., 2009).

Standard Isotopic Notation

In isotope geochemistry, abundances of isotopes in a sample are computed relatively to an international standard. The relative abundances of isotopes are expressed using “delta notation”, written as δ , in units of parts per thousand, more commonly referred to as “per mil” and denoted by ‰. By denoting X the element under consideration (with atomic number n , and whose heavier isotope has atomic number m), the “delta notation” of X is $\delta^m X$:

$$\delta^m X = 1000 \times \left(\frac{R_{sample}}{R_{standard}} - 1 \right)$$

where R_{sample} and $R_{standard}$ refer to the $\frac{mX}{nX}$ ratios of sample and standard, respectively.

For carbon, the international standard is the Vienna Pee-Dee-Belemnite, while that of nitrogen is atmospheric N_2 .

Physical, biological and chemical processes interact and results in distinct isotopic signatures in naturally occurring materials. Ecologists can take advantage of these natural processes and their predictable behaviour to track the flow of nutrient across food webs (Peterson and Fry, 1987; West et al., 2006). The elements C, N, S, H, and O all have more than one isotope, one heavier than the other due to the presence of an extra neutron in the nucleus (Fry, 2006). The lighter isotope is usually more reactive, a phenomenon known as fractionation² (Fry, 2006). For example, the lighter ^{14}N is preferentially excreted and the heavier ^{15}N is preferentially retained. This differential reactivity results in a predictable enrichment of the ratio of ^{15}N to ^{14}N from preys to consumers (Kelly, 2000). Hence $\delta^{15}N$ has been adopted by biologists to infer the trophic level of organisms (Post, 2002; Vanderklift and Ponsard, 2003).

²There are several types of fractionation: equilibrium, kinetic and mass-independent fractionation. See http://en.wikipedia.org/wiki/Stable_isotope.

In a somewhat different vein, carbon isotopes are used for identifying carbon sources and fluxes within ecosystems (Kelly, 2000; Peterson and Fry, 1987; West et al., 2006). Plants fall into different categories whether they rely on a C₃ or C₄ metabolic pathway. The isotopic signatures of these plants are distinct, with C₃ plants being more depleted in ¹³C, which allow to infer the probable diet of a consumer (Parnell et al., 2010; Semmens et al., 2009). Natural gradients in carbon isotopes occur between terrestrial and marine food webs (Schoeninger and DeNiro, 1984; Hobson et al., 1994), between inshore and offshore waters (Rau et al., 1982; Hobson et al., 1994), between benthic and pelagic foodwebs (France, 1995) or between low and high latitudes water masses (Rau et al., 1982, 1989).

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are by far the most studied elements in ecology (Kelly, 2000; West et al., 2006): they inform respectively on the origin of assimilated preys, that is the foraging location of a consumer; and on the trophic position within a food web of the consumer. Progress in mass spectrophotometry allows the use of tiny amount to measure the isotopic composition of biological samples. This is a great strength of stable isotopic ecology: the technique is a very little invasive one. Samples of various tissues such as blood, muscle, claws, hair *etc* can be easily collected on a wide range of wild animals, even endangered ones (for example Jaeger (2009); Thiebot (2011)), to study indirectly foraging ecology.

An illustrative example is the study of Popa-Lisseanu et al. (2007) who elucidated whether Giant Noctule Bats (*Nyctalus lasiopterus*) could prey on migrating birds. By measuring seasonal variations of stable isotopes in the blood of bats, Popa-Lisseanu et al. (2007) then compared these variations with the bats' potential prey: insects and birds. Bats were in fact hunting songbirds on the wing, but only so during the birds' seasonal migration. This studying exemplify the attractiveness of stable isotopes for studying foraging ecology: these bats are small-flying mammals and are nocturnal foragers, characteristics that render direct observations challenging. Thus stable isotopes are especially suited for studying animals with cryptic life-styles or life-stages (Reich et al., 2007).

1.3 Coping with Indirect Evidence

Stable isotope ecology tracks the flow of molecules through a food web. The foraging behaviour of consumers is investigated indirectly by taking advantages of naturally occurring differences in stable isotope composition between ecosystems. This reliance of natural gradients also means that stable isotopic data collected of wild animals will be more observational than experimental (Sagarin and Pauchard, 2010). The evidence provided by stable isotopes is thus indirect in that the exact identity and geographical origin of consumed preys is unknown, but can nevertheless be inferred. As exemplified by the Giant Noctule Bats, stable isotopes can yield powerful insights when direct observations are logistically impractical.

1.3.1 The Ecologist's Telescope

Stable isotopes may thus be some kind of telescope which allows ecologists to peek into remote places where wild animals forage. An analogy with Galileo and the planet Jupiter springs to mind, and is not as far stretched as one may think. Indeed, Galileo used his telescope, without having a satisfactory optical theory justifying that what he was seeing was not some sort of illusion (Kuhn, 1996). This glaring deficiency arose suspicion from his fellow scientists (just like Darwin could not provide a satisfactory theory of heredity to achieve convincing skeptics in his time (Stanford, 2006)). That is not strictly the case of stable isotopic ecology: fractionation involves chemical reactions and is backed up by healthy theoretical constructs and experimental successes (Fry, 2006). However, there remains dark corners with the use of stable isotopes when studying wildlife (Gannes et al., 1997; Martínez del Rio et al., 2009; Wolf et al., 2009b), most notably the accurate estimation of discrimination factors³ (Vanderklift and Ponsard, 2003; Caut et al., 2009; Perga and Grey, 2010; Auerwald et al., 2010; Caut et al., 2010; Ellison and Dennis, 2010). These discriminations factors can strongly influence inferences for example when estimating diet from stable isotopic data (Parnell et al., 2010; Bond and Diamond, 2011).

Because stable isotopes provide indirect evidence, the view taken in the present thesis is that their analysis will require both substantial biological knowledge and an adequate statistical analysis to account for relevant sources of variations. The first requirement is trivial, but the second one stresses that stable isotopes are typically used by ecologists to infer unobservable states (foraging) and can be affected by many sources of variations. These two features in turn calls for a statistical analysis specifically tailored to the data at hand⁴.

³Discrimination factors, denoted ΔX are the difference between a consumer and its diet $\delta^m X$, where X is the element under scrutiny.

That is $\Delta X = \delta^m X_{\text{consumer}} - \delta^m X_{\text{diet}}$.

⁴I believe this to be true when studying wild animals with little scope for a very tight and controlled experimentation. Things may be very different in the laboratory where unwanted sources of variation can effectively be neutralized.

1.3.2 The Statistician as an Interpret

After all, statistics is about knowing the unknowns
Meng (2000)

Statistics is a language used to interpret another language
Ellison (2004b)

Teasing apart different sources of variation is one of the task of statistics. Even the biologging approach to studying foraging behaviour relies heavily on statistics: state-space models of animal movements explicitly separate an observation error from the error of the underlying process of interest (Jonsen et al., 2003; Patterson et al., 2008). Variance components models are widely used in quantitative genetics to tease apart genetic variation from environmental variation (Lynch and Walsh, 1998), and have been successfully applied on wild populations where study designs are often closer to observational than experimental (Kruuk, 2004; Browne et al., 2007; Authier et al., 2011a). Impressive computing power lie within any modern computer, which, combined with the widespread availability of free statistical softwares such as the R language (R Development Core Team, 2009) means that it has never been so accessible to fit sophisticated models taylorred to specific scientific questions.

Yet, when it comes to stable isotopic ecology, sophisticated methods are still scarce (but see Semmens et al. (2009); Parnell et al. (2010); Ward et al. (2011); Jackson et al. (2011) for counterexamples), and most studies rely on analyses than emphasize null hypothesis testing over estimation (Ellison and Dennis, 2010). One detrimental aspect of testing is the sometimes excessive use of untenable null hypotheses, most often that of a zero effect (Burnham and Anderson, 2002; Gelman, 2010; Nelder, 1996). While testing hypotheses is important, estimation is often more of interest to ecologists (Burnham and Anderson, 2002; Ellison and Dennis, 2010). If stable isotopes are to reveal unobservables about wild animals, then an explicit statistical model is needed. For example, Hénaux et al. (2011) were interested in estimating the migration routes of four cougars (*Puma concolor*) across North America Great Plains. Using an explicit likelihood-based approach⁵, Hénaux et al. (2011) were able to infer the most likely dispersal route of each cougar from claw isotopes. Likewise, Van Wilgenburg and Hobson (2011) combined stable isotopic data with band recovery data to predict the origin location of migrating birds.

⁵see Appendix A

All data require some underlying scientific model (understood as an abstract idealization of the “real world”) to be intelligible (Kuhn, 1996; Chalmers, 2006). Such a scientific model needs to be translated into a statistical one, which then combined with data will help the ecologist to assess the merits of her pet theories. The statistical model in turn posits several simplifying or operative hypotheses, some less reasonable than others. Assumptions are unavoidable⁶ but they should be explicit so they can be criticized (Box, 1990). The statistician is there to help the ecologist to connect between the raw data, the (scientific) model, the (statistical) methods, and ultimately to listen to the conclusions of this triumvirate (Figure 1.2).

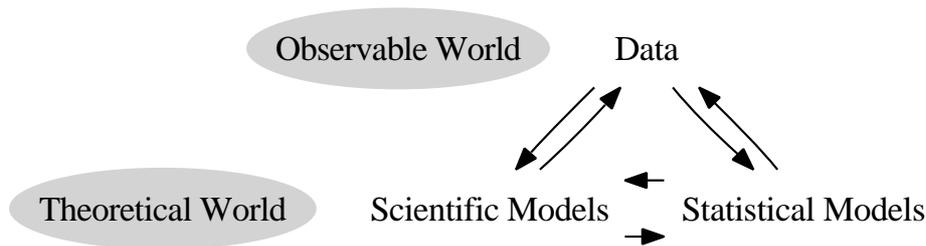


Figure 1.2: The intricate interplay of scientific, statistical models and data (modified from Kass (2011)).

Criticism is indeed a crucial part of any scientific enquiry (Box, 1990; Gelman and Shalizi, 2010; Kass, 2011) as it highlights the blindspots that need further investigations⁷. For these reasons, I favoured a Bayesian framework throughout the present work. This framework allows with relative ease to account for many sources of variations as well as to build realistic (that is, sophisticated) statistical models tailored to the scientific question at hand. The main drawback of this choice stems from model selection within the Bayesian Framework, the most current pressing open problem in Bayesian statistics (Jordan, 2011). As a consequence I had to resort to sometimes unfamiliar or even hybrid procedures in some instances. Extensive and friendly coverage of the breadth of applications of Bayesian statistics to “real-world” problems are provided in Gelman et al. (2003); Gelman and Hill (2007); Gill (2009) and MacCarthy (2007); Link and Barker (2009) for ecology in particular. A very brief and superficial description of Bayesian statistics is exposed in Appendix A.

⁶even so-called nonparametric statistics or the bootstrap make restrictive assumptions (Efron, 1979; Rubin, 1981; Johnson, 1995; Fagerland and Sandvik, 2009).

⁷or reveals that we may be wrong! See the entertaining talk by Kathryn Schulz: http://www.ted.com/talks/lang/eng/kathryn_schulz_on_being_wrong.html

1.4 Objectives of the thesis

The objectives of the present thesis was to study the ecology of an elusive marine carnivore with stable isotopes: the Southern Elephant Seal (*Mirounga leonina*, Linnaeus 1758, Figure 1.3) breeding on îles Kerguelen (49°30' S, 69°30' E), Southern Ocean. The cryptic life-style of this seal - it can spend more than 80% of its lifetime at sea (McIntyre et al., 2010), and more than 90% of that time at sea is spent submerged (Hindell et al., 1991) - makes the use of stable isotopes to study its foraging ecology especially appealing.



Figure 1.3: Southern Elephant Seals: a male, female and pup on a Kerguelen hauling-out beach, îles Kerguelen (Credit: M. Authier 2009).

1.4.1 Biological Cycle of the Southern Elephant Seal

Southern Elephant Seals are the largest extant pinnipeds, and also the mammalian species with the starkest sexual dimorphism with males being up to one order of magnitude heavier than females (Laws, 1953). Adult Southern Elephant Seals spend most of their time at sea but come ashore for two short bouts each year: to breed during the spring haul-out (September-November) and to moult during the summer haul-out (January-February) (Laws, 1960). In spring, females aggregate in dense rookeries to give birth to a single pup, wean it in three weeks and mate before returning to sea. During this foraging trip at sea, which lasts ≈ 2 or 3 months, females replenish their energy stores: lactation is very costly as a female loses on average one third (up to one half) of her post-partum mass during the 3 weeks period when she attends her pup and during which her mass loss rate is on average 8 kg per day (Arnbom et al., 1997). The summer haul-out starts in January and animals gather on beaches in loose aggregates to moult. Both juvenile males and females are to be found at this time of the year, whereas breeding bulls will arrive later in the summer (Laws, 1960; Ling and Bryden, 1981). The biological cycle of breeding females is summarized in Figure 1.4. These seals fast when they are ashore: foraging is thus temporally and spatially independent from breeding or moulting. Figure 1.4 also shows how the post-breeding foraging trip is ≈ 3 to 4 times shorter than the post-moulting trip which can last 7 months. Seals are less time-constrained for the post-moulting trip than for the post-breeding trip for which they need to quickly replenish their energy stores before the energetically demanding summer moult.

A long standing question regarding this species is why did it decline in the 1970s (Guinet et al., 1999; McMahon et al., 2005a). A population decline was observed on the major breeding grounds in the South Indian (îles Kerguelen) and South Pacific (Macquarie Island, 54°30' S, 158°57' E), but not in the South Atlantic (South Georgia, 54°15' S, 37°05' W), Oceans (McMahon et al., 2005a). Causes behind this decline are still debated, yet they most likely have to do with the foraging ecology of Southern Elephant Seals (McMahon et al., 2005a; Ainley and Blight, 2009). While 30 years ago Ling and Bryden (1981) lamented that the foraging ecology of Southern Elephant Seals was poorly known, this situation has since dramatically changed with the advent of the 'biologging revolution' (McConnell et al., 1992; Biuw et al., 2007). In an impressive coordinated effort, 85 Southern Elephant Seals from key colonies within the Southern Ocean were equipped with telemetric tags to collect data on the physical environments in which seals improve their body condition (Biuw et al., 2007). Biuw et al. (2007) evidenced differences between breeding colonies in the South Atlantic Ocean and elsewhere which could impact the energy budget of seals: seals from îles Kerguelen and Macquarie Island may have longer transit times before reaching favorable feeding grounds compared to seals breeding on South Georgia.

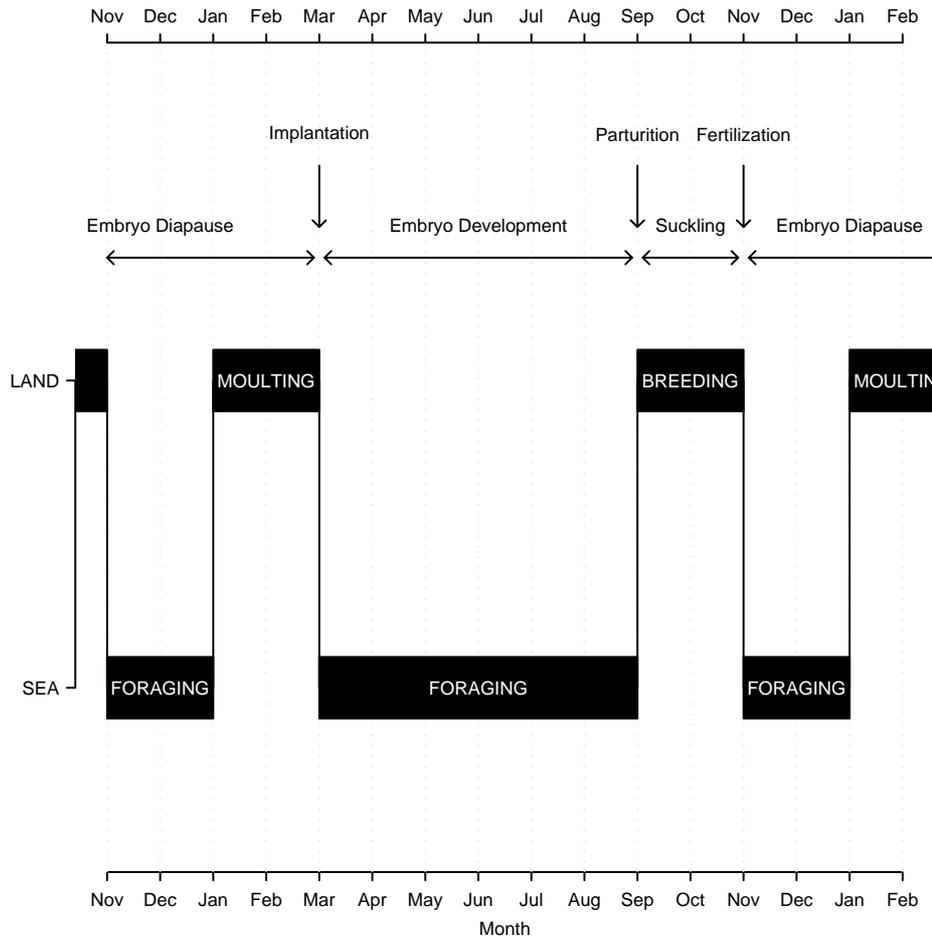


Figure 1.4: Schematic representation of the biological cycle of a breeding female Southern Elephant Seals (modified from Laws (1960))

Bailleul *et al.* (2007*a,b*) and Bailleul *et al.* (2010) further detailed the physical environment encountered by the Kerguelen seals during their foraging trips, using data collected from telemetric tags deployed on the animals. These studies detailed the oceanographic conditions associated with an improving condition of the seals, as well as the location of feeding grounds on a large scale. One drawback of these studies is that equipped seals were monitored for only one trip, and there was typically few individual level data on them. Yet, while these are philopatric, they are not strictly enfeoffed to a particular hauling-out site on îles Kerguelen: seals were sometimes retrieved far away from where they were equipped (Figure 1.5). While 'biologging' provides detailed data of a single foraging trip, in the case of the Kerguelen population where there is currently no Capture-Mark-Recapture scheme, it is hard to assess long-term trends in foraging behaviour and their consequences on individual life-histories. Here lies the potential of stable isotopes to address these blindspots.

1.4.2 Short Description of the Addressed Questions

The next chapter of this thesis will thus look into the current population trend on îles Kerguelen, updating the analysis of Guinet *et al.* (1999) with ten years of additional data. The third chapter will detail the use of stable isotopes and their relation to foraging strategy as inferred from biologging data using animals that were both equipped with telemetric tags and blood-sampled. It will also peek into the foraging strategy of breeding females as inferred from their pup blood isotopes (Ducatez *et al.*, 2008). I will then try to correlate these foraging strategies with a proxy of female fitness, the weaning mass of its pup. Pup weaning mass influences pup survival (McMahon *et al.*, 2000*a*), a life-history parameter to which population growth is very sensitive (McMahon *et al.*, 2005*b*). The fourth chapter will investigate the question of the ontogeny of foraging in Southern Elephant Seals using both a cross-sectional and longitudinal approach. This chapter will focus in particular, on the use of tooth stable isotopes as natural archives to compare foraging between seals that lived before and after the 1970s population crash. Finally, the relationship between foraging and a life-history trait, longevity, of male Southern Elephant Seals will be assessed.



Figure 1.5: Map of îles Kerguelen in the Southern Ocean. Blue dots highlight sites where seals have been equipped with telemetric tags and were recaptured, while red dots show sites where some seals were recaptured. Seals equipped at a site were not necessarily recaptured at that site: for example, one female equipped at Cape Ratmanoff was recaptured on Port-aux-Français (see Chapter 3).

Southern Elephant Seal Biology

Contents

2.1	Estimating Population Size	16
2.1.1	Breeding Female Census	16
2.1.2	Asynchronous Breeding	16
2.2	Hierarchical Modelling	17
2.2.1	Haul-Out Process	17
2.2.2	Variance Partitioning	19
2.2.3	Peak Presence and Synchrony	20
2.3	Corrected Censuses	24
2.3.1	Phenomenological shift	25
2.3.2	Population Trend	26

This chapter was published as:

Authier, M., Delord, K. & Guinet, C. (2011) Population Trends of Female Elephant Seals Breeding on the Courbet Peninsula, îles Kerguelen. *Polar Biology*, 34, 319-328.

2.1 Estimating Population Size

2.1.1 Breeding Female Census

Pregnant females are constrained to come ashore to give birth, and their breeding probability quickly rise to unity with age (McMahon et al., 2003). Thus censuses of breeding females during the spring haul-out are likely to encompass most of the breeding female population. Given the extreme mating schemes observed for males (Jones, 1981), censuses of breeding males may not yield as an accurate picture of the population status as breeding female counts. Such counts will miss the non-breeding fraction of a population. However, even when breeding females are censused, counts may be prone to a large observation error because of the large density of animals within colonies. Such observation error, if ignored, will be confounded with environmental noise and may either eclipse true biological signals or give rise to spurious results (Hovestadt and Nowicki, 2008).

2.1.2 Asynchronous Breeding

The timing of female return is spread over two months, but each female only stays ashore for three to four weeks (Van Aarde, 1980). Because the population of breeding Southern Elephant Seals is asynchronous, no census can encompass all females that may have come ashore. The latter number must be estimated along with a measure of uncertainty. Females aggregate in more or less large rookeries, and all rookeries are not formed at the same time during the breeding season; that is, there is some variability associated with breeding sites. All sites can not be logistically sampled given the large size of îles Kerguelen (approx. 7,200 km^2 with 2,800 km of coastline). Thus, there is a spatial as well as a temporal variability in counts. A last source of variability stems from field workers who are actually doing the censuses.

One aim of this thesis was to re-assess the population status of Southern Elephant Seals breeding on îles Kerguelen. This species is one of the best studied phocids, yet the exact causes behind its large decline during the second half of the twentieth century are still debated (McMahon et al., 2005a). In the most recent analysis of population trends on Kerguelen, Guinet et al. (1999) wondered whether the decline was over, but refrained from making strong statements given their relatively short time series of censuses. Here, their analysis is updated with 10 years of additional data.

2.2 Hierarchical Modelling

2.2.1 Haul-Out Process

Several models have been developed to describe the asynchronous behaviour of breeding females Southern Elephant Seals (Van Aarde, 1980; Pascal, 1981; Rothery and McCann, 1987). Among these, that of Rothery and McCann (1987) describing the timing of Southern Elephant Seal haulout with four parameters that have a straightforward biological interpretation, is particularly attractive. More specifically, the haul-out process is described as the product of a total number of breeding females coming ashore (N_{max}) and a proportion dependent on the day the census was realized. The latter proportion (p), by definition bounded between 0 and 1, is a bell-shaped function of census day (t), centred on a date of maximum presence (μ), of female synchrony (σ) and of the mean time length (pre- and post-partum) females spend ashore (S).

This proportion p corresponds to the proportion of females that have arrived to breed by day t , Arr_t , minus the proportion of females that have left by day t , Dep_t . Thus, for a census performed on day t :

$$N_t = N_{max} \times p(t, \mu, \sigma, S) \quad (2.1)$$

$$\begin{aligned} p(t, \mu, \sigma, S) &= Arr_t - Dep_t \\ Arr_t &= \Phi\left(\frac{t - \mu}{\sigma}\right) \\ Dep_t &= \Phi\left(\frac{t - S - \mu}{\sigma}\right) \end{aligned}$$

where $\Phi(\cdot)$ denotes the standard normal cumulative distribution function.

All four parameters (N_{max}, μ, σ, S) cannot be estimated simultaneously from the same data (Rothery and McCann, 1987; Galimberti and Sanvito, 2001; Condit et al., 2007). Van Aarde (1980) estimated S to be 28 days with a standard deviation of $\sqrt{5}$ days. This was derived as the sum of a 5 ± 2 day-long pre-partum stay followed by a 23 ± 1 day-long pup-caring period. If the remainder of these parameters can be estimated, then N_{max} can be estimated from a census performed on day t of the breeding season as $N_{max} = \frac{N_t}{p(t, \mu, \sigma, S)}$. Female Southern Elephant Seals breeding the Courbet Peninsula in the Western part of îles Kerguelen has been monitored since the 1950s (Figure 1.5). This census encompasses a 80 km long transect and is done by foot: the census cannot be completed in any single day. However, if accurate estimates of μ and σ can be obtained, then the number of breeding females for any date t can be estimated from a census.

2.2.2 Variance Partitioning

To estimate the parameters μ and σ related to the Kerguelen population, 6 and 9 harems of different sizes were monitored daily from September the 21st till November 16th at Cape Ratmanoff in 2008 and 2009 respectively (Figure 1.5). For any of these N_t , there are two obvious sources of variation:

1. counting errors due to the field worker (measurement error); and
2. sampling errors due to natural variability due to sampling a few harems from a larger population. Some harems are formed earlier and some later during the breeding season.

To take into account the different sources of variation, each monitored harem was given a specific set of parameters ($N_{max}^i, \mu^i, \sigma^i$, where the superscript i denotes the i^{th} harem) and the inter-harem variability, along with correlations between the different parameters, were explicitly modelled in a hierarchical model. The $(N_{max}, \mu, \sigma)^i$ were assumed to be exchangeable ¹ and to follow a multivariate normal distribution.

Some eighteen different field workers helped in counting females throughout the study period. Different distributional assumptions for the fraction of variance due to observers and the residual fraction were tested. Specifically I compared a normal versus a Student distribution for the residual variance term. Field workers helping in the field had either some or no prior experience in counting pinnipeds. To assess the impact of such heterogeneity on counts, the variance due to observer was modelled either as following a normal (that is observers were comparably skilled), a Student (that is, a few observers may have been extremely good/bad) or a Skew-normal (that is, observers on average tended to over/under-estimate females) distribution. Models thus differed by at most two parameters, and were compared using the Bayesian deviance (the smaller the deviance, the better the model fit, see the discussion by Dawid in Spiegelhalter et al. (2002)). All models were implemented with winBUGS (Lunn et al., 2000; Spiegelhalter et al., 2003): details are available in Appendix B.

¹The Bayesian justification of the random effects model reflects an *a priori* assumption of *exchangeability* about the treatment effects, that is the joint distribution of the treatment effects is independent of the identity of the actual [levels] being considered. In practice, the exchangeability assumption involves two components. First that the [effects] are unlikely to be identical, but are likely to be similar [...]. Second, that there is no reason to expect the [effect of any specified level] to be larger than the [effect of another specified level]. The second component has the consequence that an *a priori* ranking of the effect sizes is not possible (Higgins and Spiegelhalter, 2002).’ Throughout though, the qualification ‘random effect’ is avoided as it is ambiguous (Gelman and Hill, 2007) and its meaning has changed over time (Hodges and Clayton, 2011)

The model with the minimal deviance was a model with a Student distributed residual error and a normally distributed observer error (Table 2.1). Under this model, observer error represented 6 ± 9 % of the total variance. Because censuses of the Peninsula Courbet are always performed by different fieldworkers from one year to the next, quantifying the uncertainty due to observers was essential to assess the reliability of estimates. That this uncertainty is rather small (6 ± 9 % of the total variance) and normally distributed is testimony to the dedicated work of observers: they are doing their best on a hard job.

	Deviance (\bar{D})	Error _{residual}	
		Normal	Student
Error _{Observer}	Normal	10 080	10 000
	Student	10 260	10 230
	Skew-Normal	10 090	10 020

Table 2.1: Model Selection. Different distributional assumptions for residual and observer errors were made and contrasted. The best model had a Student and Gaussian distribution for residual and observer errors respectively .

The selected model was that with Student error, reflecting the occurrence of some extreme observations. These may have resulted from the frequent inclement conditions during which censuses were performed (strong winds, snow). In addition, the Courbet Peninsula shows a rather flat landscape (Figure 1.5), with no promontory points which could help in assessing the depth of harems when counting females. That the selected model suggested that counts may be intrinsically hard is thus rather pleasing and in agreement with the experience of most fieldworkers. Nevertheless, in this analysis, data from 2008 and 2009 were pooled, thus ignoring any variability due to year. However, as 2008 and 2009 were very similar (see Chapter 3) this variability is, in all likelihood, small.

2.2.3 Peak Presence and Synchrony

On îles Kerguelen, the haul-out peak occurred on October the 13^{15}_{17} ² while the synchrony for a rookery was $7.38.39.3$ days. At the harem level, N_{max} was uncorrelated with both μ ($\rho =_{-0.57} -0.08_{0.42}$, or σ ($\rho =_{-0.64} -0.09_{0.51}$). On the other hand, μ and σ were negatively correlated ($\rho =_{-0.93} -0.59_{-0.11}$)³: precocious harems were less synchronous than late ones. Model fit to the raw data is depicted on Figure 2.2

²following [Louis and Zeger \(2009\)](#), point estimates are reported bracketted by a 95% credible interval.

³This estimate is likely an overestimate arising from the use of an Inverse Wishart prior for the covariance matrix. See Appendix B

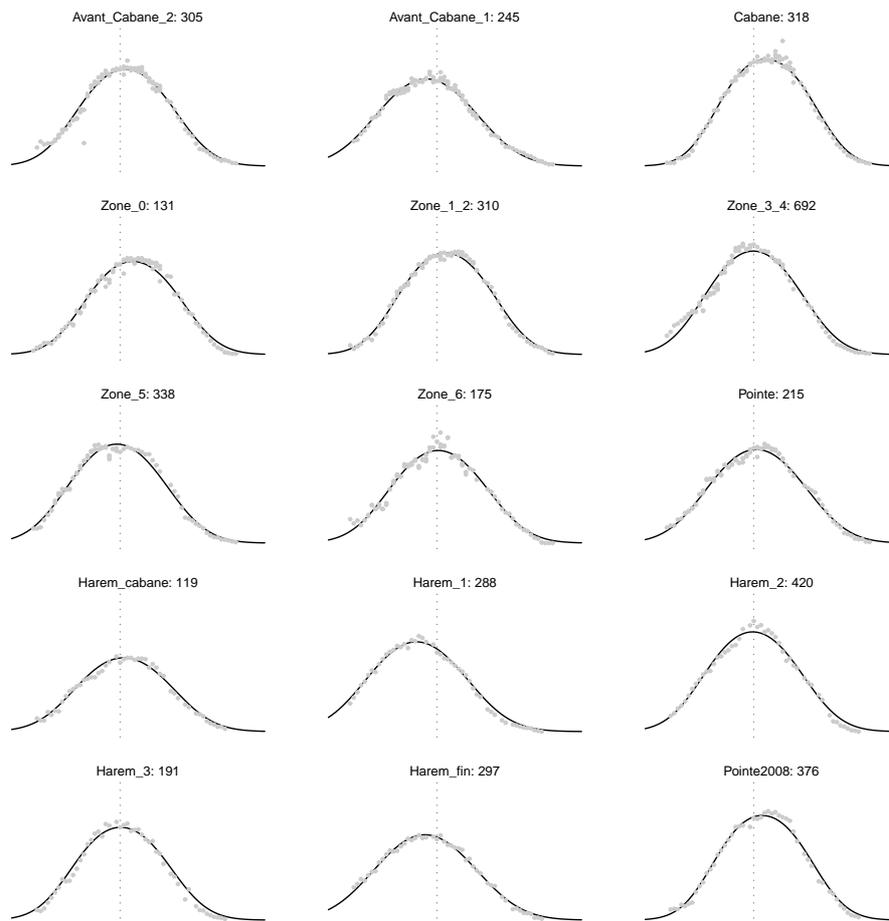


Figure 2.2: Plots of all surveyed harems in 2009 (3 first rows) and in 2008 (2 last rows) at Cape Ratmanoff. Harem name is followed by the estimated N_{max} . The x-axis corresponds to census date, and the vertical, dotted grey line symbolize the 15th of October. Light grey dots correspond to raw data, and the black solid to the posterior mean number of hauled-out female at date t .

The hierarchical model fitted the data well. However, [Condit et al. \(2007\)](#) recently highlighted some shortcomings of this model, specifically the assumption of symmetry in the haul-out process, that is that females are returning to the sea at the same rate as they hauled-out. This assumption does not hold, a fact already noted by [Galimberti and Sanvito \(2001\)](#), because there is a small, but practically significant, negative correlation between female arrival and departure dates from the rookery ([Condit et al., 2007](#)). I nevertheless chose to focus on [Rothery and McCann \(1987\)](#)'s model as it has been widely used so that comparisons to published results from other populations of Southern Elephant Seals are possible.

To assess the magnitude of the bias in estimated N_{max} , the total number of pups produced (dead, weaned, and unweaned) on the censused harems was recorded in 2009. In 2009, all harems between Cape Ratmanoff and another, unnamed Cape (located between Cape Ratmanoff and Cape Sandwich). These natural boundaries prevented to some extent an influx of pups from adjacent areas. Because some pups were also tagged, I could observe them moving around within the studied area, and found only one (out of 220) outside it. Also, because of the flatness of the landscape and the short *Acaena*-dominated vegetation (no tussocks), a lot of weaned pups actually moved inland, and aggregated around the banks of the nearby Manchot river and mud holes. Because of these landscape features at the studied sites, I feel confident the direct pup counts were accurate. These direct counts were then compared to the predicted number of females. Although, this estimate of pup production had its own uncertainties, the latter were expected to be smaller than that of females because pups tends to remain on their natal rookery for 3-8 weeks upon weaning ([Lenglart and Bester, 1982](#)).

In 2009, the selected model estimated $_{2580}^{2730}_{2870}$ females to have hauled-out on the study area. On November the 1^{st} , 2^{nd} , 3^{rd} and 5^{th} , I counted an average of $_{2840}^{2960}_{3080}$ pups on the study area. Thus, the model underestimated the total number of females that have hauled-out during the breeding season. [Rothery and McCann \(1987\)](#)'s model has shortcomings: the model underestimated the number of females ashore at peak haul-out (positive residuals), and overestimated this number at the close of the breeding season (negative residuals). This behaviour resulted in a wave-like pattern in a plot of residuals against census date, apparent for most surveyed harems but the smallest, and was most pronounced in the largest harem (Figure 2.3). Such a deficiency stems from the symmetry assumption of the model while there is in fact a small, but practically significant, negative correlation between female arrival and departure dates from the rookery ([Condit et al., 2007](#)). This correlation thins the right tail of the bell-shaped curve (see Figure 2.3), and results in an underestimation of the proportion of females present at peak haul-out. Thus the correction factors $p(t, \mu, \sigma, S)$ will tend to produce under-estimates.

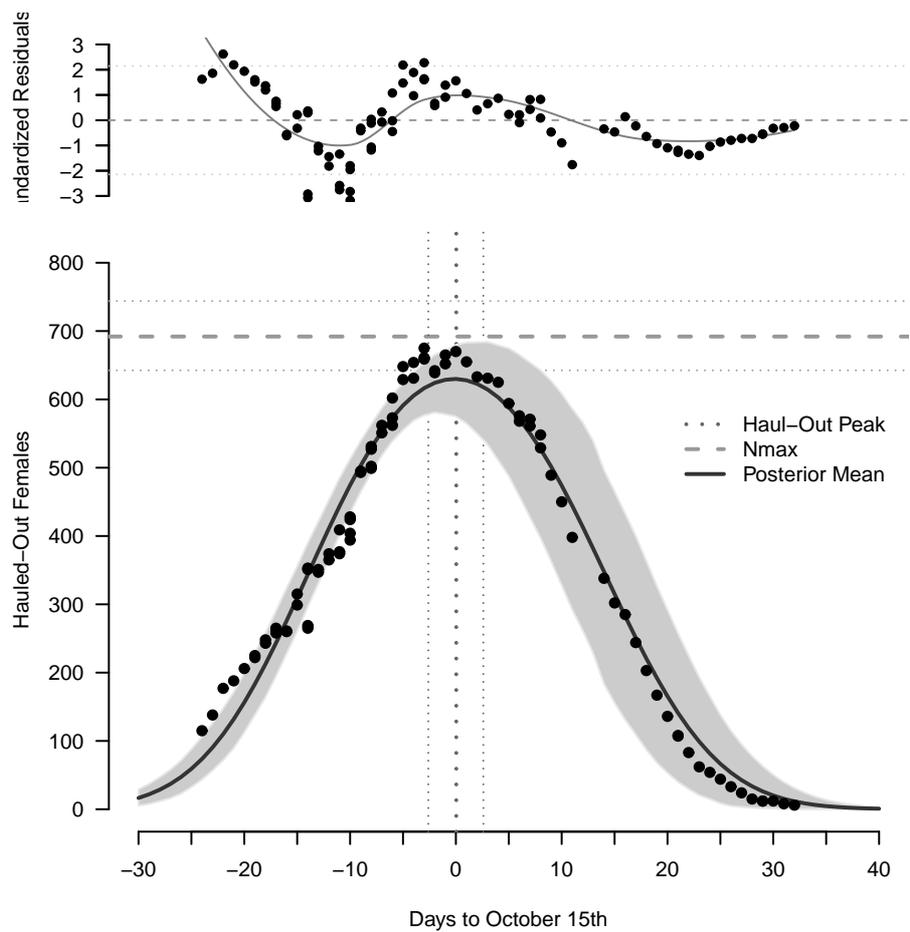


Figure 2.3: Haul-Out Process at the Largest Rookery Surveyed in 2009. Dotted grey lines along with the light-grey envelope picture 95% CI. Standardized residuals are depicted on the upper part of the plot. The wave-like pattern in the residuals indicates model misfit. This misfit can also be seen from the way the fitted curve overestimated the number of hauled-out females at the close of the breeding season.

2.3 Corrected Censuses

There is room for improving the model, as described in [Condit et al. \(2007\)](#). Most problematic may be the underestimates produced by biased corrections factors. Yet, [Galimberti and Sanvito \(2001\)](#) reported this bias to be small: the difference between estimated and observed N_{max} was less than 5% of observed N_{max} , which is acceptable in a practical sense. A set of parameters for a 'new' harem was predicted from the posterior distribution and used to compute corrections factors for single-day censuses of females breeding between Cape Digby and Cape Molloy (≈ 80 km, Figure 1.5). As the Bayesian framework allows the incorporation and trickling down of uncertainties across levels, 95% credible intervals were accordingly computed for each census.

Thirty-two censuses, starting from 1952 and spanning 60 years, were available (CEBC CNRS database). They were usually performed within a week around the 15th of October. However, among these censuses, three were incomplete (in 1952, 1970 and 1984). In 1952 and 1984, a large and important part of the Courbet Peninsula was not sampled. These years were thus excluded from further analysis. The 1970 census missed a small part of the Courbet Peninsula, that around the permanent field station of Port-Aux-Français. This census is thus incomplete, but was nevertheless retained as the fraction of unrecorded females is proportionally small compared to the total number of females ($\approx 5 - 7\%$). Moreover, this missing fraction is smaller than the standard error of the corrected estimate. Also the original field report of the 1970 census was found in the Kerguelen scientific library while doing fieldwork in 2009. This report revealed a mistake in census dates for 1970 reported in previous works (for example [Guinet et al. \(1999\)](#)) that used data from secondary sources (for example [Pascal \(1981\)](#)). Since correction factors can have a dramatic influence on counts depending on whether the census was performed close to peak haul-out date or not, these mistakes in census dates resulted in a gross over-correction of the 1970 census in previous publications.

To assess the population trend in female Southern Elephant Seals breeding on the Courbet Peninsula, linear penalized-splines at fixed knot locations ([Gurriñ et al., 2005](#)) were used on the thirty corrected censuses of the Courbet Peninsula. This semi-parametric regression does not require any *a priori* assumption on the trend. However, as the posterior distribution of corrected estimates was sometimes heavily skewed, I subsampled 1,000 datasets from the posterior distributions of corrected estimates and analyzed them with Bayesian p-splines. The 1,000 results were then used to approximate the true posterior distribution. While this procedure actually ignores the uncertainty in estimating the parameters, this source of uncertainty is negligible compared to that due to correction factors. Posterior median and median absolute deviation are reported instead of posterior mean and standard deviation to account for the skewness in these corrected censuses.

2.3.1 Phenomenological shift

These data encompass censuses performed up to 60 years ago, but were corrected with estimates from the current population of Southern Elephant Seals. To assess whether a phenological shift has taken place, a small literature survey was performed to find estimates of female peak haul-out date (μ) and synchrony (σ). Five relevant publications (Rothery and McCann, 1987; Hindell and Burton, 1988; Boyd et al., 1996; Slip and Burton, 1999; Galimberti and Sanvito, 2001) reported Iteratively Weighted Least-Square estimates of N_{max}, μ, σ from five Subantarctic islands, including îles Kerguelen (Table 2.2), and covering the three currently recognized stocks of Southern Elephant Seals (Slade et al., 1998).

Island	Latitude	Longitude	N	Year
Kerguelen	49°30' S	69°30' E	2	1970-1971
Falkland	52°26' S	59°05' W	5	1995-1999
Heard	53°05' S	73°30' E	7	1949-1992
South Georgia	54°15' S	37°05' W	15	1951-1995
Macquarie	54°30' S	158°57' E	3	1959-1985

Table 2.2: Populations of Southern Elephant Seals for which published estimates are available. These estimates may correspond to different sites on these islands. Some sites were monitored many years.

For most estimates, standard errors were not reported and each estimate could not be weighted by its standard error in a small meta-analysis. Because estimates came from different islands, this factor was explicitly modelled in my analysis to avoid the potentially confounding effect of latitude (Galimberti and Boitani, 1999). I was specifically interested in the correlation between μ and σ within each island where females haul out, to compared it with my own estimate from data collected in 2008 and 2009. There was no correlation between μ and σ across different islands ($\rho =_{-0.35} 0.00_{0.38}$), but again there was a trend for a negative correlation within each island ($\rho =_{-0.96} -0.50_{0.32}$), suggesting that harems forming early in the breeding season were less synchronous than harems forming later. Older females tend to haul-out later in the season (Arnbom et al., 1997) and breeding experience could explain this a correlation. Embryo implantation is delayed in Southern Elephant Seals (Figure 1.4) and occurs at the close of the summer moult (Laws, 1960). Older, more experienced females may adjust to current environmental conditions at the end of moulting better than primiparous or inexperienced females, thus becoming more synchronized. Finally, estimates of peak haul-out date on îles Kerguelen for the 1970s ($_{13}18_{22}^{\text{th}}$ of October) and the 2000s ($_{13}15_{17}^{\text{th}}$ of October) are not different but the estimate for the 1970s has a large uncertainty.

2.3.2 Population Trend

Results from the spline analysis are depicted on Figure 2.4. The linear penalized-splines accounted for $35 \pm 17\%$ of the variance, and the smoothing parameter, λ , was large ($\lambda = 82 \pm 49$). After a large decrease (\approx one third) during the 1960-80s, the population is now stable.

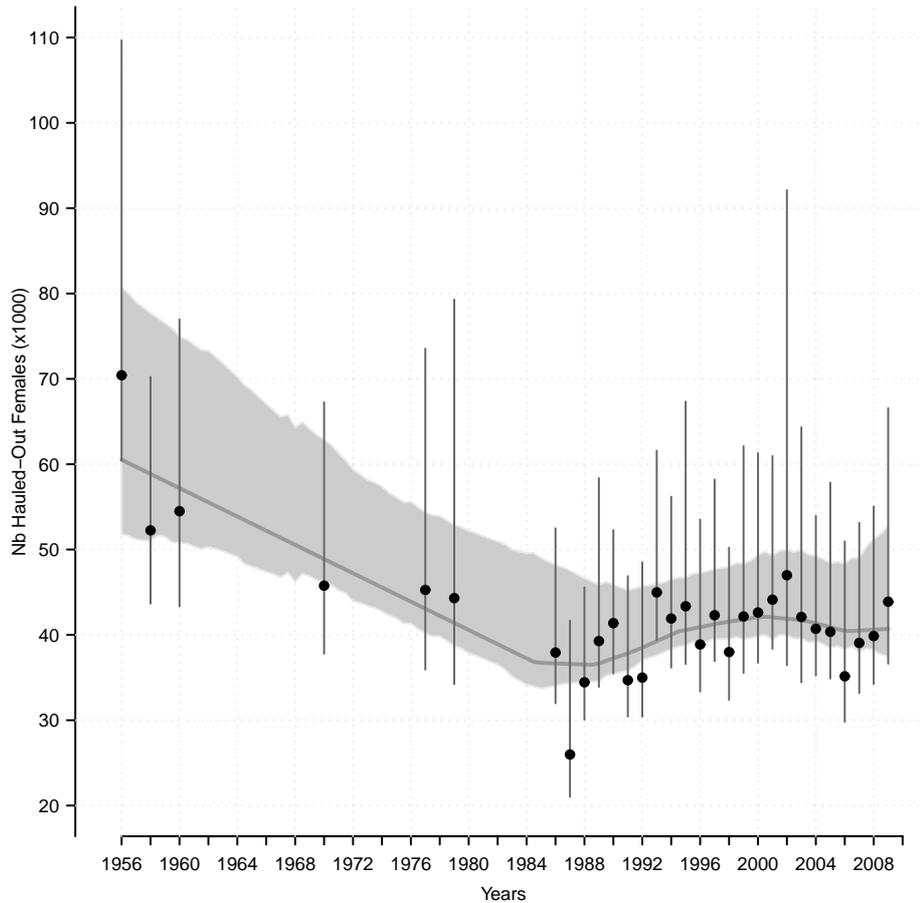


Figure 2.4: Population trend in female Southern Elephant Seals breeding on the Courbet Peninsula, îles Kerguelen since the 1950s. Posterior medians of breeding female counts, corrected for census date, along with their 95% CI are depicted. The grey envelope and the continuous darker grey line represent a 95% CI and the posterior median value of the trend respectively.

The Kerguelen population has been stable around 40,000 individuals over the last 20 years. However, the spline smoothness penalty was large, betraying oversmoothing. Model fit, as measured by the coefficient of determination, was also modest. This oversmoothing was a consequence of the large uncertainties in corrected estimates. Thus, oversmoothing may not be an issue here as most of the variation results from correction factors *per se*, and true biological variation, unless very large, may be veiled when correcting censuses. There was in fact a large decrease in Southern Elephant Seal numbers during the 1960-70s across several Subantarctic islands (Guinet *et al.*, 1999; McMahon *et al.*, 2005a). On îles Kerguelen, the present work suggests this decrease was of approximatively one third.

McMahon *et al.* (2005a) reviewed and listed 8 possible causes behind the population decrease of Southern Elephant Seals:

1. antropogenic disturbances when seals are ashore;
2. a male paucity preventing the fertilization of all females;
3. large-scale disease outbreaks;
4. population overshoot following the end of sealing activities;
5. increased juvenile predation by killer whales as a consequence of the reduction of their preferred preys (the great whales);
6. interspecific competition;
7. competition with fisheries; and
8. a large-scale regime shift in the Southern Ocean ecosystem.

Causal inference with observational data is fraught with pitfalls (Glymour, 1998). However, certain causes are more reasonable than others, and among the ones listed above, (1), (2) and (3) can be ruled out (McMahon *et al.*, 2005a). Causal explanations (4), (5) and (6) are unlikely to have triggered such a large and widespread decrease as the observed one. However, these hypotheses are hard to test given the paucity of data for the period of interest and the logistic difficulties associated with observing seals at sea. Finally, the last two hypotheses emphasize how resources became scarce in the Southern Ocean during the 1970s, either due to overexploitation by commercial fisheries (Ainley and Blight, 2009) or to a large-scale ecosystem regime shift (Weimerskirch *et al.*, 2003). Thus the most likely explanation for the observed decrease on îles Kerguelen is linked to the foraging of Southern Elephant Seals, which is apprehended through the use of stable isotopes in the next chapter.

Foraging Strategies

Contents

3.1 Foraging Locations	29
3.2 Integrating Stable Isotopes and Satellite Telemetry	33
3.2.1 Track Data Analysis	33
3.2.2 Temporal Resolution	33
3.2.3 Southern Ocean Isoscapes	37
3.3 Maternal Strategies	43
3.3.1 Fitness Proxy	43
3.3.2 Data Collection	44
3.3.3 Blood Stable Isotopes	44
3.3.4 Inferring Foraging Strategy	46
3.3.5 Environmental Conditions	53
3.4 Concluding Remarks	57

Section 3.3 is under revision after having been submitted to *Proceedings of the Royal Society Series B* :

Authier, M., Dragon, A., Richard, P., Cherel, Y. & Guinet, C. (in revision) O'Mother, Where Wert Thou? Maternal Strategies in the Southern Elephant Seal: a Stable Isotope Investigation.

3.1 Foraging Locations

For the Kerguelen population of Southern Elephant Seals, [Bailleul et al. \(2010\)](#) identified two main foraging zones using ARGOS location data: pelagic waters of the Polar Front (Figure 3.1) and oceanic waters around the Antarctic. Mesoscale features, such as fronts and eddies, structure and enhance primary productivity ([Bakun, 2006](#)). These fronts and eddies influence the spatial structure of prey fields and determine the preferred foraging grounds of oceanic top-predators ([Bost et al., 2009b](#)). The interfrontal zone, between the Polar Front and the Subtropical Front, is especially dynamic with locally productive eddies. South of the Polar Front, the vast Antarctic zone present important seasonal variations in sea-ice extent. The interactions between sea-ice extent and the local oceanographic conditions determine the dynamics of key Antarctic species such as krill ([Loeb et al., 1997](#)).

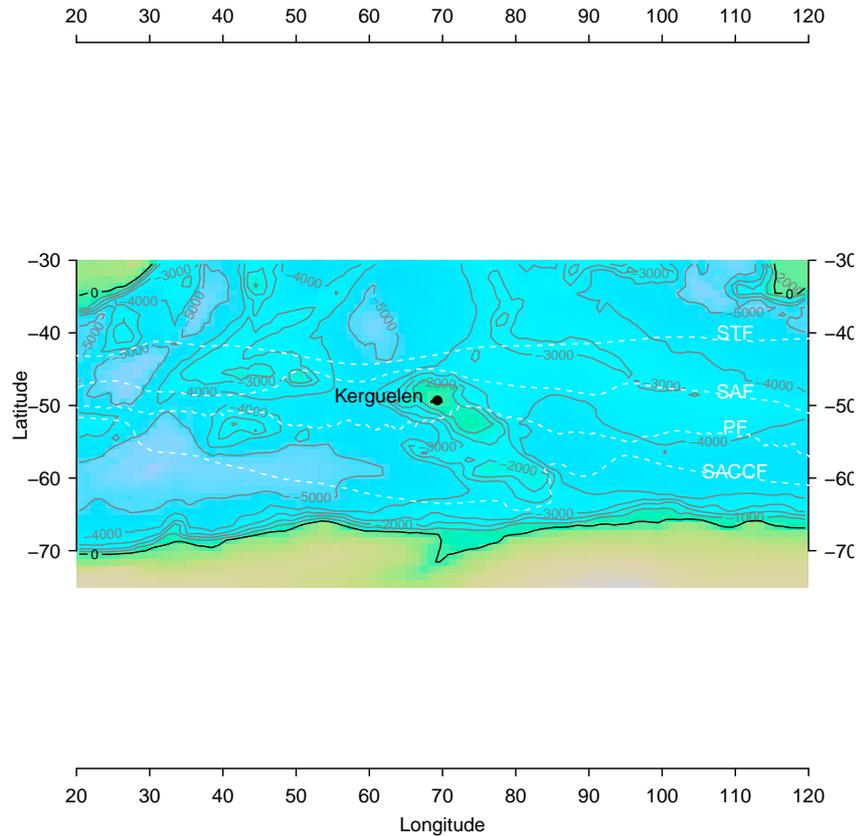


Figure 3.1: Frontal Structures around îles Kerguelen. White dashed lines symbolized frontal structures within the Southern Ocean: Southern SubTropical Front (SSTF), Sub-Antarctic Front (SAF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF) (Orsi et al., 1995). The Interfrontal zone corresponds to water masses between the SSTF and the SACCF. îles Kerguelen are also surrounded by a large continental Plateau, which harbours a large primary productivity.

The use of carbon stable isotopes to infer the foraging location of marine predators depends on the assimilation of preys with isotopically distinct values. While for terrestrial ecosystems, so-called isoscapes¹ can be mapped (for example [Hobson et al. \(1999\)](#); [Van Wilgenburg and Hobson \(2011\)](#)), there are comparatively fewer data to compile such maps for marine ecosystems ([Jaeger et al., 2010](#)). The latitudinal gradient in $\delta^{13}\text{C}$ observed in the Southern Ocean has been measured on suspended Particulate Organic Matter ([Bentaleb et al., 1998](#); [Trull and Armand, 2001](#)). The enrichment in $\delta^{13}\text{C}$ across trophic links is usually deemed negligible ([Kelly \(2000\)](#) but see [Rau et al. \(1984\)](#); [Caut et al. \(2009\)](#)). Yet the complex trophic relationships of the Southern Ocean biota (Figure 3.2) introduce uncertainties on the cumulative impact of even small enrichments between adjacent trophic levels. Directly assessing the relationship between the $\delta^{13}\text{C}$ values of predators and where they have foraged is thus desirable to establish the accuracy of isotopic data.

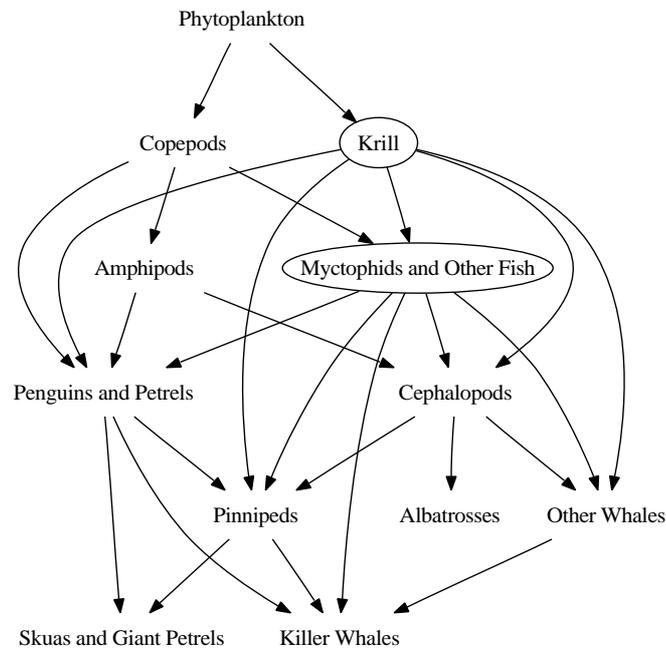


Figure 3.2: Simplified food web of the Southern Ocean marine ecosystem to illustrate the main relationships between different taxonomic groups and the importance of krill and myctophid fish (Modified from [Péron \(2011\)](#)).

¹Isoscapes are geographical regions with known differences in isotopic composition.

A priori, the $\delta^{13}\text{C}$ Antarctic signature is expected to be smaller than the $\delta^{13}\text{C}$ interfrontal signature (Rau et al., 1982; Cherel et al., 2007); the $\delta^{13}\text{C}$ interfrontal signature itself is expected to be smaller than the $\delta^{13}\text{C}$ Kerguelen Plateau signature because of the increased primary productivity on the Kerguelen Plateau (Blain et al., 2001; Michener and Kaufman, 2007; Cherel and Hobson, 2007). However, the large bloom over the Kerguelen Plateau is carried eastward by currents (Figure 3.3), forming a long plume that extends into oceanic waters of the Interfrontal Zone (Blain et al., 2001). Thus, large differences between the carbon isotopic signature of the Interfrontal zone and the Kerguelen Plateau are not likely and the following relationship with carbon isotopes may be expected: $\delta^{13}\text{C}_{\text{Antarctic}} < \delta^{13}\text{C}_{\text{Interfrontal}} \leq \delta^{13}\text{C}_{\text{Plateau}}$.

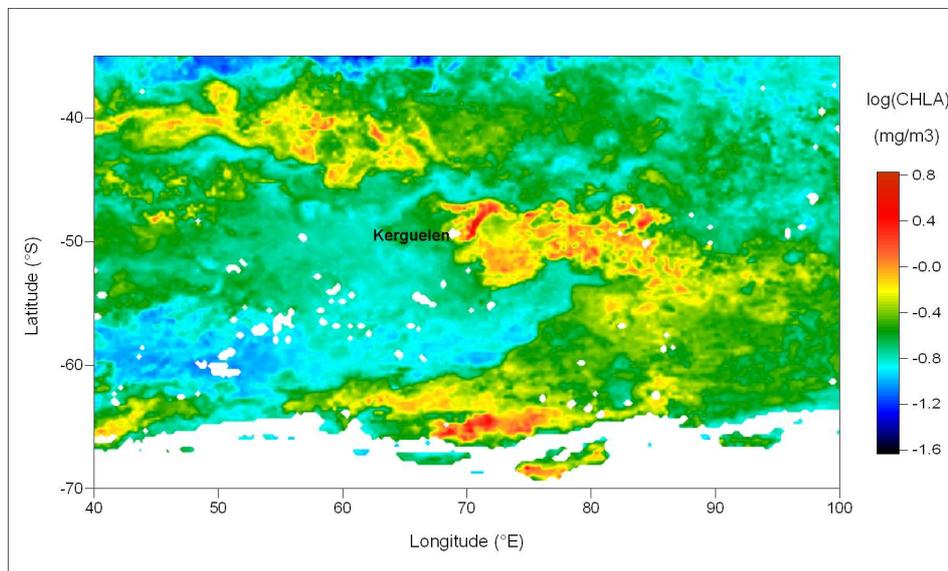


Figure 3.3: Chlorophyll heatmap of the Southern Ocean around îles Kerguelen during the summer phytoplankton bloom. The influence of the highly productive Kerguelen Plateau extend eastward in a long plume (Credits C. Péron).

3.2 Integrating Stable Isotopes and Satellite Telemetry

From 2003 to 2011, 80 Southern Elephant Seals were captured on îles Kerguelen at the end of the breeding (October-November) or moulting (February to April) seasons. They were anaesthetised using a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100) which was injected intravenously (McMahon et al., 2000b). Before logger deployment, seals were blood sampled and weighed. Data loggers were then glued quick-setting epoxy (Araldite AW 2101) on seals' head after cleaning the hair with acetone. Deployed tags were satellite-relayed-data devices that collected and transmitted Argos locations during the seals' post-breeding or post-moulting trips at sea. Upon returning to îles Kerguelen, 26 animals were recaptured and blood sampled but only 19 were weighed. Blood was collected from the dorsal venous sinus using 90×1.2 mm needles. Seventy percent ethanol was added for sample preservation before laboratory analysis (see Appendix C).

3.2.1 Track Data Analysis

To take into account measurement errors, Argos locations from the 26 complete tracks were analyzed using a switching-state-space model (Jonsen et al., 2003; Patterson et al., 2008). State-space models were implemented in winBUGS as part of the Ph.D. thesis of Anne-Cécile Dragon. Whole details are provided in Dragon et al. (2011a). Here, the primary aim was to standardize location data and to take into account satellite measurement errors. These tracks are represented on Figure 3.4).

3.2.2 Temporal Resolution

To assess the temporal resolution that $\delta^{13}\text{C}$ can provide to infer the foraging location of Southern Elephant Seals, I used the complete track of 26 individuals which were blood sampled both upon tag deployment and retrieval. The mean latitude of a track² was computed for each seal before its tag was retrieved. Because blood turn-over is a continuous physiological process, this computation was done for each cumulative month before haul-out, that is I computed the mean latitude of the foraging trip for the last month, the two last months, and so forth, before a seal came back on land. We then sequentially correlated this mean latitude with the $\delta^{13}\text{C}$ value obtained upon tag retrieval. We expected any significant relationship between latitude and $\delta^{13}\text{C}$ to gradually wear off because of blood turn-over. The lag at which this significant relationship disappears would then indicate the temporal resolution of blood $\delta^{13}\text{C}$.

²A more sophisticated approach using a switching-state-space model to distinguish between foraging modes, intensive (low speed, increased sinuosity) and extensive (high speed, decreased sinuosity), yielded similar results when I used only the mean latitude of intensive foraging locations.

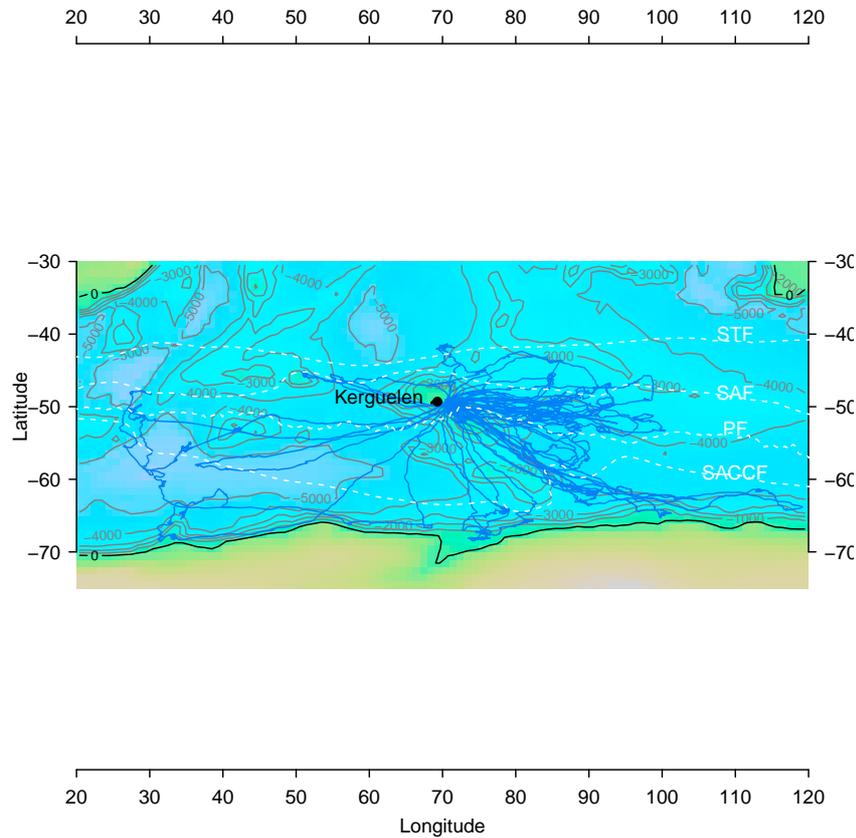


Figure 3.4: Satellite tracking of Southern Elephant Seal breeding on îles Kerguelen. 26 ARGOS tracks are represented (solid lines) to illustrate the different strategies: seals mainly forage close to the Antarctic or in pelagic Polar Frontal waters. Juvenile males also use extensively both the Antarctic Shelf (depth < 500 metres, (Bailleul et al., 2007a)) and the Kerguelen Plateau (depth < 1000 metres, (Bailleul et al., 2010)). White dashed lines symbolized frontal structures within the Southern Ocean: Southern SubTropical Front (SSTF), Sub-Antarctic Front (SAF), Polar Front (PF) and Southern Antarctic Circumpolar Current Front (SACCF) (Orsi et al., 1995). The Interfrontal zone corresponds to water masses between the SSTF and the SACCF.

Tissue isotopic turn-over scales with body mass (Carleton and Martínez del Rio, 2005), and because body mass correlates with body length, which is easier to measure in the field ($\rho = 0.87$, $p < 0.001$), I included body length as a covariate in the models. We also included whether a seal performed a post-moult or post-breeding trip as a covariate. Sex was not included as it was confounded with trip type: equipped juvenile males were always instrumented at the end of the summer moult.

Month before haul-out	N	$\bar{\theta}$	se	z_{score}	p_{value}
1	26	1.49	0.18	8.3	< 0.01
2	26	1.69	0.72	2.4	< 0.01
3	26	1.66	0.71	2.3	< 0.01
4	13	1.65	0.15	11.0	< 0.01
5	7	0.90	0.41	2.2	< 0.05
Whole Trip	26	2.04	0.29	7.0	< 0.01

Table 3.1: Regression coefficients for the relationship between blood $\delta^{13}C$ value and latitude in Southern Elephant Seals.

There was a statistically significant relationship between $\delta^{13}C$ and mean foraging latitude up to 4 months before hauling-out ($p < 0.001$, Table 3.1). Small sample size prevented to draw conclusions about this relationship beyond 4 months before haul-out. In fact, there was a statistically significant relationship $\delta^{13}C$ and the mean latitude of the *whole trip* (Figure 3.5 and Table 3.1). Blood $\delta^{13}C$ value thus seemed to reflect the whole previous trip of a Southern Elephant Seal. In contrast, when longitude was included in the regression, its coefficient never reached statistical significance and was close to 0.

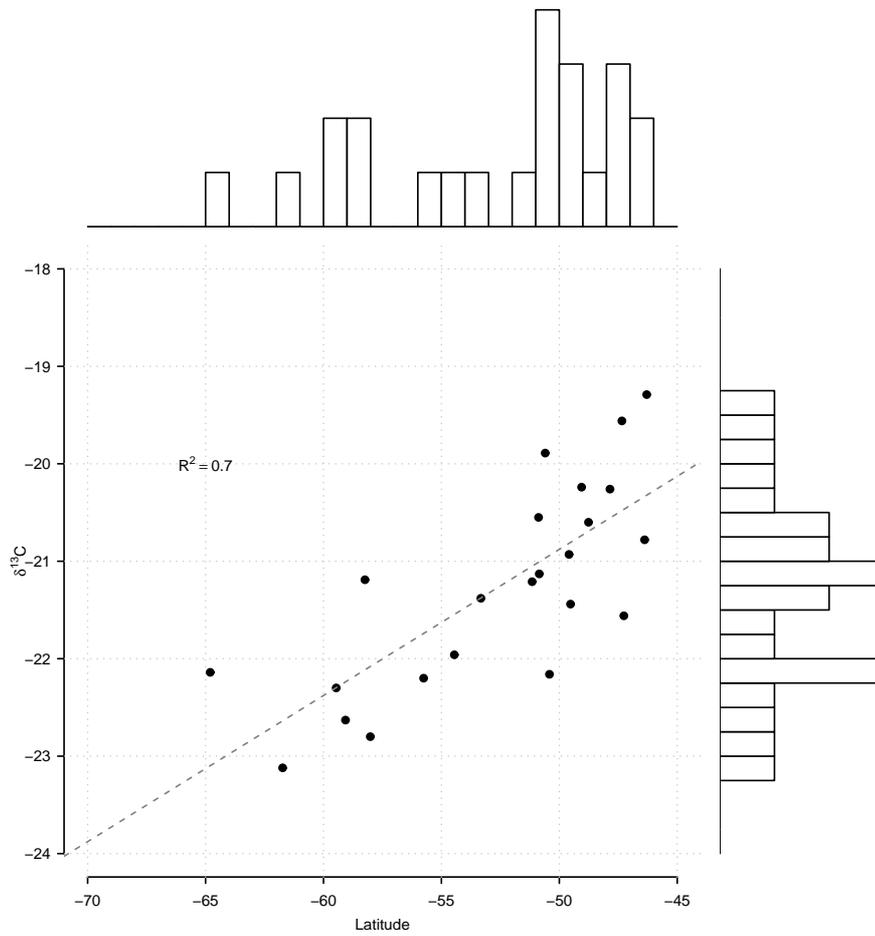


Figure 3.5: Relationship between the mean latitude of a foraging trip and blood $\delta^{13}\text{C}$ value in Southern Elephant Seals from îles Kerguelen. Marginal distributions are depicted on the margins of the plot.

Upon assessing the temporal resolution of $\delta^{13}\text{C}$, I then included the $\delta^{13}\text{C}$ value corresponding to tag deployment, that is the value reflecting the previous foraging trip to assess foraging fidelity (denoted $\delta^{13}\text{C}_{t-1}$). If seals are faithful to a foraging strategy, I can expect a slope of 1 between $\delta^{13}\text{C}_t$ and $\delta^{13}\text{C}_{t-1}$, and latitude to lose its statistical significance.

When $\delta^{13}\text{C}_{t-1}$ was included in the regression model, the relationship with latitude disappeared ($\bar{\theta}_{se} = 0.01_{0.26}$, $p = 0.97$). The coefficient of regression for $\delta^{13}\text{C}_{t-1}$ was $\bar{\theta}_{se} = 0.987_{0.005}$, which was statistically different from either 0 ($p < 0.001$) or 1 ($p = 0.004$). Whether $\delta^{13}\text{C}_{t-1}$ was included or not, trip type (post-moult *vs* post-breeding) was a statistically significant factor: post-moult trips were associated with smaller $\delta^{13}\text{C}$ values. However, this factor is confounded with sex. It is likely that males foraged in higher latitudes waters than females during the austral winter: Bailleul et al. (2007a) showed how tagged males ventured into the Antarctic pack-ice while females stuck to the marginal sea-ice zone. Yet, even when males were removed from the sample this effect persisted. It may reflect that at the end of the summer, all sea-ice has melted and the animals may wander further south than during spring.

3.2.3 Southern Ocean Isoscapes

Because the temporal resolution of $\delta^{13}\text{C}$ was at least 4 months and because seals were faithful to a strategy, I analyzed isotopic data collected upon tags deployment. Using track data, I was able to determine whether a seal foraged predominantly on the Kerguelen Plateau, in the Interfrontal zone or in Antarctic waters for 80 equipped seals whose foraging track was not necessarily complete (thus assuming the observed part to be representative of the whole track). We used Linear Models to determine the isotopic signature of these three water masses (Plateau, Interfrontal and Antarctic), and tested the effect of sex, body length, trip type (post-moulting versus post-breeding trips), foraging location and all interactions between sex and other covariates. Since males foraged over the Antarctic Shelf or Kerguelen Plateau (Bailleul et al., 2007a, 2010), statistically significant interactions between sex and foraging location may be expected.

This data set, while large with respect to biologging studies, is not balanced: there was twice as much females (54) as males (26), only 5 males were tracked over a post-breeding trip, and only one female foraged over the Kerguelen Plateau. This imbalance means that some covariates (or combination thereof) are largely correlated. To circumvent this issue, variable selection was performed using spike-and-slab regression (Ishwaran and Rao, 2005; Ishwaran et al., 2010)³. My aim here was to select the most important factors affecting the blood $\delta^{13}\text{C}$ value of Southern Elephant Seals. The stability of the selected variable was further checked by cross-validation: a value of 1.00 means that this variable was always selected during the cross-validations because it helped minimizing prediction mean squared error. The original data set was randomly split in two halves, one for training and the other one for prediction, and this procedure was repeated 40 times. Results are summarized in Table 3.2 and Figure 3.6.

Parameter	Posterior Mean		OLS	Stability
	Standardized	Scaled		
Antarctic	-0.77	-1.7	-2.0	0.900
Trip	-0.64	-1.3	-1.6	0.800
Male \times Snout-to-Tail Length	-0.38	-0.9	-1.9	0.675
Plateau	0.08	0.2	0.2	0.675
Male \times Interfrontal	0.07	0.3	-0.1	0.650
Male \times Plateau	0.10	0.1	NA	0.600
Snout-to-Tail Length	0.20	0.4	-0.1	0.500
Male	0.03	0.1	0.1	0.475
Male \times Antarctic	-0.05	-0.2	-0.2	0.475
Male \times Trip	0.02	0.1	0.4	0.475

Table 3.2: Spike-and-Slab Regression Summary. Regression coefficients for 10 variables/interactions are reported relative to a baseline taken as the $\delta^{13}\text{C}$ value of a female seal of average Snout-to-Tail length of 250 cm that foraged in Interfrontal waters ($\delta^{13}\text{C} = -20.2 \text{‰}$). Standardized coefficients allow to assess the relative importance of each variable, while the scaled one are useful for predictions. For example, a seal that foraged into Antarctic waters has a carbon signature of $-20.2 - 1.7 = -21.9 \text{‰}$. Snouth-to-Tail Length was standardized following Gelman (2008): the scaled regression coefficient correspond to the value for being 50 cm larger than average. OLS stands for the 'Ordinary Least Square' regression coefficient and are reported to illustrate shrinkage.

³The expression *spike-and-slab* refers to a mixture prior for the regression coefficients: this prior is made up of a diffuse and vague distribution (the slab) and a degenerate distribution at 0 (the spike). This spike ensures that some coefficients are effectively shrunk to 0, thus achieving variable selection.

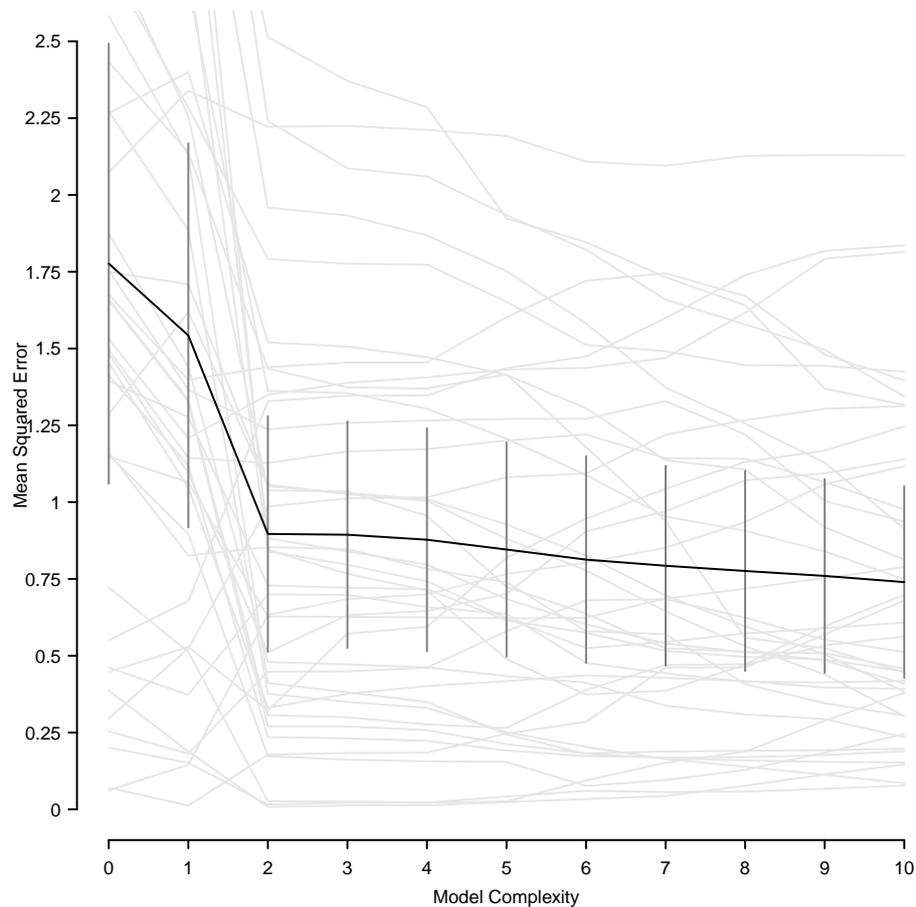


Figure 3.6: Cross Validation procedure to select model complexity. The greatest gain in minimizing prediction mean-squared error (MSE) was achieved with two covariates: Antarctic foraging and trip type. Additional covariables only marginally reduced MSE, and were selected in less than 80% of the 40 cross-validations. Grey lines in the background correspond to the MSE of each of the 40 cross-validations. Mean MSE and 95% confidence intervals are depicted in black.

The stability analysis suggested that the two most important variables were whether a seal foraged in Antarctic waters and the trip type (Figure 3.6). As expected, Antarctic foraging was associated with a smaller $\delta^{13}\text{C}$ value than foraging in the Interfrontal zone. As previously, post-moult trips were associated with smaller $\delta^{13}\text{C}$ values than post-breeding trip, but in this case, sex was not confounded with trip type (5 juvenile males out of 26 were instrumented for a post-breeding trip). The post-moult trip can last 7 months while the post-breeding one lasts a shorter 2 months (Figure 1.4). Breeding females lose on average one third of their body mass through lactation (Arnbom et al., 1997), but seals take 3 weeks to reach Antarctic waters (Biuw et al., 2007). Thus foraging in Antarctic waters may not be an option for most females that need to restore their condition before moulting.

There were no other variables with a stability greater than 0.8 but the next most stable variables were whether seals foraged on the Kerguelen Plateau and an interaction between sex and body length. The carbon isotopic signature of the Kerguelen Plateau is very similar to that of the Interfrontal zone being enriched by an estimated 0.2 ‰. This difference is small and given the residual standard deviation of 0.8 ‰, the Kerguelen Plateau and the Interfrontal $\delta^{13}\text{C}$ signatures are indistinguishable with my data. However the estimated difference with a modest data set is still plausible both in size and magnitude: the Kerguelen Plateau is expected to have an enriched signature in carbone isotopes due its large productivity (Blain et al., 2001). It is also noteworthy that the estimated difference has not been shrunk toward 0 with the spike-and-slab prior. The modest size of my data may have prevented an unambiguous assessment of the Kerguelen Plateau signature compared to the Interfrontal Zone signature.

The interaction between sex and body length suggests that bigger males had a more negative blood carbon isotopic value (-0.9‰ for a 3 metres-long seal compared to an average 2.5 metres-long one⁴). This interaction is plausible: these seals have an indeterminate growth (Laws, 1953; McLaren, 1993; Bell et al., 2005), and body length can thus be used as a proxy for age. This interaction term could reflect a tendency for older male to forage at higher latitudes compared to other individuals (juvenile males or females).

⁴The posterior mean of this coefficient is considerably shrunk toward 0 compared to the OLS estimate. The latter is overly influenced by a single datum with high leverage corresponding to the largest male (3.8 metres long) with a blood $\delta^{13}\text{C}$ of -22.2‰ .

Foraging in Antarctic waters and elsewhere is characterized by a relative difference in isotopic value of 1.7‰ for whole blood. Jaeger et al. (2010) studied Southern Ocean isoscapes with blood plasma of Wandering Albatrosses (*Diomedea exulans*) and found that a difference of 10°S of latitude was associated with a difference of 3.1‰. Considering Antarctic waters to lie at -60°S and îles Kerguelen at -50°S, I may have expected a difference of 3.1‰ in Southern Elephant Seal too. However, the estimate I found is almost half of that (Tables 3.1 & 3.2). This discrepancy may result from the different turn-over rates of whole blood and blood plasma, the huge different size in the compared species, extrapolation⁵, or type-M errors⁶.

With the spike-and-slab regression I used, overestimation is less an issue because of shrinkage (see Appendix C). Four data points with high leverage are visible on Jaeger et al. (2010)'s Figure 2, and their data show 3 distinct clusters. The Southern Elephant Seals is comparatively smoother (Figure 3.5), but could also be compatible with a slight non-linear relationship between latitude and $\delta^{13}\text{C}$: a steeper slope may be observed for low latitudes in agreement with Francois et al. (1993). Francois et al. (1993) found a very steep negative relationship between Particulate Organic Matter $\delta^{13}\text{C}$ and latitudes between -40°S and roughly -45°S, followed by a less steep relationship below -45°S. Very few animals among the 80 tagged ones went into subtropical waters, and I may deem this strategy to be minor. A linear relationship between the range of latitudes covered by Southern Elephant Seals and $\delta^{13}\text{C}$ thus seems reasonable. In contrast, Wandering Albatrosses studied in Jaeger et al. (2010) flew north of -45°S of latitude which, in light of the results from Francois et al. (1993), suggests the slope they found may overestimate the relationship between $\delta^{13}\text{C}$ and higher latitudes. Finally, I note that my estimate is in agreement with that of Bentaleb et al. (1998) who measured the $\delta^{13}\text{C}$ values of Particulate Organic Matter between -40° South and -50° South, in the vicinity of îles Kerguelen and found an average decrease of ≈ -2 ‰.

⁵Among the 45 Wandering Albatrosses studied by Jaeger et al. (2010), none went as south as -60°S.

⁶Type-M errors are errors in the estimation of the magnitude of an effect: if an effect is statistically significant, it's likely to be an overestimate (Gelman and Tuerlinckx, 2000; Whittingham et al., 2006). It is sometimes referred to as the 'Winner's Curse'. See the blog entry <http://andrewgelman.com/2011/09/the-statistical-significance-filter/> of the statistician Andrew Gelman.

In summary, the present analysis shows how the carbon isotopic signature of Antarctic waters is reflected in Southern Elephant Seal tissues, thus allowing one to infer where a seal has been feeding. Whereas an Antarctic signal was statistically detectable, it seems not possible to distinguish the Kerguelen Plateau $\delta^{13}\text{C}$ signature from that of the Interfrontal zone with my current data. This may be a consequence of the important productivity of the Kerguelen Plateau that is carried away eastward in a long plume that extends in oceanic waters (Blain et al., 2001) (Figure 3.3), and of the capital breeding strategy of Southern Elephant Seals. This latter fact combined with the large body size of seals means that seals store large amount of resources: the recovered isotopic signal that may be considerably smoothed out of small variations, which can explain why the $\delta^{13}\text{C}$ signatures of the Kerguelen Plateau and of the Interfrontal Zone were not distinguishable with my current data, probably too modest to estimate precisely small differences.

3.3 Maternal Strategies

3.3.1 Fitness Proxy

The existence of several foraging strategies in the Kerguelen population begs the question of the individual fitness consequences of each strategy: do seals foraging in Antarctic waters have a different fitness than those foraging in the Interfrontal Zone? Despite being a key ecological and evolutionary concept, biological fitness (or the currency of natural selection) is difficult to define both operationally (Link et al., 2002; Metcalf and Parvard, 2006; Brommer et al., 2002, 2004) or philosophically (Ariew and Lewontin, 2004; Matthen and Ariew, 2002; Rosenberg and Bouchard, 2010). The definition adopted here is that biological fitness is a measure of the propagation rate of genotypes into future generations (Link et al., 2002), which emphasizes both the ability of organisms to survive long enough to reproduce, and the ability to contribute offsprings that are subsequently recruited into the population.

Survival and reproduction are thus two important components of biological fitness. In the population of Southern Elephant Seals on îles Kerguelen, the current study design does not allow to individual identify seals, and thus to assess their survival. However, elephant seals are capital breeders, meaning resources acquisition and expenditure for reproduction are separated in time (and space) (Jönsson, 1997). Females forage and accumulate energy stores for ≈ 7 months (Figure 1.4) before hauling-out in the Austral spring for giving birth to single pup. Twinning is extremely rare in this species and a single pup can triple its mass within the three weeks of maternal attendance (Arnbom et al., 1997). Resources that a female may accumulate during the post-moult foraging trip are crucial for her reproductive success: weaning mass correlates positively with juvenile survival in Southern Elephant Seals (McMahon et al., 2000a).

A pup weaning mass may thus be viewed as a proxy of the reproductive fitness of a breeding female. How large is a pup upon weaning reflects the ability of a female to extract resources from the environment. That there is individual variability in foraging strategy (Antarctic, Interfrontal or Kerguelen Plateau) may reflect an underlying variation in reproductive fitness among females. In other words, does foraging in Antarctic or Subantarctic waters pay-off differently in terms of stored energy? We can assess the effect of maternal foraging strategies on pup fitness by looking for relationships between a pup weaning mass and its blood isotopic ratio. Ducatez et al. (2008) showed how the blood $\delta^{13}\text{C}$ value of pups, which are easy to handle and to weigh, accurately reflected that of their cow. Using carbon stable isotopes, I may then infer maternal foraging grounds before hauling-out, and evaluate how this affects pup weaning mass. *A priori*, the Antarctic strategy seems more profitable for females given the observed gradient of increased pup weaning mass with latitude (Burton et al., 1997).

3.3.2 Data Collection

Data on pup weaning mass and blood sampling took place during the austral spring (September–November) of 2006–2009 on the Courbet Peninsula, îles Kerguelen. Except in 2007 due to logistics, a cohort of ≈ 200 pups was monitored daily from birth to weaning (Table 3.3). Each pup was individually marked upon birth on the trailing edge of one hind-flipper with a numbered plastic tag (Dalton Rototag, Nettlebed, UK), which was removed upon weaning. Before weaning, pups are within harems and defended by their mother from other females. As soon as a female leaves a harem, her pup is expelled by the other females and hangs for some days around this harem. Because the pups were tagged at birth, and because harems were daily checked, a weaned pup was spotted within 12–24 hours of its mother departure time. When found outside a harem, any marked pup was immediately captured, weighed and blood sampled. Blood was collected from the dorsal venous sinus using 90×1.2 mm needles. Seventy percent ethanol was added for sample preservation before laboratory analysis (see Appendix C). Body weight was measured with a weighing-scale with a precision of 0.1 kg in 2006–2008, but of 2 kg in 2009. This measurement error was taken into account in subsequent analyses.

Year	N	Mean	Median	Std Dev.	Skewness	Kurtosis
2006	193	105	104	19	0.03	−0.29
2007	57	106	106	19	0.08	0.27
2008	202	110	114	23	−0.25	0.02
2009	234	111	112	23	−0.14	−0.18
2006–2009	686	109	110	22	−0.11	−0.13

Table 3.3: Summary statistics of weaning mass (kg) of pups from îles Kerguelen. Bowley’s skewness coefficient, which varies between -1 and 1 is reported (Kim and White, 2003). The kurtosis estimator is computed according to An and Ahmed (2008) (their $\hat{\gamma}^{N^2}$), with the value 0 corresponding to the kurtosis of normal distribution. Both the skewness and kurtosis coefficients are dimension-less.

3.3.3 Blood Stable Isotopes

Carbon isotopic ratio for pups ranged from -23.9 to -18.8 ‰ with a mean value of -21.1 ‰, while those of nitrogen ranged from 10.1 to 12.8 ‰ with a mean value of 11.4 ‰. Variations in both carbon and nitrogen isotopic values were small: the absolute coefficient of variation was less than 5% for both isotopes. Across years, the distribution of $\delta^{15}\text{N}$ was very stable (except for 2007 due to small sample size). Distributions of $\delta^{13}\text{C}$ were comparatively more variable (larger yearly deviations from the overall median, Figure 3.7) but the magnitude of deviations from the overall mean was small (< 0.5 ‰ for all years).

Ducatez et al. (2008) evidenced linear relationships between a pup's blood carbon isotopic signatures and those of its mother: the mean predicted isotopic ratios for breeding females were $-21.4 \pm 0.1 \text{ ‰}$ and $10.1 \pm 0.1 \text{ ‰}$ for carbon ⁷ and nitrogen ⁸ respectively.

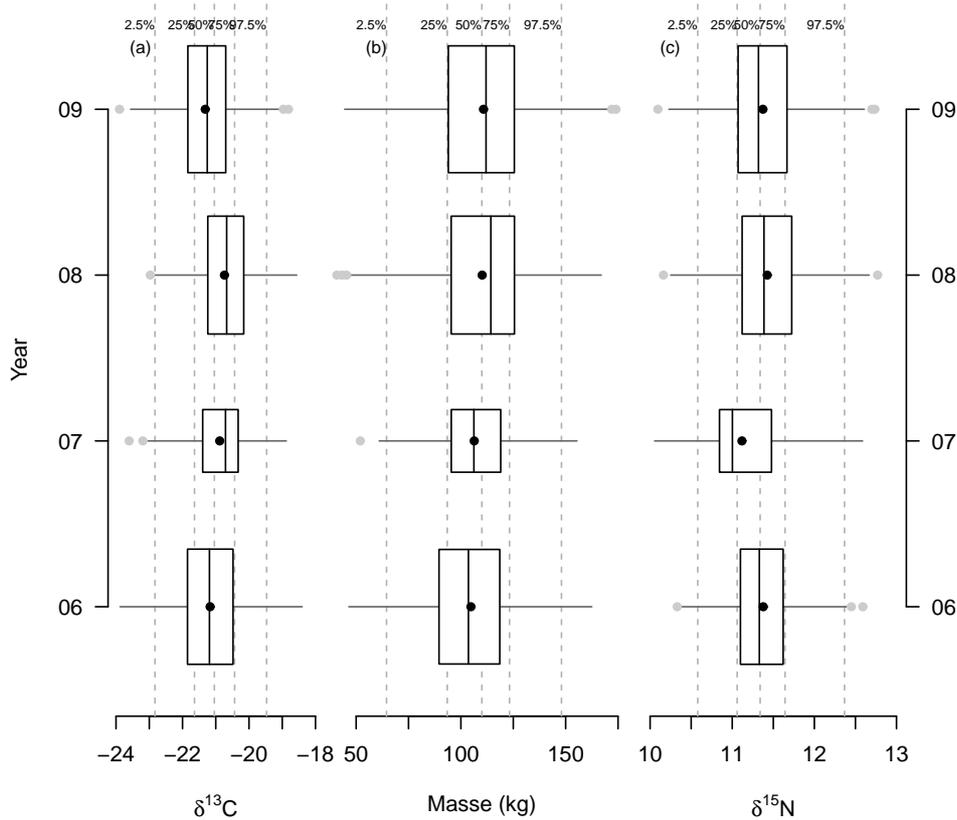


Figure 3.7: Tukey plots of the distributions of blood carbon (a), nitrogen (c) isotopic values and (b) weaning mass of Southern Elephant Seal pups from îles Kerguelen. Areas inside a box are proportional to the square root of sample size and represent 50% of the data for a given year. Black points within each box symbolize the mean isotopic signature for a given year. Grey points highlight outliers which were defined as in Dümgen and Riedwyl (2007). Dotted lines in the background show percentiles of the whole data set. These plots show the little between-year variation observed in the data.

$${}^7\delta^{13}\text{C}_{\text{Female}} = 0.4 + 1.0 \times \delta^{13}\text{C}_{\text{Pup}}$$

$${}^8\delta^{15}\text{N}_{\text{Female}} = 4.7 + 0.4 \times \delta^{15}\text{N}_{\text{Pup}}$$

3.3.4 Inferring Foraging Strategy

Both Skewness and kurtosis of the distribution of pup weaning mass tended to be negative, which may be suggestive of a mixture of two distributions (Figure 3.8 and Table 3.3, (Darlington, 1970; Hilderbrand, 1971)). Such a mixture of two distributions could reflect the two main foraging strategies of females⁹. We thus hypothesized weaned pups to form an heterogeneous aggregate of small and large individuals. We further modelled weaning mass, which was not normally distributed (Figure 3.8), as a mixture of two normal distributions¹⁰:

$$\text{Mass}_i = (1 - p_i) \times (\bar{\text{Mass}}_1 + \text{Sex}_1 + \eta_{\text{Year},1}) + p_i \times (\bar{\text{Mass}}_2 + \text{Sex}_2 + \eta_{\text{Year},2}) + \varepsilon_i \quad (3.1)$$

where $\bar{\text{Mass}}_2 > \bar{\text{Mass}}_1$; p_i ($1 - p_i$) denotes the probability for a pup i to belong to the latent group of large (small) weanlings, and ε_i denotes the residuals which are assumed to follow a normal distribution of mean 0 and variance $\sigma_{\text{residual}}^2$. The $\eta_{\text{Year},k \in (1:2)}$ are drawn for a normal distribution of mean 0 and variance $\sigma_{\text{Year},k \in (1:2)}^2$.

Equation 3.1 above defines a Mixture Model. This model has varying intercepts for each component: between-year variation is thus taken into account (the $\eta_{\text{Year},k \in (1:2)}$) and allowed to be different for each component. If each component of the mixture maps to a foraging strategy, then I can expect different environmental variation between the Interfrontal Zone and the Antarctic. Likewise, sex differences may be expected given the extreme sexual dimorphism in this species. The group membership of each pup i is not directly observed (this is too late since pregnant females were at sea), but it can be conceptualized as missing data to be estimated from their blood stable isotopic values¹¹:

$$\text{robit}(p_i) = \text{Intercept} + \delta^{13}\text{C}_i + \delta^{13}\text{C}_i^2 + \delta^{15}\text{N}_i + \delta^{15}\text{N}_i^2 + \text{Weaning Date}_i \quad (3.2)$$

where the robit is a robust link function (Liu, 2004). Other link functions (probit and logit) were initially considered but led to convergence problems¹². The robit corresponds to the cumulative distribution function of a Student distribution with 7 degrees of freedom and scale parameter 1.5484, chosen to closely mimic a standard logistic distribution (Liu, 2004). In contrast to clustering methods such as *k-means*, this model accounts for the uncertainty in assigning a pup to belong to one latent group or the other.

⁹Because females do not forage very much on the Kerguelen Plateau (Bailleul et al., 2010), the focus is here on the Interfrontal Zone.

¹⁰A simpler regression model with no mixture had virtually not predictive power ($R^2 = 0.07$) even though all the considered covariates were statistically significant at the 5% level.

¹¹We previously showed that Snout-to-Tail Length is not a strong predictor of foraging strategy for females

¹²Hence the choice of the robit to remedy these convergence issue. The idea here was not to use a 'fancy' link function for the sake of generalizing familiar estimators (Achen, 2002).

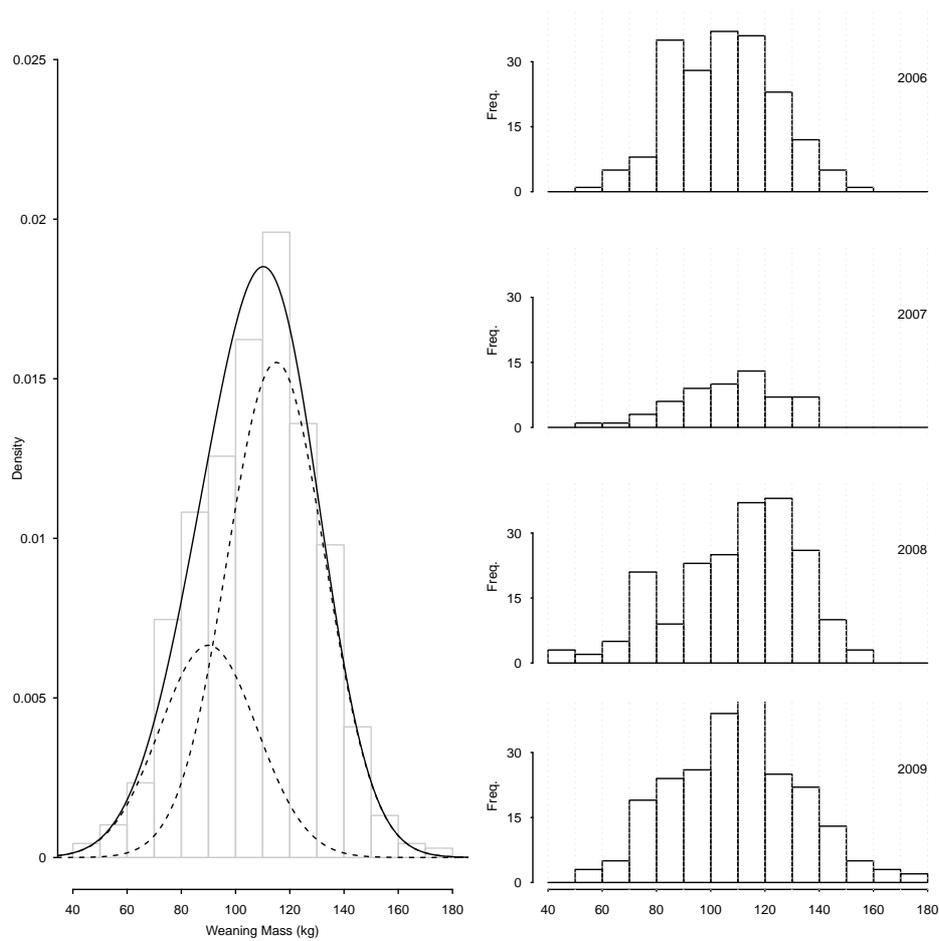


Figure 3.8: Distribution of the raw weaning mass data. The left panel shows the whole dataset (grey bars in the background) along with a two-component mixture of Gaussian distributions that reproduces the skewness and kurtosis of the observed data. The right panel shows the same data stratified by year (on a frequency scale).

Squared values of blood isotopic values in Equation 3.2 allowed for a non-linear functional response, whose appropriateness was checked with splines in a preliminary analysis. For example, a concave function of $\delta^{13}\text{C}$ may be interpreted as the Interfrontal Zone being a highly profitable foraging zone for females as they would transfer more energy to and wean a larger pup compared to females that may have forage at either higher or lower latitudes. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were included as covariates since they did not greatly correlate ($\rho =_{0.25} 0.32_{0.39}$). Weaning date was included as (1) it was not largely correlated to any other covariates, and (2) it is a loose proxy for maternal age: older (and larger) females haul-out later than young (and smaller) ones (Kirkman et al., 2004). Ducatez et al. (2008) found a statistically significant positive correlation between weaning date and $\delta^{13}\text{C}$, but the estimated effect size was very small ($\rho = 0.14$) and cannot trigger multi-collinearity issues.

Pup snout-to-tail body length (STL), although recorded on the field, was not included as weaned pups are still growing. At weaning, the arrow of causality points both from STL to mass and from mass to STL: STL is an intermediate outcome and should not be 'controlled for' (Green, 2001). Weaning STL and mass were largely correlated ($\rho =_{0.58} 0.63_{0.67}$), and the distribution of STL was asymmetric and similar to that of weaning mass (data not shown).

Modelling weaning mass as in Equation 3.1 accounted for nearly one-third of the observed variability. All considered predictors of (latent) group membership as in Equation 3.2 were important (Figure 3.9). Carbon isotopic value was a strong predictor of group membership, but in a non-linear way. Pups with either the largest or smallest blood $\delta^{13}\text{C}$ were very likely to have a large weaning mass, compared to pups with an intermediate value. In contrast, a greater $\delta^{15}\text{N}$ consistently depressed the probability of a pup to have a large weaning mass. Finally, weaning date had a modest positive effect: pups weaned later in the season were also more likely to have a larger weaning mass. This last relationship was expected since older females tend to haul-out later than young ones (Arnbom et al., 1997; Kirkman et al., 2004); being more experienced and larger, they can store more energy to transfer to their pup.

These data thus supported the idea of Southern Elephant seal weanlings being an heterogeneous aggregate: about $_{17}29_{40}\%$ of weanlings had an average mass of $_{82}89_{99}$ kg, while the remaining $_{60}71_{83}\%$ had an average mass of $_{107}115_{24}$ kg (Figure 3.8). Given that an extra 5 kg may sustain a fasting pup for ten days at sea (McMahon et al., 2000a), this difference is biologically significant. The mixing proportions were relatively stable across years with $_{56}70_{84}$, $_{53}73_{88}$, $_{64}76_{86}$ and $_{53}67_{81}\%$ of large pups in 2006, 2007, 2008 and 2009 respectively.

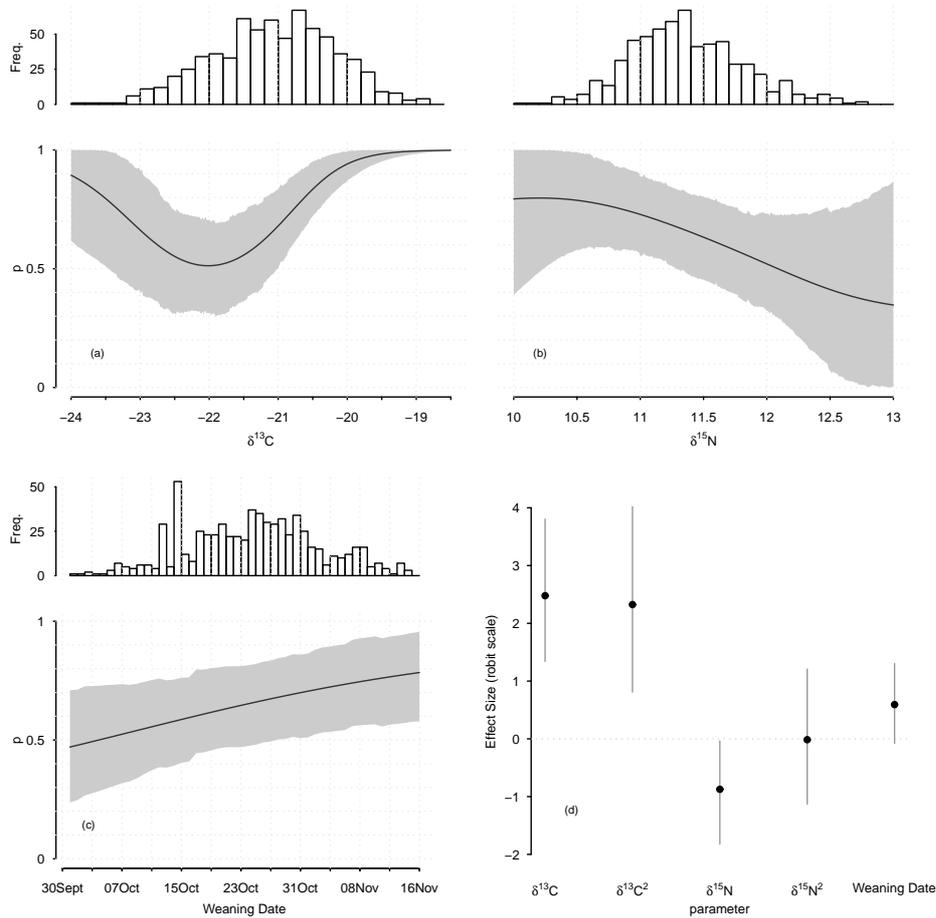


Figure 3.9: Graphical representation of the robit regression coefficients for predicting latent group membership. Carbon (panel *a*) and nitrogen (panel *b*) isotopic signatures had a significant effect on predicting whether a pup’s weaning mass was small ($p = 0$) or large ($p = 1$). The effect of weaning date was also suggestive (panel *c*), although not statistically significant at the 95% level. Histograms of the raw data are depicted above each plot (*a*, *b*, *c*). On panel *d*, effect size of the estimated regression coefficients (on the robit scale) are depicted. Reported estimates are for standardized variables. The grey envelope corresponds to a 95% credibility interval, and the black line to the posterior mean.

Stable isotopes of pup blood proved to be strong predictors of their weaning mass, and allowed me to infer maternal foraging strategies. Females foraging at high (inferred from smaller $\delta^{13}\text{C}$ values) or low (inferred from larger $\delta^{13}\text{C}$ values) latitudes, had a greater probability of weaning a large pup than females foraging in the Interfrontal Zone (Figure 3.9a). This non-monotonic relationship between a pup's blood carbon isotopic ratio and its probability to have a large weaning mass was surprising. We suspected *a priori* that the Antarctic strategy, because of the high productivity around Antarctica (Ainley and DeMaster, 1990), was more profitable for females; but I anticipated a monotonic relationship (Burton et al., 1997) such as the smaller $\delta^{13}\text{C}$, the greater the probability for a pup to be large. Using the results of Table 3.2 and discrimination factors from Ducatez et al. (2008), I can predict the mean foraging latitude of a breeding female from the $\delta^{13}\text{C}$ value of her pup (Figure 3.10).

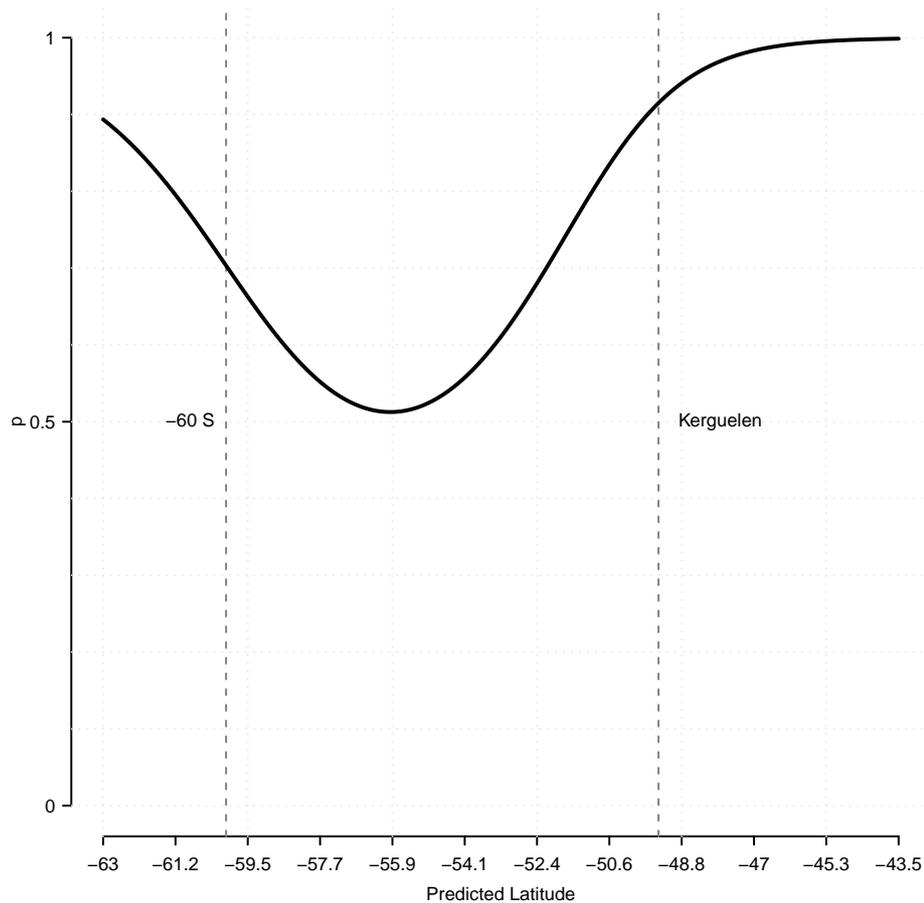


Figure 3.10: Predicted relationship between group membership probability of pup (large or small) and the mean latitude of its cow foraging trip after moulting.

High and low $\delta^{13}\text{C}$ values predicted with certainty a pup to be a large weanling. Yet, only 1% pups had a carbon signature lower than -23.0‰ , suggestive of a true Antarctic maternal strategy. Likewise, only 3% pups had a carbon isotopic ratio higher than -19.5‰ . Such a large value may suggest foraging in subtropical waters, yet considering how little females seem to go north to the Sub-Tropical Front (Figure 3.4), high $\delta^{13}\text{C}$ values may in fact reflect the Kerguelen Plateau signature, which is a very productive zone within the Indian sector of the Southern Ocean (Blain et al., 2001). From the results of Table 3.2, I concluded that I could not distinguish between Interfrontal and Kerguelen Plateau $\delta^{13}\text{C}$ signatures, although there was some consistent support for my *a priori* expectations¹³. These results stemmed from the analysis of 80 incomplete tracks. Here the data on pups is one order of magnitude higher ($N \approx 700$) so finer details are detectable. In addition, I assumed that the incomplete tracks were still representative albeit seals may be continuously feeding during a foraging trip (Thums et al., 2011). Incomplete tracks lacked the homeward part to îles Kerguelen, that is the part where females crossed the Kerguelen Plateau. Given how few equipped females went into subtropical waters (Figure 3.4), it is more likely that the high $\delta^{13}\text{C}$ values were in fact reflective of the Kerguelen Plateau.

If both foraging in Antarctic oceanic waters and on the Kerguelen Plateau are so profitable, why do most females still bother to forage in the Interfrontal Zone as much as they do (Bailleul et al., 2010; Dragon et al., 2010)? Females foraging in Antarctic waters may face extra costs linked to the variability in sea ice extent as females avoided threading into the pack ice and stuck to the marginal ice-free zone during the Austral winter (Bailleul et al., 2007a). Going South could be a risky, but profitable, strategy so that only high quality females may favour this strategy. The Kerguelen Plateau is extensively used by juvenile males, but not by adult females (Bailleul et al., 2010). This sexual segregation in space may reflect harassment by males, or an increased risk of predation by killer whales (*Orcinus orca*, Guinet (1992)) or sleeper sharks (*Somniosus antarcticus*, van den Hoff and Morrice (2008)) such that females avoid foraging on the Kerguelen Plateau despite its biological richness. The advanced mechanisms to explain this sexual segregation are rather speculative, but direct observations of interactions when foraging are not available¹⁴.

¹³and it is noteworthy that there was no shrinkage for the effect size, suggesting a robust signal in these data.

¹⁴A way to obtain such data would be to equip some individuals with recording cameras.

Nitrogen isotopic ratio negatively correlated with the probability for a pup to be large. This pattern may suggest that, within the Southern Ocean foodweb, lower trophic level preys (for example: myctophid fish, $\delta^{15}\text{N}$ ranged between 7.6 and 10.2‰ (Cherel et al., 2008)) are of higher quality compared to upper level ones (for example: squids, $\delta^{15}\text{N}$ values ranged between 10.0 and 10.9‰ (Cherel et al., 2008)¹⁵). Traditional stomach content analyses concluded of the preponderance of squids in the diet of Southern Elephant Seals (Rodhouse et al., 1992), yet these studies are biased due to an over-representation of hard-to-digest items, such as cephalopod beaks, in the otherwise empty stomach of a fasting animal.

Using stable isotopes, Cherel et al. (2008) challenged this view and suggested that adult Southern Elephant Seals may be feeding mainly on myctophid fish species. These fish are cornerstones of oceanic foodwebs (Figure 3.2), and represent the bulk of the mesopelagic fish biomass within the Southern Ocean (Cherel et al., 2010). Their high fat and protein contents (Catul et al., 2011) probably make them all the more suitable to female Southern Elephant Seals compared to squids. Another line of evidence backing this view comes from (Newland et al., 2009) who reported an increased in fish fatty acids in the blubber of adults females compared to juveniles.

An alternative, but not exclusive, explanation might be the occurrence of a gradient in $\delta^{15}\text{N}$ within the Southern Ocean due to different baseline $\delta^{15}\text{N}$ in inshore (Cherel and Hobson, 2007) or sub-tropical (Jaeger et al., 2010) waters. As previously mentioned, pup's blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ did modestly correlate ($\rho = 0.25$ – 0.32 – 0.39), supporting this idea. However, there was no statistical support for a quadratic relationship between $\delta^{15}\text{N}$ and the probability for a pup to be large at weaning. Thus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are providing complementary information. The most likely pattern is that of both a decreasing gradient in $\delta^{15}\text{N}$ with latitude or land proximity, and of lower trophic level preys, such as myctophids, being more profitable in terms of energy content.

¹⁵It is worth emphasizing that these values correspond to fish and squids sampled on the Kerguelen Plateau during oceanographic campaigns.

3.3.5 Environmental Conditions

We estimated two year-level variances with the model defined by Equation 3.1. For small pups, $\sigma_{\text{Year},1}$ was equal to 0.4_{11}kg , whereas $\sigma_{\text{Year},2}$ was equal to 2.7_{16}kg for large pups. Thus year-level variability was smaller in the group of small pups, which may suggest the Interfrontal Zone harbours more predictable resources. The Interfrontal Zone is highly dynamic with locally rich productive eddies (Blain et al., 2001; Moore and Abbott, 2000). Many top-predator species target fronts and mesoscale eddies to forage on mesopelagic fish whose spatial distribution is much more predictable close to frontal structures (Bost et al., 2009a). That there was a sex difference in weaning mass among large pups ($\Delta_{\text{M-F}} = 1.4\text{kg}$) but none among small ones ($\Delta_{\text{M-F}} = -0.5\text{kg}$) in such a highly dimorphic species where differences can be detected from an early age (for example, Field et al. (2007a)), may also hint at the Interfrontal Zone being a safer, though poorer bet for breeding females compared to other locations.

We refined Equation 3.1 by considering environmental covariates operating at the year level. Assuming a bottom-up effect in Southern Ocean food webs, I hypothesized that years with high primary production during active pregnancy (that is after blastocyst implantation, Figure 1.4) should be more profitable for females, and be reflected in a larger pup weaning mass.

Available total surface Chlorophyll *a* concentration, from SeaWiFS sea colour maps, was used as a proxy for primary production. Maps of the zones visited by tag-equipped seals (Figure 3.4) were computed with a ground resolution of $4\text{ km} \times 4\text{ km}$ (<http://oceancolor.gsfc.nasa.gov/>). Due to cloud cover causing a large percentage of missing pixels, I used monthly data in the Interfrontal Zone ($40^\circ\text{ S} - 60^\circ\text{ S} - 0^\circ : 125^\circ\text{ E}$) but did not get data for the Antarctic Zone (south of 60° S). In the Interfrontal Zone, Chlorophyll *a* anomalies about the monthly mean were calculated for each pixel. In sub-Antarctic waters, the bulk of main Chlorophyll *a* production occurs during the austral summer (Mongin et al., 2008). A proxy of the total surface Chlorophyll *a* production was therefore calculated yearly from cumulated anomalies between October 2005 and May 2009.

Dragon et al. (2011b) evidenced a positive correlation between Sea Ice Extent and Chlorophyll *a* concentration in Antarctic waters. Since Sea Ice Extent is assessed from microwave energy, its measurement is unaffected by cloud cover. Hence, Sea Ice Extent is more readily available than Chlorophyll *a* concentration in Antarctic waters. We investigated the influence of Sea Ice Extent (extracted over the zone $> 60^\circ\text{ S} - 0^\circ$ and 125° E , see Dragon et al. (2011b) for a full description of the methodology) on weaning mass for the group of large pups. As females do not thread into the Antarctic Pack Ice (Bailleul et al., 2007a), an extended Sea Ice cover during winter may limit their foraging habitat, and a negative effect of Sea Ice Extent on pup weaning could be expected *a priori*.

Although I only disposed of four years of data, a year effect j specific to each latent group $k \in \{1, 2\}$ was thus modelled as:

$$\eta_{j,k} = \begin{cases} \text{Chlorophyll } a_j \\ \text{Sea Ice Extent}_j \end{cases} + v_{j,k} \quad (3.3)$$

where $v_{j,k}$, the residuals for group k , are assumed to follow a normal distribution of mean 0 and variance $\sigma_{\text{Year}, k \in \{1, 2\}}^2$.

To assess the relevance of the chlorophyll a concentration and Sea Ice Extent in Mixture Models, I computed a R_{Year}^2 -statistic at the year level (Gelman and Pardoe, 2006). This coefficient of determination can be interpreted as a measure of the between-year variation accounted for by an environmental covariates. Thus three Mixture Models were fit: one with no environmental covariate at the year level, one with Chlorophyll a anomaly and one with both Chlorophyll a anomaly and Antarctic Sea Ice Extent. Model Selection was done using Posterior Predictive Checks (see Appendix C), using three test-statistics: minimum, maximum and kurtosis. Extrema descriptive statistics were chosen to assess whether a model could predict the observed (large) range of weaning mass (Table 3.3), while kurtosis was chosen because it can betray bimodality (Darlington, 1970; Hilderbrand, 1971), and thus testify of the appropriatedness of the two-component mixture models.

Statistic	Null	Mixture	Mixture _{Chl_a}	Mixture _{Chl_a,SIE}
minimum	0.45	0.42	0.48	0.46
maximum	0.67	0.38	0.32	0.25
kurtosis	0.80	0.57	0.53	0.58

Table 3.4: Posterior Predictive Checks of the fitted models (Null: model with no mixture; Mixture: Mixture Model without environmental covariates; Mixture_{Chl_a}: Mixture Model with Chlorophyll a as a year-level covariate, and Mixture_{Chl_a,SIE}: Mixture Model with Chlorophyll a and Sea Ice Extent as year-level covariates). Values close to 0 or 1 betray misfit, while a value of 0.5 indicates a good fit. The selected model is in bold.

Including year-level covariates slightly improved model fit (Table 3.4). Posterior Predictive Checks favoured the mixture model with only Chlorophyll *a* concentration at the Interfrontal Zone. Chlorophyll *a* anomalies at the Interfrontal Zone accounted for some 33% of the year-level variance for small weanlings. This figure was down to 0% for large weanlings as expected under the hypothesis that foraging strategies map exactly to latent groups (Figure 3.11).

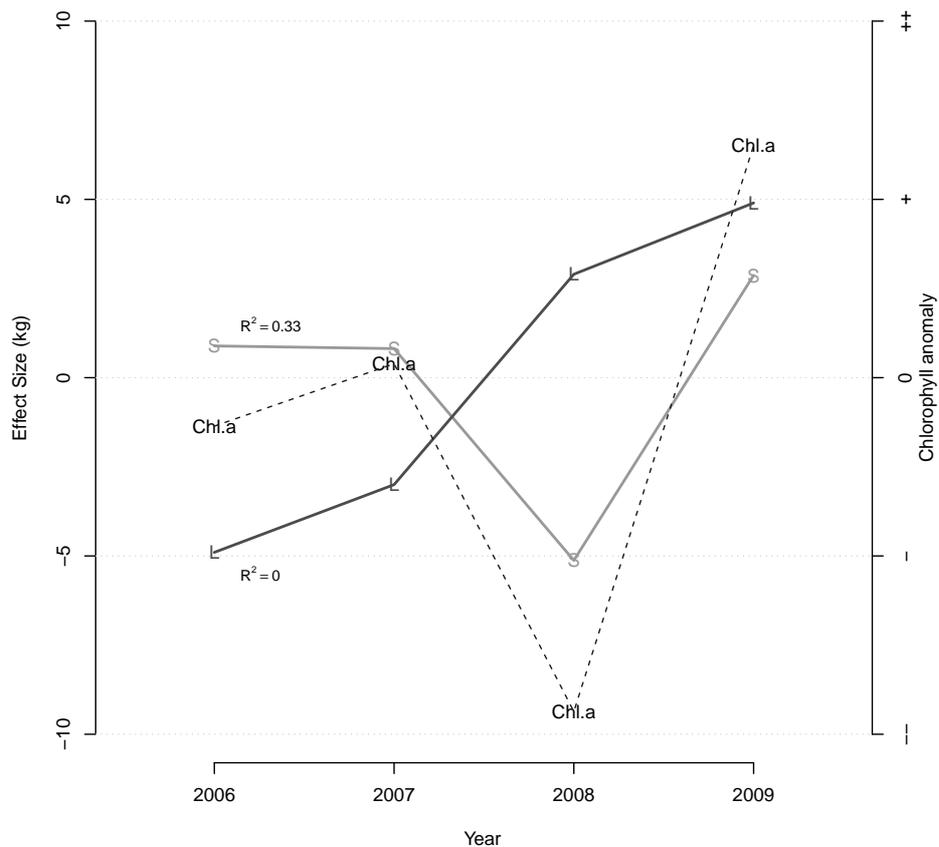


Figure 3.11: Year effect on the weaning mass of each estimated group of pups: S and L stand for small and large weanlings respectively. The two groups differed in their response to environmental conditions. Yearly deviations from mean weaning mass for small pups, but not for large pups, positively covaried with cumulated Chlorophyll *a* anomalies in the Interfrontal Zone. Solid lines correspond to posterior means.

Antarctic Sea Ice Extent accounted for 80% of the variability of mass within large weanlings. Yet adding this covariate to the model did not improve model fit either judging from Posterior Predictive Checks, or from residual plots (wave-like pattern in a plot of residuals against fitted values, not shown). Moreover, the sign of the relationship was opposite to that expected *a priori*: I found a positive relationship between Sea Ice Extent and weaning mass while a negative one was anticipated as breeding females are limited by sea ice when foraging in Antarctic waters (Bailleul *et al.*, 2007a). The non-monotonic relationship between latent group membership probability and $\delta^{13}\text{C}$ value (Figure 3.10) argues against a perfect match between foraging locations and the amount of resources a female managed to transfer to her pup. This adds skepticism toward any strong relationship between Sea Ice Extent and year-level variability.

That my data encompassed only four years limits any strong conclusions about the impact of environmental factors on maternal foraging behaviour. Nonetheless, I uncovered a small correlation between small weanlings and a proxy of productivity in the Interfrontal Zone. This correlation is biologically plausible both in sign and in effect size: Southern Elephant Seals do not feed on chlorophyll so a large effect would be unsound. Due to data unavailability on Chlorophyll *a* concentration around Antarctica, I assessed the effect of Sea Ice Extent on the weaning mass of large pups and found a suspiciously large correlation of the wrong sign. The effect size is probably an overestimate arising from the short time series I currently have: the shorter the time series the larger the odds a large correlation can arise by chance alone. This is corroborated by my Posterior Predictive Checks, which did not suggest a real model improvement of including Sea Ice Extent.

Finally, maximum weaning mass was always underestimated by all mixture models, testifying that I am still lacking an important predictor for large pups.

3.4 Concluding Remarks

Starting with the assumption that the foraging strategy of a breeding female determine the amount of resources she will be able to extract, store and eventually transfer to her single pup, I built a mixture model to assess whether the population of weaned pups could be composed of several latent groups, each group mapping to a foraging strategy. The actual mapping was done using indirect evidence of foraging that stable isotopes can provide. The distribution of weaning mass among pups was not normal but left-skewed, which I modelled as a two-component mixture. The smaller component encompassed about 30% of pups with a mean mass of 90kg and a blood $\delta^{13}\text{C}$ value suggestive of an Interfrontal signature. Yearly variation around that mean may be linked to primary productivity at the Interfrontal Zone, which suggested that the cows of these pups did forage in Interfrontal waters.

In contrast, the other component did not map to a single foraging strategy. The blood $\delta^{13}\text{C}$ value of large pups (about 115kg) suggested either foraging in Antarctic waters, in Sub-tropical waters or on the Kerguelen Plateau. This result underscores a limitation of stable isotopes as there exists many gradients (latitudinal, inshore/offshore) within the Southern Ocean that influence an isotopic signature. Recently, [Thums et al. \(2011\)](#) disclosed how Southern Elephant Seals were in fact continuously feeding during a foraging trip, without displaying obvious area-restricted patterns. When tracking data revealed how females headed straight back to the Kerguelen before parturition, it was first assumed that they would not feed extensively on the way ([Ducatez et al., 2008](#)). With the new evidence from [Thums et al. \(2011\)](#), females might in fact take advantage of the very productive Plateau around Kerguelen and feed as previously suggested by [Bailleul et al. \(2010\)](#). This behaviour complicates the interpretation of stable isotope data, and may in fact explain why using a robust link function, which downweights occasional outliers ([Gelman and Hill, 2007](#)), was necessary for analyzing these data.

The bell-shaped relationship between $\delta^{13}\text{C}$ and pup weaning mass suggested that foraging in Antarctic oceanic waters and on the Kerguelen Plateau were very profitable, but were not widely used by most females. I speculated that females foraging in Antarctic waters may face extra costs linked to the variability in sea ice extent so that only high quality females may favour this strategy. It may also be that the Kerguelen Plateau is avoided by adult females because of harassment by males, or of an increased risk of predation. Harassment by males is likely given how a few males exclude all the other from mating with females on land and given recent evidence that both primiparous and multiparous can mate at sea ([de Bruyn et al., 2011](#)).

Thus contrary to the initial assumption of a perfect match between resources transfer to a pup and foraging strategy, several foraging strategies may have (unsurprisingly) similar pay-offs, although foraging in the Interfrontal Zone seems to be a 'conservative' option: less variable but also less profitable in terms of energy ultimately transferred to a pup. The Kerguelen population of breeding Southern Elephant Seal females crashed during the 1960s-1980s (Chapter 2). Causes behind this decline are still unclear (McMahon *et al.*, 2005a), although the hypothesis of an ecosystem regime shift affecting the Southern Ocean and impacting many species of upper marine predators is favoured (Weimerskirch *et al.*, 2003; McMahon *et al.*, 2005a). My results are consistent with this hypothesis: under a regime shift, secondary productivity declined (Weimerskirch *et al.*, 2003), shrinking to nil the larger fitness pay-offs enjoyed by females foraging in the marginal sea-ice zone or on the Kerguelen Plateau compared to other females. As a result, all females would wean smaller pups with dimmer prospects of post-weaning survival. The large population decrease on îles Kerguelen could have stemmed from such a small juvenile recruitment rate (McMahon *et al.*, 2005b). It is also noteworthy that this period of decline witnessed also an excessive fishing effort around the Kerguelen Plateau which was never to be repeated (Ainley and Blight, 2009). Decreased productivity and overfishing may both have increased juvenile mortality, either because females could not extract find enough resources to wean a pup with good survival prospects, or because pups themselves were unable to find enough resources once weaned.

My analysis points to a potentially important role for maternal foraging strategies in shaping population trends on îles Kerguelen (McMahon *et al.*, 2005b). Evidence from biologging (Bradshaw *et al.*, 2004) and stable isotopes suggest Southern Elephant Seal females are faithful to their foraging grounds. The relatively stable mixture proportions across years observed in this study could reflect a stable commitment of females to a foraging strategy. Yet, this may have adverse fitness consequences both in the short- and long-term. Females committed to a foraging strategy in the Interfrontal Zone may well never contribute to the next generation, having only weaned small (and frail) pups. This then begs the question of the ontogeny of foraging behaviour.

Foraging and Life History

Contents

4.1 Ontogeny of Foraging	60
4.1.1 Cross-Sectional Data	60
4.1.2 Trophic Level of Southern Elephant Seals	65
4.2 The Importance of Study Design	66
4.3 Ontogenetic Shifts	67
4.3.1 Isotopic Data Collection	67
4.3.2 Change-point Models	69
4.3.3 Hierarchical Formulation	71
4.3.4 Results	72
4.4 Ecological Correlates of Longevity	79
4.4.1 Longevity in the Wild	79
4.4.2 Joint Longitudinal/Survival Models	80
4.4.3 Results	83
4.4.4 Life-History Consequences of Early Life	85

Section 4.1 is under review for publication in *Marine Ecology Progress Series* :

Chaigne, A., Authier, M., Richard, P., Cherel, Y. & Guinet, C. (submitted) Shift in Foraging Grounds and Diet Broadening during Ontogeny in Southern Elephant Seals from Kerguelen Islands.

Section 4.3 is awaiting a final decision from *Methods in Ecology and Evolution*:

Authier, M., Martin, C., Ponchon, A., Steelandt, S., Bentaleb, I. & Guinet, C. Breaking the Sticks: a Hierarchical Change-Point Model for Estimating Ontogenetic Shifts with Stable Isotope Data.

Section 4.4 is to be submitted to *PLoS One*:

Authier, M., Bentaleb, I., Ponchon, A., Martin, C. & Guinet, C. Foraging and Longevity in Male Southern Elephant Seals.

4.1 Ontogeny of Foraging

In the preceding chapter, I suggested that seals were faithful to a foraging strategy but my data were limited owing to the cost of 'biologging'. Having demonstrated how carbon stable isotopes reflect the latitude at which a seal forages, I can investigate the ontogeny of foraging in Southern Elephant Seals using stable isotope data only. That is I can investigate the development of foraging behaviour with age, taking a complementary approach to that of Bradshaw et al. (2004) who investigated the faithfulness to feeding grounds in 6 year-old females tracked over several foraging trips. Bradshaw et al. (2004) found females from Macquarie Island to return to the same foraging grounds in several foraging trips. These authors chose to focus on same-aged females to avoid any confounding due to age if animals change their behaviour as they age. This latter question is more easily answered with stable isotopes using cross-sectional data on a wide panel of animals: since Southern Elephant Seals have an indeterminate growth, Snout-to-Tail Length may be used as a proxy for age. Thus by blood-sampling individuals of varying body size, I may investigate whether foraging strategy (Antarctic *versus* Subantarctic for the Kerguelen population) changes with age.

4.1.1 Cross-Sectional Data

From 2004 to 2011, a total of 404 randomly-chosen seals (136 males and 268 females) present on hauling-out sites (mainly Cape Ratmanoff, Pointe Suzanne, Port-aux-Français, see Figure 1.5) were blood sampled opportunistically year round, but a large majority of seals were sampled during the summer moult, that is after a post-breeding trip. Blood was collected from the dorsal venous sinus using 90×1.2 mm needles. Seventy percent ethanol was added for sample preservation before laboratory analysis (see Appendix D). Snout-to-Tail Length was also recorded for each individual (Figure 4.1).

I investigated whether blood stable isotopes changed with Snout-to-Tail Length in Southern Elephant Seals from îles Kerguelen with mixture models. Specifically, to classify individuals as foraging either at Subantarctic (because I can't distinguish clearly between the Interfrontal Zone or the Kerguelen Plateau on the basis of carbon stable isotopes only, I lumped these two zones into a Subantarctic Zone) or Antarctic latitudes, I modelled the carbon stable isotopes value, $\delta^{13}\text{C}$, as a mixture of two distributions:

$$\delta^{13}\text{C}_i = (1 - q_i) \times (\bar{\delta}^{13}\text{C}_{\text{Sub}}) + q_i \times (\bar{\delta}^{13}\text{C}_{\text{Ant}}) + \varepsilon_i \quad (4.1)$$

where q_i is the probability that the i^{th} seals foraged in the Antarctic Zone and ε_i are the residuals drawn from a Gaussian distribution of mean 0 and standard deviation σ_{residual} . Given my previous results, I can expect $\bar{\delta}^{13}\text{C}_{\text{Ant}} - \bar{\delta}^{13}\text{C}_{\text{Sub}} \approx -1.7\text{‰}$.

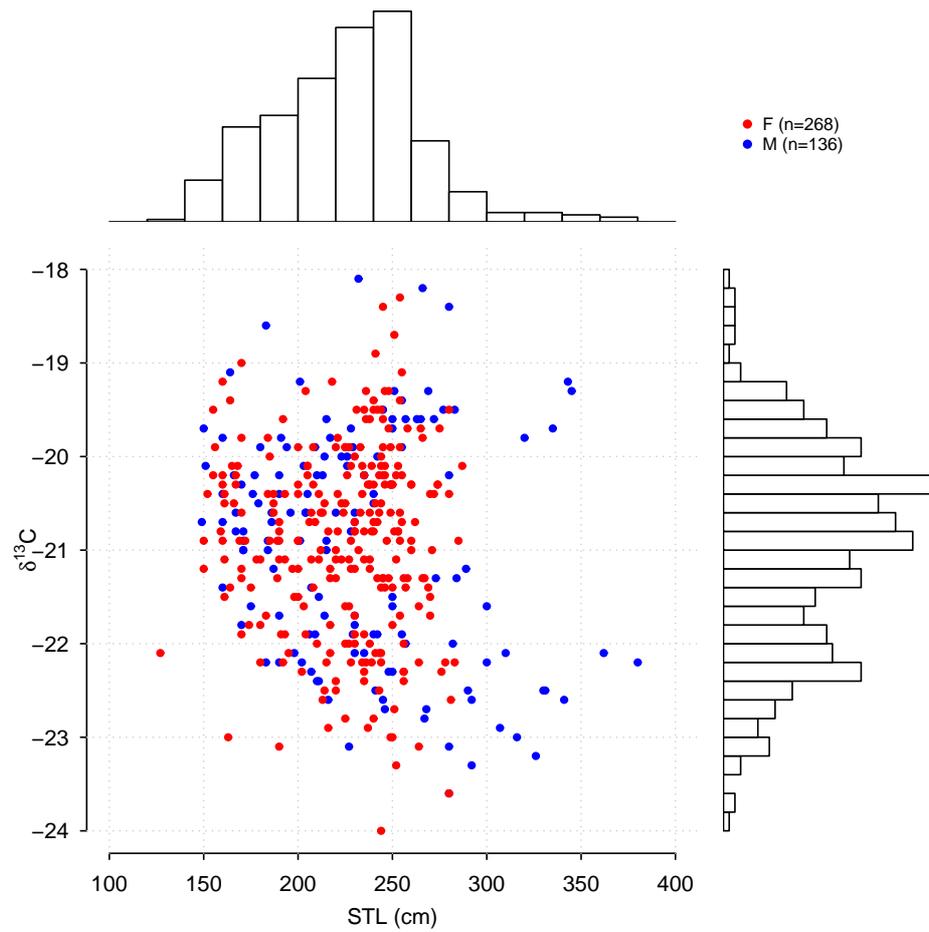


Figure 4.1: Cross-Sectional data collected on 404 seals on îles Kerguelen. The $\delta^{13}\text{C}$ value is represented as a function of Snout-to-Tail Length, along with their observed marginal distributions.

To investigate whether seals may switch between strategy with age, I modelled q_i as a function of Snout-to-Tail Length:

$$\text{logit}(q_i) = \alpha_1 + \alpha_2 \times \text{Snout to Tail Length} \quad (4.2)$$

I analyzed males and females separately (see Appendix D). For males, foraging strategy changed with Snout-to-Tail Length (standardized $\alpha_2 =_{-2.2} -1.3_{-0.6}$): bigger males were more likely to have a blood $\delta^{13}\text{C}$ value indicative of an Antarctic strategy ($\bar{\delta}^{13}\text{C}_{\text{Ant}} =_{-22.3} -22.1_{-21.8}$) while smaller one were more likely to have a blood $\delta^{13}\text{C}$ value indicative of a Subantarctic strategy ($\bar{\delta}^{13}\text{C}_{\text{Sub}} =_{-20.3} -20.1_{-19.9}$, Figure 4.2). This pattern begs the question whether the observed change between the two foraging strategies is due to individual changing their behaviour or to a differential survival of males depending on their foraging strategy. The analysis in Chapter 3 suggested that seals were faithful to a foraging strategy. However these conclusions stemmed from a dataset dominated by females. To answer unambiguously the question of a differential survival in males, longitudinal data is required.

A change in foraging grounds with increased Snout-to-Tail Length was seen in males but not in females¹. This seems to corroborate the results in Chapter 3 that females were faithful to a foraging strategy. I could distinguish between Antarctic ($\bar{\delta}^{13}\text{C}_{\text{Ant}} =_{-22.2} -21.9_{-21.5}$) or Subantarctic ($\bar{\delta}^{13}\text{C}_{\text{Sub}} =_{-20.6} -20.4_{-20.3}$) foraging strategy in females, but the pattern was not as clear cut as for males: a lot of females had an intermediate $\delta^{13}\text{C}$ value. The difference in isotopic signatures found with the male data ($-2.3 - 2.0_{-1.7}\%$) or the female data ($-1.8 - 1.5_{-1.1}\%$) is close to the one I found previously (see Chapter 3).

I also investigated whether there was any change in trophic level, as inferred with $\delta^{15}\text{N}$, with Snout-to-Tail Length. Sexes were analyzed separately: I first classified seals as foraging in either the Antarctic or Subantarctic Zone on the basis of their $\delta^{13}\text{C}$ value, and then assess whether there was a correlation between Snout-to-Tail Length and both the mean $\delta^{15}\text{N}$ and residual standard deviation (that is, I modelled the residual error as heteroskedastic, Figure 4.3) within each group of seals. Results are summarized on Figure 4.3.

¹In fact, the model did not converge for females.

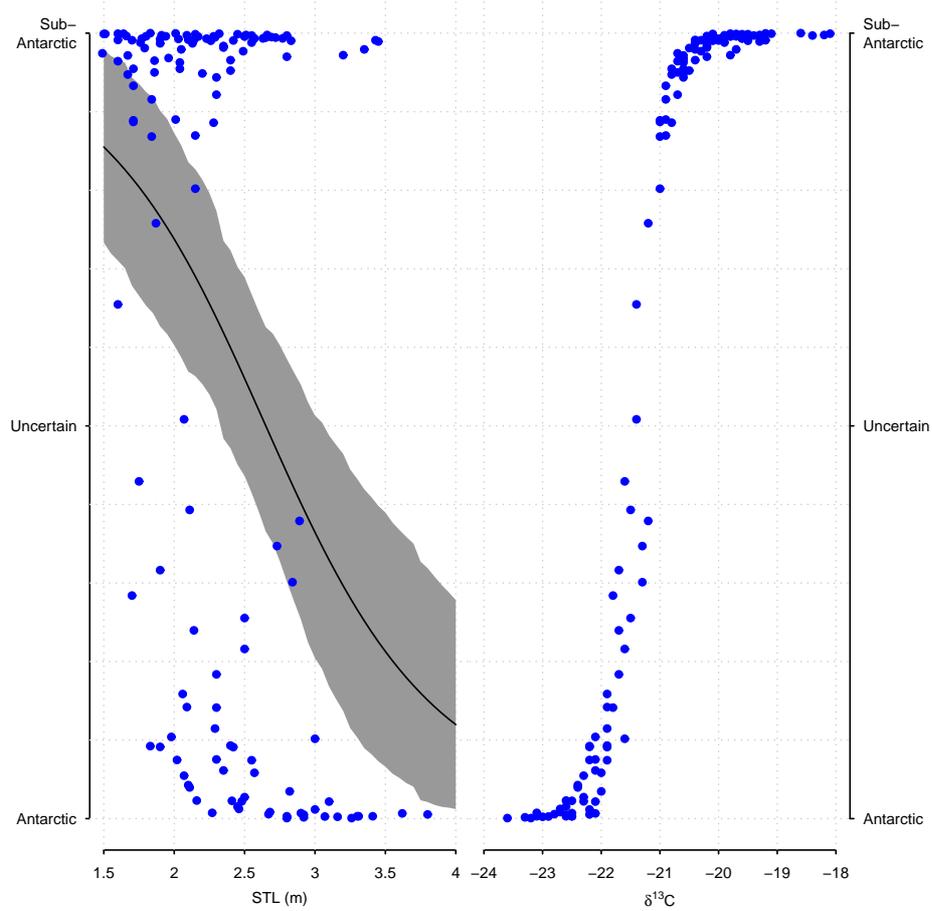


Figure 4.2: Shift in foraging strategy in male Southern Elephant Seals: bigger males had an Antarctic $\delta^{13}\text{C}$ signature. The grey envelope corresponds to a 95% credibility interval.

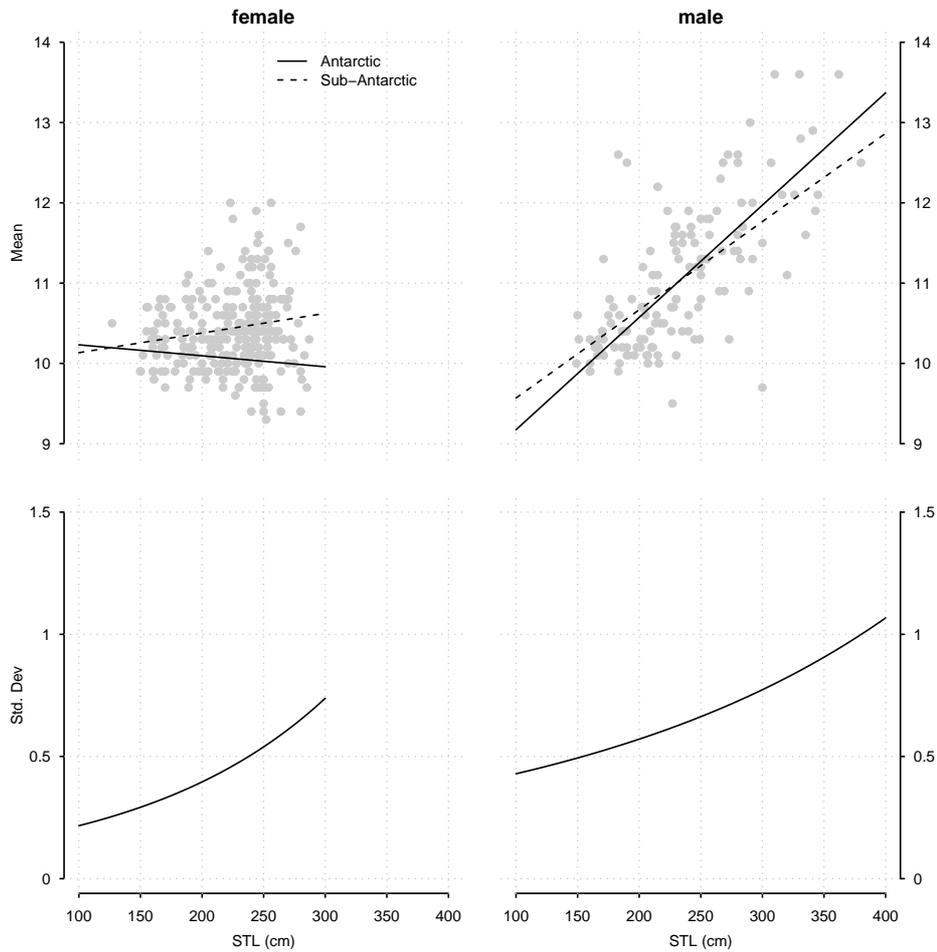


Figure 4.3: Shift in trophic level in male Southern Elephant Seals: bigger males had an a larger $\delta^{15}\text{N}$ value. The upper panels show the predicted mean $\delta^{15}\text{N}$ for a given body length, while the lower panels show the relationship between the residual standard deviation and Snout-to-Tail Length. For both males and females, the spread of the data increased with Snout-to-Tail Length suggesting that older seals were feeding on greater panel of preys than younger seals.

4.1.2 Trophic Level of Southern Elephant Seals

Whether seals foraged at Antarctic or Subantarctic latitudes, there was a strong relationship between Snout-to-Tail Length and $\delta^{15}\text{N}$ value in males (standardized coefficient for Snout-to-Tail Length, Antarctic: $0.81.1_{1.5}$; Subantarctic: $0.60.9_{1.1}$) but not in females (standardized coefficient for Snout-to-Tail Length, Antarctic: $-1.7 - 0.1_{0.9}$; Subantarctic: $0.10.2_{0.3}$). Bigger males had also a larger $\delta^{15}\text{N}$ value, which suggested that these males were feeding on prey from a higher trophic levels than smaller males. There was no strong statistical support from a similar pattern in females. However, for both males and females there was a statistically significant (at the 5% level) relationship between the residual variance in $\delta^{15}\text{N}$ values and Snout-to-Tail Length. This increase in the spread of $\delta^{15}\text{N}$ values suggested that older seals were feeding on greater panel of preys than younger ones.

These cross-sectional data clearly suggested that young males were predominantly foraging at Subantarctic latitudes than older males. This pattern was not found in females which are also similar in morphology to young males. Thus the data suggested a shift in foraging strategy with age for males, which may then become faithful to a foraging strategy later in life than females (Bradshaw et al., 2004). I previously inferred seals to be faithful to a foraging strategy, but this came from a much smaller data set ($N=26$) with only 3 males (one of which was 4 metres long). The present analysis suggests that females are indeed probably faithful to a foraging strategy from an early age but males start as foraging in Subantarctic latitudes before switching to Antarctic latitudes as they age. This effect was suggestive in my previous analysis of track and stable isotopes data: the interaction between Snout-to-Tail Length and Antarctic foraging had a plausible effect size both in sign and magnitude ($\approx -1\%$, see Table 3.2). The present analysis is, however, quite different as it relied on a mixture model to classify individuals as either Antarctic or Subantarctic foragers. It thus allows to make probabilistic statement on whether a given individual with an observed stable isotope value has been foraging in Antarctic waters or not. My previous analysis with track established that there were indeed differences in the $\delta^{13}\text{C}$ blood value of Southern Elephant Seals, which my present analysis with a mixture model exploited² to infer in the absence of track data the foraging locations of seals.

A broadening of the $\delta^{15}\text{N}$ with Snout-to-Tail Length is a novel finding. I can speculate that this broadening may reflect either individual specialization (Bolnick et al., 2003) if a seal consistently target the same preys at a specific trophic level, or else may reflect an widespread opportunism. The nature of the data I used, that is cross-sectional data, cannot answer this question as it requires repeated observations on the same individual.

²Although I did not use any informative prior from the previous analysis, I still found roughly the same difference in $\delta^{13}\text{C}$ between the two strategies with an expanded dataset.

4.2 The Importance of Study Design

The previous section investigated the ontogeny of foraging using blood stable isotopes. Because there is no Capture-Recapture study design on îles Kerguelen for logistic reasons, the data I used was cross-sectional. This design however precludes to follow individual trajectories over time, and to unequivocally assess the life-history consequences of foraging, that is questions such as what is the Lifetime Reproductive Fitness of females that are foraging in Antarctic waters compared to that of females foraging elsewhere? To provide solid answer to such question, detailed longitudinal knowledge of the whole life-history of individual animal is required.

The sheer size of îles Kerguelen (approx. 7,200 km² with 2,800 km of coast-line; Figure 1.5) prevents an exhaustive search. While being philopatric to the island where they were born, Southern Elephant Seals breeding on îles Kerguelen are not philopatric to a specific hauling-out site in the same way as other pinnipeds species may be (for example the Subantarctic Fur Seal, *Arctocephalus tropicalis* (Beauplet et al., 2006)). For example, seals equipped with telemetric tags at Cape Ratmanoff were subsequently recaptured 40 km away, at the main base of Port-aux-Français or in the Baie Norvégienne (Figure 1.5). Such behaviour coupled with the large number of individuals that haul-out every year (Chapter 2), render any effort to recapture individually mark animals with plastic tags haphazard³.

How to obtain longitudinal data then? Some tissues, once synthesized, are metabolically inert, and thus may be compared to a snapshot of the biochemical environment in which it was synthesized. Such so-called 'archive tissues' naturally lend themselves to repeated isotopic measurements. For example, fish otoliths have been successfully used to infer the stock origin of commercial fish species (Edmonds and Fletcher, 1997; Correia et al., 2011). Carapace scutes revealed the migrations of early juvenile lifestages of the marine Green Turtle, *Chelonia mydas* (Reich et al., 2007), while whiskers evidenced those of Antarctic Fur Seals, *Arctocephalus gazella* (Cherel et al., 2009). The list of species for which stable isotope analysis of archive tissues proved useful is in fact long⁴. For marine mammals, one archive tissue which may be particularly attractive is the dentin found in teeth: specimen may be aged with a tooth sample (Laws, 1952). Thus repeated sampling of tooth growth layers creates time-series of isotopic measurements and generates longitudinal data (Hobson and Sease, 1998).

³Successful Capture-Mark-Recapture studies have been carried out on Marion and Macquarie Islands, see for example (Pistorius et al., 1999b; McMahon and Burton, 2005)

⁴The interested reader is referred to Newsome et al. (2010) for more references on marine mammals.

4.3 Ontogenetic Shifts

An ontogenetic shift is defined as 'the patterns in an organism's resource use that develop as it increases in size from birth or hatching to its maximum' (Werner and Gilliam, 1984). In their review on ontogenetic shifts, Werner and Gilliam (1984) focused on changes in habitat use and diet, both of which are apprehended in isotopic ecology via carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes respectively. Individual time-series of isotopic measurements may be used then to investigate such ontogenetic shifts and to infer indirectly foraging locations and trophic position (Reich et al., 2007; Estrada et al., 2006; Hobson and Sease, 1998; Mendes et al., 2007).

One attractive feature of studying stable isotopes of archive tissues is that one may use historic samples from museum or private collections to 'go back in time' (for example, Hilton et al. (2006)). Going back to the 1970s is extremely relevant in the case of the Southern Elephant Seals given the large population decline that occurred at that time (Guinet et al., 1999; McMahon et al., 2005a; Ainley and Blight, 2009).

4.3.1 Isotopic Data Collection

Teeth were collected from elephant seals that died of natural causes on îles Kerguelen. Canines grow continuously throughout the whole life without closing of the pulp cavity, allowing for age determination (Laws, 1952, 1993). Canines from 47 males and 20 females were analyzed and sampled for isotopic analysis. All these animals were also aged (Martin et al., 2011). 18 teeth were sampled on animals that died before a population crash in the 1970s, while the remaining 49 were sampled in the 2000s, after the population had stabilized (see Chapter 2).

Each tooth was longitudinally cut and observed under diffused light to count growth layers (Figure 4.4). Translucent bands are enriched in vitamin D and synthesized when seals are ashore to breed and to moult, while opaque ones are synthesized when at sea (Wilske and Arnborn, 1996). Given the patterns of foraging trips at sea punctuated by either moulting or breeding on land (Figure 1.4), two opaque and two translucent bands correspond to one year of life. In the end (see Appendix D), a total of 1,414 (1,115 from males and 299 from females) dentin isotopic measurements from 67 individuals (47 males and 20 females) were available. It should be stressed that females are under-represented in this data set, and that the analysis of samples collected on dead females revealed these females were predominantly young ones. On the field, large males were preferentially sampled.

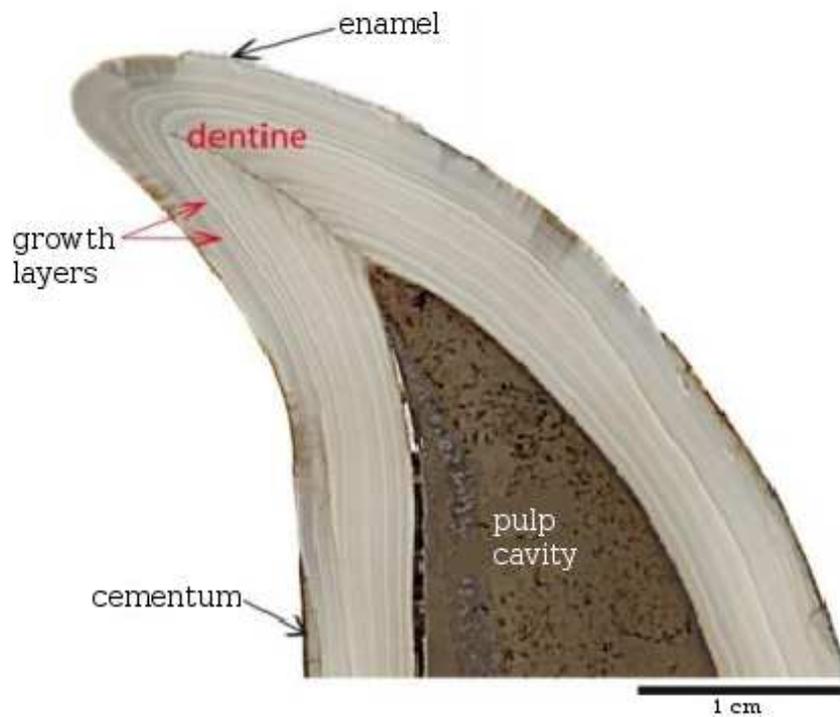


Figure 4.4: Histological structure of a Southern Elephant Seal canine tooth (Martin et al., 2011). An alternate pattern of translucent and opaque growth layer is discernible: Translucent bands are enriched in vitamin D and synthesized when seals are ashore to breed and to moult, while opaque ones are synthesized when at sea (Wilske and Arnbom, 1996). Two opaque and two translucent bands correspond to one year of life.

4.3.2 Change-point Models

To investigate ontogenetic shifts, I used change-point models. Change-point, or broken-stick, models aim at finding an abrupt rupture in a time-series. The time-series is assumed to be the juxtaposition of piece-wise linear homogeneous segments, each segment separated from the next by a change-point. For example, [Beckage et al. \(2007\)](#) used a change-point model to study allometric relationships between tree height and tree diameter or to study seedling recruitment with respect to canopy cover along a transect. [Da-Silva et al. \(2008\)](#) studied post-reproductive survival in a partially semelparous marsupial using such models⁵.

Change-point models are very flexible as they allow to specify different probability distributions to describe different parts of a time series. This is relevant for estimating ontogenetic shifts when they are conceptually defined as abrupt changes separating lifetime into two distinct components. Exploratory Data Analysis suggested a change-point model would be suitable for my data set and I use sparklines⁶ ([Tufte, 2006](#)) to illustrate my point. $\delta^{13}\text{C}$ time-series looked like ; or . Both isotopic profiles suggested a change-point model is reasonable. However, a profile such as  shows a cyclical pattern that a change-point model will not accommodate. Similarly, the $\delta^{15}\text{N}$ time series suggested a change-point model was reasonable: ; or . The issue of cyclical patterns also arose, . Yet there were also few such profiles within the data set.

I was in fact very surprised that there were not more cyclical patterns in these data. I expected a priori given the two yearly migrations of southern elephant seals to recover time-series with a periodicity, as was found in Antarctic fur seals ([Cherel et al., 2009](#)) or Southern Right Whale, *Eubalaena australis* ([Best and Schell, 1996](#)). For the few time-series with cyclicity (there were more such time series for $\delta^{13}\text{C}$: ; ; ), the cyclic pattern was apparent for 2-3 years, that is 8 to 12 data points. This was too sparse to try to fit complex models to describe this periodicity. A change-point model then seemed reasonable as an overarching model. The whole data to be analyzed with change-point models is represented in [Figure 4.5](#).

⁵Change-point models have been used in epidemiology to infer the onset of cognitive decline ([Hall et al., 2000](#); [Muniz-Terrera et al., 2011](#)), of prostate cancer ([Bellera et al., 2008](#)) or of HIV immunologic response decline ([Ghosh and Vaida, 2007](#)).

⁶Sparklines are 'data-intense, design-simple, word-sized graphics' ([Tufte, 2006](#)). Since this is exploratory, omission of the x- and y-axis is not problematic.

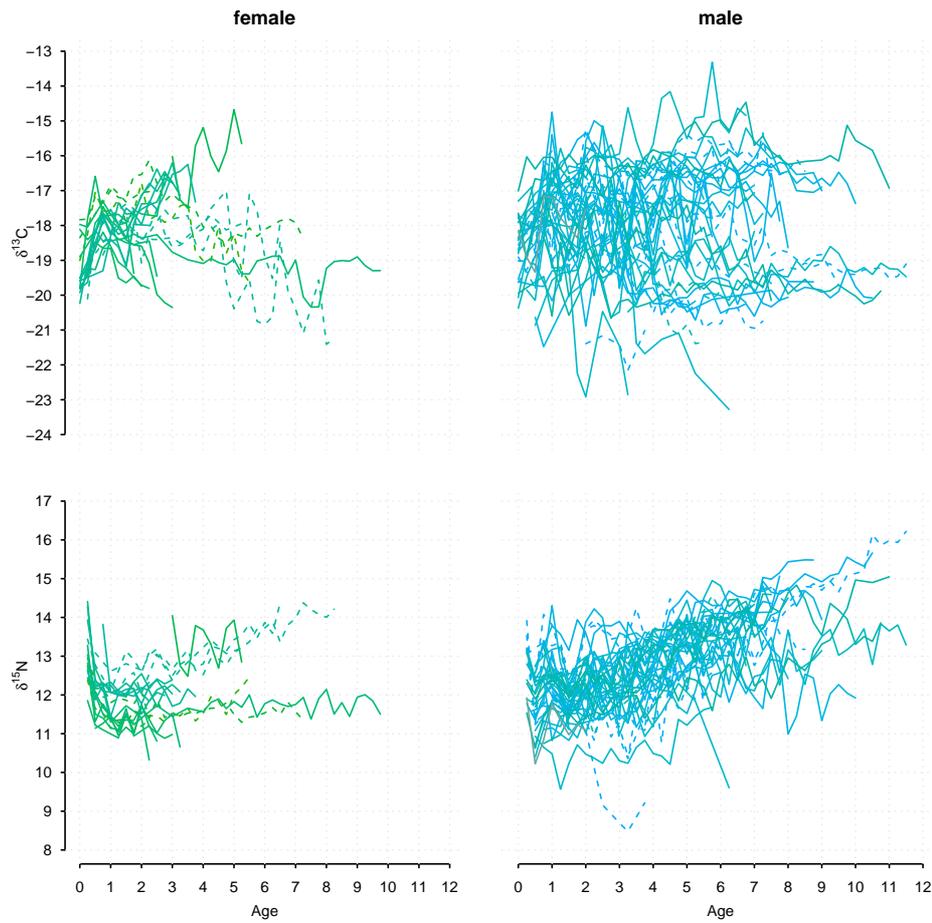


Figure 4.5: Spaghetti plots of the raw data for the Southern Elephant Seal data. Dotted lines represent animals that died before the population crash in the 1970s, while continuous lines are for animals sampled in the 2000s.

4.3.3 Hierarchical Formulation

With the data set I gathered from canine teeth, I was interested in answering the following questions about Southern Elephant Seals:

1. Are seals faithful to a foraging strategy (Bradshaw et al., 2004)?
2. When do they become faithful?
3. Are ontogenetic shifts in carbon (foraging habitat) and nitrogen (diet) isotopes concomitant?
4. Are there notable sex differences?
5. Can I detect differences in stable isotope values before and after the 1970s population crash?

To answer all these questions I used a hierarchical random change-point model: each individual was given its own set of 4 parameters describing a change-point model. For the j^{th} individual, let n_j denotes the number of available isotopic measurements. Let $K_j^{\delta^{13}\text{C}}$ ($K_j^{\delta^{15}\text{N}}$) denotes the age of the j^{th} individual when an ontogenetic shift in foraging habitat (diet) occurs.

$$\text{for } i \in [1 : n_j], \delta^{13}\text{C}_{i,j} = a_{1,j} + (\text{Age}_{i,j} - e^{a_{3,j}}) \times \begin{cases} a_{2,j} + \varepsilon_{i,1}, & \text{Age}_{i,j} \leq e^{a_{3,j}} \\ a_{4,j} + \varepsilon_{i,2}, & \text{Age}_{i,j} > e^{a_{3,j}} \end{cases} \quad (4.3)$$

$$\text{where } \begin{cases} a_{1,j} = \text{isotopic value at ontogenetic shift} \\ a_{2,j} = \text{slope before the ontogenetic shift} \\ a_{3,j} = \log(K_j^{\delta^{13}\text{C}}) \\ a_{4,j} = \text{slope after the ontogenetic shift} \\ \varepsilon_{i,1} \sim \mathbf{N}(0, \sigma_{\delta^{13}\text{C},1}) \text{ are the residuals before the ontogenetic shift} \\ \varepsilon_{i,2} \sim \mathbf{N}(0, \sigma_{\delta^{13}\text{C},2}) \text{ are the residuals after the ontogenetic shift} \end{cases} \quad (4.4)$$

and $\sigma_{\delta^{13}\text{C}}$ is the residual standard deviation, which is allowed to be different before and after the ontogenetic shift. A logarithmic transformation is used to guarantee positive values for all $K_j^{\delta^{13}\text{C}}$ or $K_j^{\delta^{15}\text{N}}$. The model implicitly assumes that only the consumer, not its prey, can experience an isotopic shift. The model described in Equation 4.3 cannot be used to infer whether it is the prey or the consumer which is moving isotopically (Matthews and Mazunder, 2004).

The individual coefficients $a_{k \in [1:4],j}$ are assumed to be exchangeable and drawn from a multivariate normal distribution of vector mean $\alpha_{k \in [1:4]}$ and covariance matrix of dimension 4:

$$\begin{pmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{pmatrix}_j \sim \text{MVN} \left(\begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \\ \alpha_4 \end{bmatrix}, \begin{bmatrix} \sigma_1^2 & \sigma_{1,2} & \sigma_{1,3} & \sigma_{1,4} \\ \sigma_{2,1} & \sigma_2^2 & \sigma_{2,3} & \sigma_{2,4} \\ \sigma_{3,1} & \sigma_{3,2} & \sigma_3^2 & \sigma_{3,4} \\ \sigma_{4,1} & \sigma_{4,2} & \sigma_{4,3} & \sigma_4^2 \end{bmatrix} \right) \quad (4.5)$$

This formulation allows to directly estimate correlations between parameter of interest via the covariance matrix. To answer questions about any differences between males and females, or between animals living before and after the population crash, I can further specify that the vector of means ($\alpha_{k \in [1:4]}$) depends on the sex of seals and whether they lived *before* or *after* the population crash:

$$\alpha_{k \in [1:4],j} = \alpha_{1,k} + \alpha_{2,k} * \text{Sex}_j + \alpha_{3,k} * \text{Crash}_j.$$

The same broken-stick model can be applied to $\delta^{15}\text{N}$: this model then calls for the estimation of two independent covariance matrices each of dimension 4: one for $\delta^{13}\text{C}$ and one for $\delta^{15}\text{N}$ (hereafter referred to as $2 \times 4 \times 4$). An obvious question is whether ontogenetic shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are simultaneous or correlated. Answering this question requires the estimation of covariance matrix Σ of dimension 8, as represented on Figure 4.6 (this model is referred to as 8×8 hereafter). Estimating a matrix such as represented in Figure 4.6 demands to constrain some elements at 0. I used a Cholesky decomposition in this end (see Appendix B).

4.3.4 Results

A hierarchical change-point model provided an adequate fit to the Southern Elephant Seal isotopic data (Figure 4.7 & Appendix D). Ontogenetic shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were generally supported, except for short time-series and a few individuals. The broken-stick model provided a better fit than a null model with no change-point (see Appendix D). The model with the most complex covariance structure (8×8 model) did not greatly improve predictive ability (Appendix D). Moreover, the estimated correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were small, with a posterior mean of ≈ 0.1 in absolute magnitude (Figure 4.6). Overall changes in $\delta^{13}\text{C}$ were not correlated with changes in $\delta^{15}\text{N}$: I can thus safely consider these correlations to be 0, which answers my question (3). There was no statistical support for distinguishing between sexes or between individuals sampled *before* or *after* the population crash: the posterior distribution of regression coefficients for both factors was as diffuse as that of its prior and included 0. This provides a straight answer to my questions (4) and (5) above: with the data set I gathered there is no difference between sexes or between seals that lived before or after the population crash.

		$\delta^{13}\text{C}$				$\delta^{15}\text{N}$				
		σ_1^2	ρ_{12}	ρ_{13}	ρ_{14}	ρ_{15}				Intercept
		0.7	σ_2^2	ρ_{23}	ρ_{24}		ρ_{26}			Slope Before
		0	-0.4	σ_3^2	ρ_{34}			ρ_{37}		Age
		0	0.1	-0.4	σ_4^2				ρ_{48}	Slope After
Intercept		0.1				σ_5^2	ρ_{56}	ρ_{57}	ρ_{58}	
Slope Before			-0.1			0.7	σ_6^2	ρ_{67}	ρ_{68}	
Age				0.1		0.5	0.6	σ_7^2	ρ_{78}	
Slope After					0.1	-0.2	0	0.2	σ_8^2	

Figure 4.6: Covariance matrix for a joint random change-point model of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Light gray squares symbolize free parameters to estimate from the data, whereas squares left blank represent parameters with no biological interpretation that are thus constrained to 0. Estimated mean correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ parameters for the Southern Elephant Seal data are shown below the diagonal.

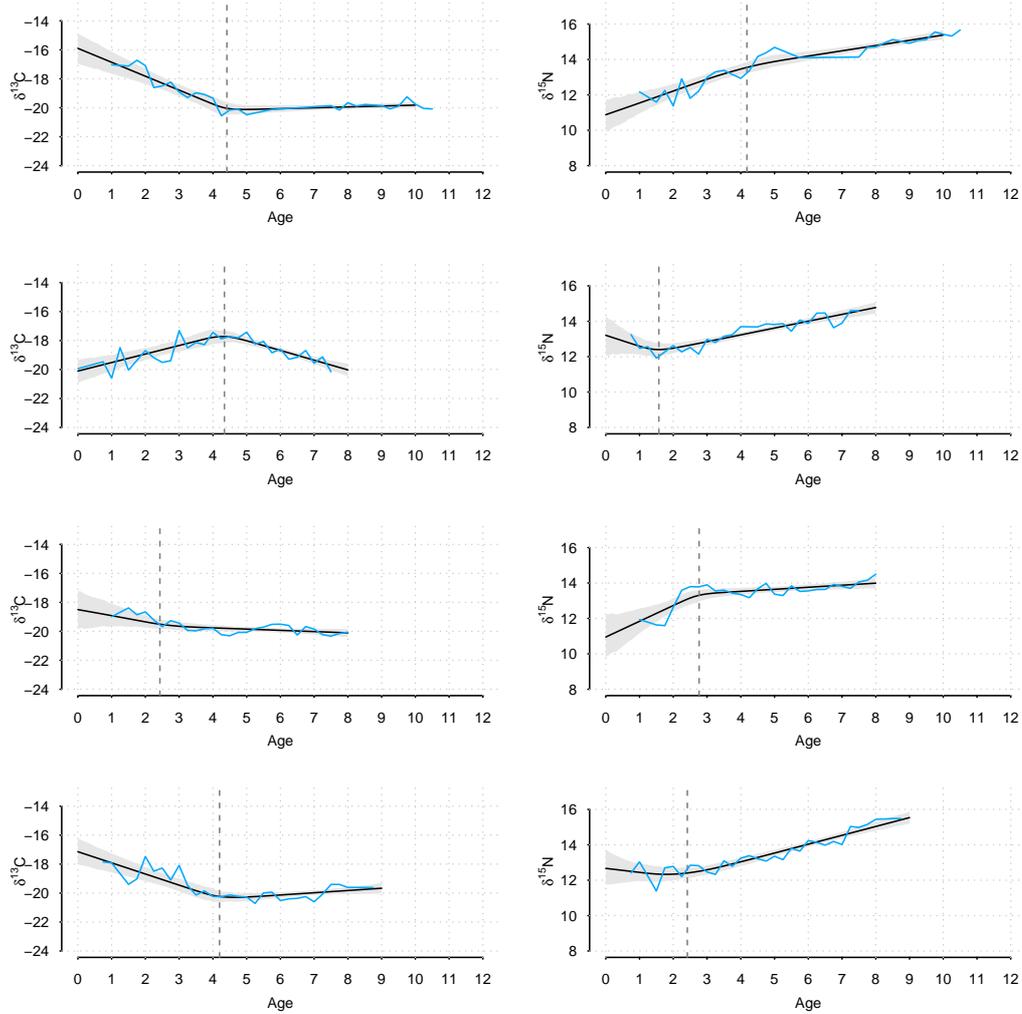


Figure 4.7: Change-point model fitted to 4 individual time-series of isotopic measurements. Each row corresponds to a different individual. $\delta^{13}\text{C}$ ($\delta^{15}\text{N}$) profiles are depicted on the left (right) panel. Grey-shaded areas represent a 95% confidence interval, while the dark line shows the posterior mean.

Results for the selected hierarchical change point model are summarized in Tables 4.1 & 4.2. The residual variances for both isotopes were larger before the ontogenetic shift (Table 4.1). I found individual heterogeneity in all four parameters $a_{k \in [1:4]}$: all variance components were well estimated (Table 4.2). The estimated age at ontogenetic shift was larger for $\delta^{13}\text{C}$ values (3.2 years) than for $\delta^{15}\text{N}$ values (1.9 years, Table 4.1). This difference was statistically significant at the 5% level. The variability in age at ontogenetic shift was similar for the two elements (Table 4.2). There is a sign reversal in slopes before and after the ontogenetic shift in both carbon and nitrogen isotopes (Table 4.1): the slope was positive and then negative for $\delta^{13}\text{C}$ and the opposite for $\delta^{15}\text{N}$. Slopes were more variable before than after the ontogenetic shift for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Table 4.2). There was respectively a small and no correlation between slopes before and after the change-point in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 4.6).

Parameter	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			Unit
	2.5%	Mean	97.5%	2.5%	Mean	97.5%	
$\sigma_{\varepsilon,1}$	0.75	0.81	0.86	0.46	0.52	0.57	‰
$\sigma_{\varepsilon,2}$	0.29	0.32	0.35	0.33	0.36	0.39	‰
α_1	-18.4	-18.0	-17.6	11.9	12.1	12.3	‰
α_2	0.01	0.21	0.43	-0.79	-0.46	-0.13	‰ per year
α_4	-0.42	-0.24	-0.08	0.11	0.20	0.30	‰ per year
K^δ	2.2	3.2	4.2	1.3	1.9	2.4	years

Table 4.1: Estimated marginals from the hierarchical change-point model fit to the Southern Elephant Seal data. $\sigma_{\varepsilon,1}$ and $\sigma_{\varepsilon,2}$ are respectively the residual standard deviations before and after the shift; α_1 and K^δ the isotopic value and age at the shift respectively, and α_2 and α_4 the slopes before and after the shift respectively.

Variance	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			Interpretation
	2.5%	Median	97.5%	2.5%	Median	97.5%	
α_1	1.81	2.88	4.08	0.46	0.72	1.03	Value at Shift
K^δ	1.13	1.56	2.29	1.27	1.60	2.17	Age at Shift
α_2	0.18	0.31	0.49	0.19	0.48	0.91	Slope before
α_4	0.03	0.20	0.41	0.04	0.08	0.13	Slope after

Table 4.2: Estimated individual-level variances in all 4 parameters governing the broken-stick model fit the Southern Elephant Seal data. Medians are reported instead of means because some posterior distributions were slightly asymmetric.

Overall, a hierarchical change-point model was supported. The ontogenetic shifts I identified can be the result of several processes, such as complete independence from maternal resources acquired before weaning (Hobson and Sease, 1998; Polischuk et al., 2001) or a shift in foraging habitat (interfrontal *versus* Antarctic waters) and diet (Bailleul et al., 2010). If the estimated shift solely resulted from a decay of maternal resources, I would not expect a difference in residual variances before and after a shift. In the case of Southern Elephant Seals, not only residual variances, but also slope variances were larger before the shift (Tables 4.1 & 4.2). This pattern may be interpreted as an individual switching from a very variable state to a more stable one, or in other words for carbon isotopes, in seals becoming faithful to a foraging strategy.

For carbon isotopes, after a juvenile stage characterized by a large residual variance, Southern elephant seals became faithful to a foraging strategy. Inferences drawn from longitudinal isotopic data are in agreement with those of biologging studies (Bradshaw et al., 2004), but the former involved a larger sample over a longer time-period than the latter. This commitment to a foraging strategy occurred at an early age, on average at about 3 years, but there was substantial individual heterogeneity (Table 4.2, Figure 4.7).

The posterior mean for the marginal slope after the ontogenetic shift was negative (for example, $\delta^{13}\text{C}$), which I interpreted as individuals foraging in Antarctic waters. These seals have to haul out on îles Kerguelen for reproduction and moulting, and they are very likely to feed on the way (Thums et al., 2011), thus diluting a “pure” antarctic signature for $\delta^{13}\text{C}$. Hence a negative slope, as the Antarctic signal becomes preponderant over the years. These data are thus in agreement with the cross-sectional data on males presented before: older seals seem to favor the Antarctic Zone. The estimated individual variability showed that some slopes after the shift were null or slightly positive, which can be a reflection of seals foraging always in the same water mass, for example in oceanic Interfrontal waters (or in Antarctic waters) (Bailleul et al., 2010).

Finally, a few individuals had a large positive slope before the shift and a shift late in life. The large positive slope before the shift may be a reflection of seals foraging in Subtropical waters before switching to an alternative strategy.

Concerning diet inferred from $\delta^{15}\text{N}$ values, the shift occurred on average earlier than for the $\delta^{13}\text{C}$ data (Table 4.1). Slopes before the shift were negative, yet they reversed sign after. Their magnitude also halved before and after the shift, with very few individual variability left after the shift (Table 4.2). This pattern suggested the shift in $\delta^{15}\text{N}$ values to mostly reflect the gradual decay of maternal influence on $\delta^{15}\text{N}$ (Hobson and Sease, 1998), followed by a gradual elevation in the trophic web as seals grew in size. Growth is indeterminate in these seals: they keep growing until their death although growth is very slow in adults (McLaren, 1993). This continuous growth means that older seals can physically catch bigger preys, which may explain why I observed a gradual elevation in trophic levels (Field et al., 2007b). This pattern was previously observed in males with blood data (Figure 4.3). Additionally, the large energy stores males must accumulate before the breeding season may also drive a shift toward large and energetically profitable preys. Residual variances were also larger before than after the shift but the decrease was not as dramatic as for $\delta^{13}\text{C}$ values (Table 4.1). Thus this shift may mostly reflect complete independence from maternal inputs.

This pattern of an elevation in trophic level with age (for example, ) does not conflict with blood isotopic data for males (Figure 4.3), but was not expected for females (for example, ). My previous analysis of blood data evidenced an elevation in $\delta^{15}\text{N}$ with increasing snout-to-tail length, a proxy for age, only in juvenile males (Figure 4.3). The discrepancy found here with dentin stable isotopes probably results from the imbalance of the female data compared to males: few time-series for females span more than 4 years (Appendix D). The limited number time-series spanning more than 4 years means that the male pattern largely dominates the population-level pattern in my hierarchical model. Thus blood isotopic data is more reliable to infer the female pattern (Bailleul et al., 2010), although the dentin isotopic analysis suggested that a few females too underwent an elevation in trophic position as they aged (that is, individuals with increasing slope after the ontogenetic shift).

A hierarchical random change-point model allowed me to answer all 5 questions I formulated:

1. Southern Elephant Seals were globally faithful to foraging strategy as inferred from their dentin $\delta^{13}\text{C}$ profile. A juvenile phase characterized by large variations and an overall increase in $\delta^{13}\text{C}$ was followed by more stable values. There was also an ontogenetic shift in diet, but this shift was most likely a reflection of complete independence from maternal resources acquired before weaning. Once completely emancipated from maternal resources, seals fed at increasing trophic levels with age.
2. The timing of the ontogenetic shift varied for each individual but occurred on average around 3 years for foraging strategy ($\delta^{13}\text{C}$) and 2 years for diet ($\delta^{15}\text{N}$).
3. The timing of the two ontogenetic shifts were not correlated.
4. There were no detectable sex differences in the data set I used. This finding was surprising, even suspicious in light of my previous results with blood isotopic data. It is more likely a reflection of the imbalance between the number of observations for each sex (1115 *versus* 299 for males and females respectively). In addition, sampled females were younger than males which may have prevented an accurate assessment of their isotopic ecology. Thus my data is more suitable to investigate foraging patterns in males.
5. I did not find any effect of the population crash in the isotopic values of dentin. The dentin isotopic data was collected on dead animals recovered on land; animals that died at sea are missing. In addition these data are biased toward large males and against young age classes. Because of the lack of information on these missing fraction of the population, the data only suggested that there were no difference between adult males that lived before and after the population crash.

Taken together, these results suggest that my ability to draw inferences on females is limited in this data set. The model I used was useful to investigate indirectly with stable isotopes the development of foraging. One implicit assumption of the model, worth repeated, is that I assumed that the seals and not their preys were moving isotopically. This seems reasonable given the large foraging range of Southern Elephant Seals (Figure 3.4) and the fact that they feed on prey much smaller than themselves, such as myctophid fish or cephalopods (Rodhouse *et al.*, 1992; Cherel *et al.*, 2008). One obvious extension of the model is to incorporate age-at-death, or longevity, of males and assess whether it correlates with their foraging strategy.

4.4 Ecological Correlates of Longevity

4.4.1 Longevity in the Wild

As previously mentioned, sampling teeth from mammals also yields information on their age. If teeth are sampled on dead marine mammals, it becomes possible to estimate the age-at-death of the specimen. Age-at-death or longevity has long been a life-history trait of considerable scientific interest (Gompertz, 1825; Beeton and Pearson, 1901). In wild animal population, Capture-Mark-Recapture data collected over several decades now point to the importance of longevity as a component of individual fitness (Berubé et al., 1999; Descamps et al., 2006; Gaillard et al., 2000; Kruuk et al., 2000; Weladji et al., 2006; Pettoirelli and Durant, 2007; Kjellander et al., 2004). In the case of mammal species, most studies investigating the relationship between longevity and fitness have focused on females (Berubé et al., 1999; Descamps et al., 2006; Gaillard et al., 2000; Weladji et al., 2006; Pettoirelli and Durant, 2007; Beauplet and Guinet, 2007; Kjellander et al., 2004; Hamel et al., 2009, 2010) (but see Kruuk et al. (2000) for a counterexample), most likely because estimating male fitness is even harder to measure and often demands genetic analysis. These studies, which mainly concerned large terrestrial herbivores, usually found evidence of long-lived females having a larger fitness, assessed via their offspring production, than short lived ones (but see Descamps et al. (2006) for a counter example).

The data set I gathered may actually be not suitable to investigate longevity in female Southern Elephant Seals, but it is for males. Southern Elephant Seal are the most dimorphic and polygyneous mammal among extant species. Given that they can spend up more than 80% of its lifetime at sea (McIntyre et al., 2010), seals are simply not observable most of the time. Moreover, when ashore during the breeding season, males fight for holding harems of numerous females. The distribution of male reproductive success is severely right-skewed with most males never reproducing but a few mating with a large number of females (Galimberti et al., 2002). Body size is a critical component for holding and fighting over a harem. Since these seals can grow all their life (McLaren, 1993), breeding for a male very likely depends on surviving long enough to reach an adequate size to pretend at holding a harem. I may therefore expect a strong relationship between longevity and fitness in males (Jones, 1981). Yet, assessing longevity in the male Southern Elephant Seal using Capture-Mark-Recapture methods may prove too demanding: less than 4% of a cohort may survive up to 9 years-old (Pistorius et al., 1999b), when they may become harem-holders (Jones, 1981; Galimberti et al., 2007). Moreover the question of why these males manage to outlive the other is left open since what they are doing at-sea remains elusive. Indirect evidence provided by stable isotopes may here allow me to shed light on any relationship between foraging and longevity in male Southern Elephant Seal breeding on Îles Kerguelen.

4.4.2 Joint Longitudinal/Survival Models

Survival analysis deals with the analysis of time-to-event data (Clark et al., 2003). Longevity, or age-at-death, is rarely normally distributed, nor is the distribution usually symmetric (Clark et al., 2003). Longevity is the result of cumulative survival until death occurs. The concept of hazard refers to the probability of an individual, having survived up to time t , dies at time $t+dt$, that is hazard represents the instantaneous rate of mortality at time t . In wild populations of vertebrates, the hazard function usually has a bathtub shape (\cup) with many individuals dying young (very high hazard), few dying in their prime-age and a spurt in mortality for late age-classes (Choquet et al., 2011). Such data are also censored, that it is more common to know that an individual has lived up to a certain age, than to know precisely its age-at-death. These peculiarities of time-to-event data have motivated the development of a devoted methodology to their analysis (Bradburn et al., 2003a; Clark et al., 2003).

In the data set gathered on Southern Elephant Seals, there is no censored observation and the distribution of age-at-death is actually not extremely skewed:  where the histogram starts at age 0 and ends at age 12 and the two highest bars correspond to age-classes 6 and 8. This results from the bias against young individuals, probably dying at sea, and thus not sampled from canine teeth recovered on land. Age-at-death is one part of the data I gathered and the other part is a longitudinal isotopic profile of seals that reflect their foraging strategy. The question is then to assess whether the longitudinal variable ($\delta^{13}\text{C}$) is correlated with the survival endpoint (longevity). A joint modelling approach consists of linking two submodels: a *measurement model* describing the longitudinal process and an *intensity model* describing the survival process (Henderson et al., 2000; Guo and Carlin, 2004). As Guo and Carlin (2004) remarked '[w]hen association between the two processes exists, I should obtain less biased and more efficient inferences by using this joint model'.

The longitudinal data for $\delta^{13}\text{C}$ values is depicted of Figure 4.8 which illustrates the dual foraging strategy of Southern Elephant Seals. The hierarchical random change-point model (see Equation 4.3) I described in the preceding section provided an adequate description of the $\delta^{13}\text{C}$ profile of each individual: it described with two linear segment a juvenile stage followed by an adult one wherein seals are faithful to a foraging strategy. I choose to model the intensity process with an Accelerated Failure Time model. The AFT model is an alternative of the more commonly used Cox Proportional Hazard (PH) model (Cox, 1972). With the AFT, survival times are directly modelled which eases the interpretations of coefficients, but a parametric distribution family must be specified (Bradburn et al., 2003a; Swindell, 2009) in contrast to the semi-parametric PH model. The core assumption of the AFT is a monotonic hazard function (Bradburn et al., 2003b), which seems reasonable for these data (empirical hazard function: \cup).

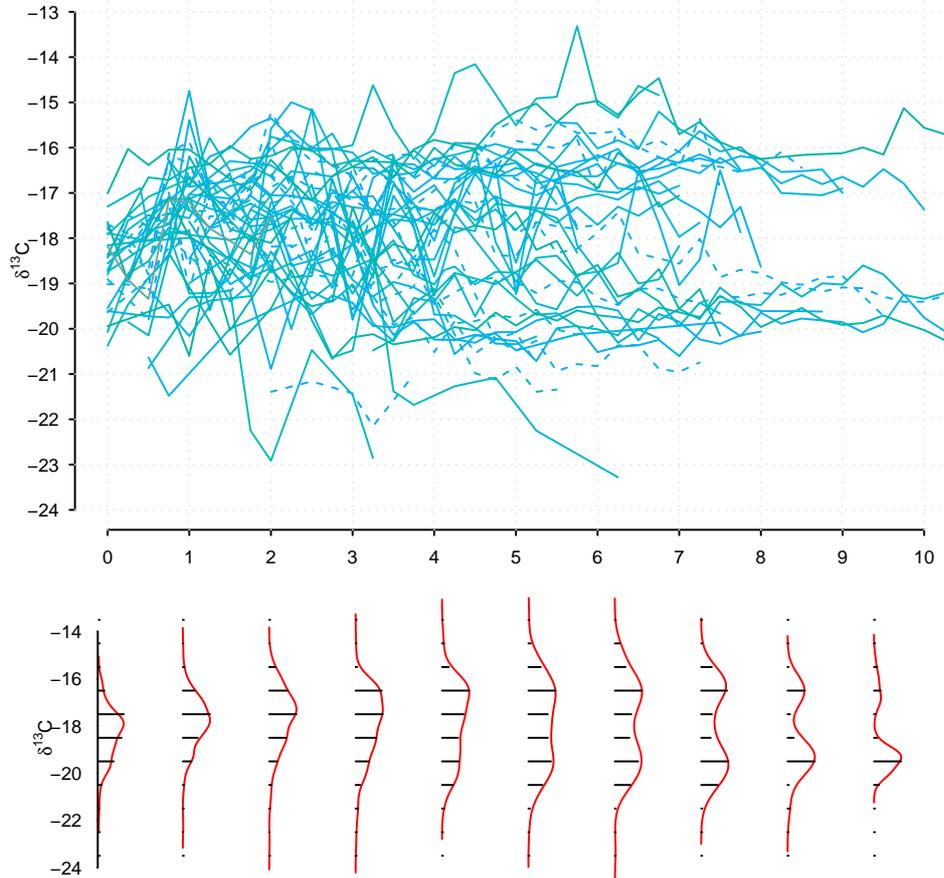


Figure 4.8: Spaghetti and density plots of the tooth $\delta^{13}\text{C}$ values from male Southern Elephant Seals from îles Kerguelen stratified by age. The distribution is unimodal up to age 3 but changes to a bimodal distribution afterwards.

Let's denote the survival time of the j^{th} male by Longevity_j . I assumed the Longevity_j to follow a Weibull distribution of shape parameter r and scale parameter λ_j :

$$\text{Longevity}_j \sim \text{Weibull}(r, \lambda_j) \quad (4.6)$$

$$\log(\lambda_j) = \beta_0 + \beta_1 * a_{1,j} + \beta_2 * a_{2,j} + \beta_3 * a_{3,j} + \beta_4 * a_{4,j} \quad (4.7)$$

$$\text{where } \begin{cases} a_{1,j} = & \text{isotopic value at ontogenetic shift} \\ a_{2,j} = & \text{slope before the ontogenetic shift} \\ a_{3,j} = & \log(\text{age at ontogenetic shift}) \\ a_{4,j} = & \text{slope after the ontogenetic shift} \end{cases} \quad (4.8)$$

The shape parameter r controls the hazard rate with $r > 0$ (resp. < 0) describing an increasing (resp. decreasing) hazard with time. With my data, I expected $r > 0$ (empirical hazard function: ) . The parameters $\beta_{1,2,4}$ then quantify the association between foraging location (via $\delta^{13}\text{C}$) and longevity. The parameter β_3 captures the relation between age at ontogenetic shift and longevity. The parameter I am particularly interested in is β_4 as it reflects the correlation between the stable foraging habitat of adults and their longevity. In the AFT, a positive $\beta \times x$, where x is the covariate value, accelerates the occurrence of the event (death), while a negative value retards it. Thus, a negative β_4 means that individuals foraging in two different water masses (negative slope) die earlier than those males which have a very stable strategy (null slope).

I compared this joint model with 3 other AFT survival models: a null model with no individual-level covariate; a model with the mean $\delta^{13}\text{C}$ value of each individual incorporated as a covariate; and lastly I used a mixture model to assign each male to a foraging strategy depending on its mean $\delta^{13}\text{C}$ value and then group membership was included as a covariate for the AFT model.

Model comparison was done using the Akaike Information Criterion with a small sample correction, AIC_c^7 (Burnham and Anderson, 2004). My sample size is modest ($N = 47$) and the most complex AFT model considered had 6 parameters, keeping the ratio of sample size to parameter number above ≈ 8 which is slightly below the recommended 10 (Bradburn et al., 2003b). The goodness-of-fit of the selected model was checked by comparing the predicted longevity with the observed one using Kolmogorov-Smirnov test. I investigated in a preliminary analysis whether males born before and after the 1970s population crash (Guinet et al., 1999) had different longevity and found none (Likelihood Ratio Test: $\chi_1^2 = 0.03$, $p = 0.86$).

⁷ AIC_c was chosen because the number of parameters within each AFT models was easily enumerable.

4.4.3 Results

The best model for male longevity was the joint change-point/survival model (Table 4.3)⁸, yet model fit as assessed using Kolmogorov-Smirnov test, was poor ($D = 0.5745$, $p < 0.001$). Further investigations also revealed large correlations (> 0.6) between the $\beta_{k \in [1:4]}$ (see Figure D.4 in Appendix D). Close inspection of the individual-specific parameters $a_{k \in [1:4]}$ revealed that the only parameter to truly covary with longevity was a_4 , the slope after the ontogenetic shift (Figure 4.9, Appendix D). Hence only the posterior estimate of β_4 is reported: $\beta_4 =_{-2.8} -1.4_{-0.1}$. Since β_4 was negative, males with a very stable foraging strategy ($a_4 \approx 0$) had on average a larger life-span than the other males.

Model	K	Deviance	AIC _c	Δ_{AIC_c}	w _{AIC_c}
Joint	6	202.2	215.6	0.0	94.5
Null	2	218.4	222.5	6.9	3.0
Mixture	4	215.6	224.1	9.0	1.4
Mean $\delta^{13}\text{C}$	3	218.3	224.6	9.5	1.1

Table 4.3: Accelerated Failure Time (AFT) model selection. Δ_{AIC_c} is each model AIC_c minus the minimum AIC_c, and w_{AIC_c} are model weights (Burnham and Anderson, 2004). The best model in term of predictive ability was the joint change-point/survival model.

The sophisticated joint modelling approach confirmed what an “eye-ball” analysis suggested: isotopic profiles with the littlest variation were the longest (Figure 4.8). Seals that exhibited little variation in their tooth $\delta^{13}\text{C}$ profile were also the most long-lived. My change-point model previously described evidenced a negative correlation between the age at ontogenetic shift and the slope after this shift (Figure 4.6): seals that had an early shift were constant in their foraging behaviour for the rest of their life (that is a null slope). The two modes that progressively appear with age on Figure 4.8 reflects how seals that became faithful to a foraging strategy early on lived longer than the others.

⁸I also computed the Deviance Information Criterion. Model selection with DIC was unchanged, but the Mixture model ranked higher than the Null model. The effective number of parameters seemed too low for the Mixture model though.

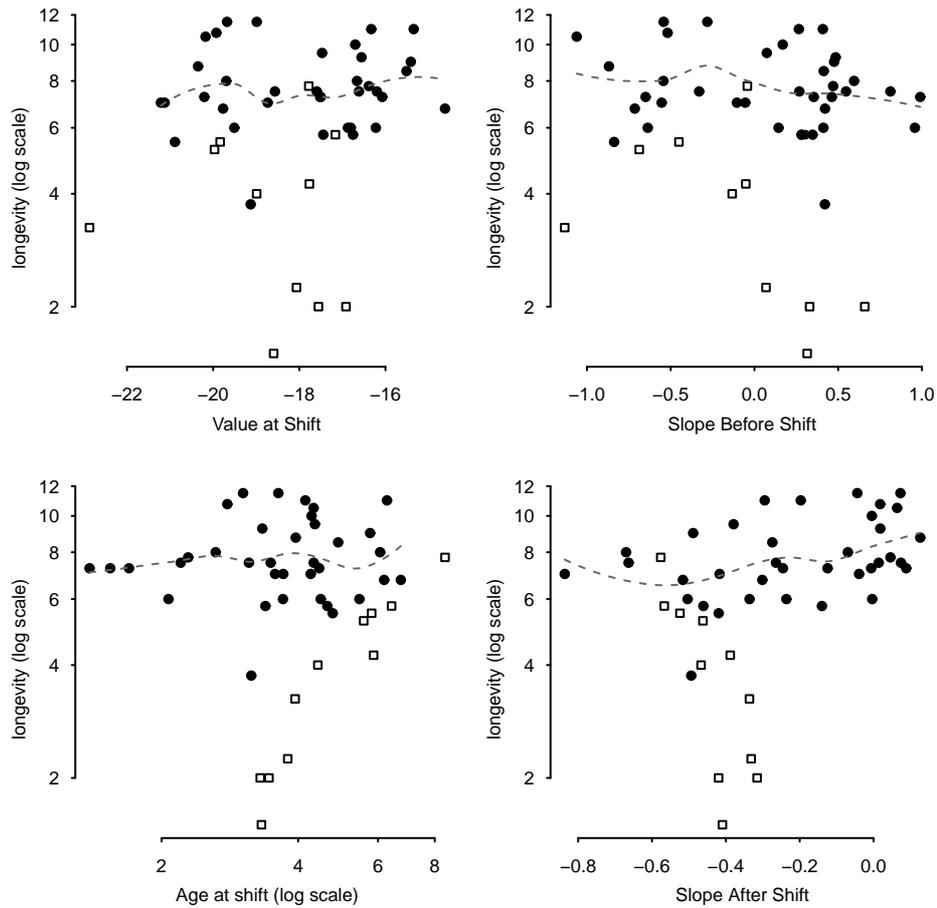


Figure 4.9: Checking of the joint change-point/AFT model. Longevity of male Southern Elephant Seals are plotted against their individual-specific parameters describing a broken-stick time series of $\delta^{13}\text{C}$ values. The dashed gray line is a loess curve, fitted to reveal any trend. Data points depicted with an open square-symbol symbolized individual for which the change-point model was not supported: the model predicted a larger age at ontogenetic shift than the life-span of the animal.

4.4.4 Life-History Consequences of Early Life

This pattern of an early shift in life associated with far-reaching consequences in later-life underscore how crucial are the first years of life in this species (McMahon *et al.*, 2005*b*). The change-point model previously revealed that the mean slope before the shift was positive (Table 4.1). The positive slope before the shift was expected because weaned pups rely exclusively on maternal milk before weaning. Phociid milk is very rich in lipids (Carlini *et al.*, 1994; Hindell *et al.*, 1994), which are depleted in the heavier carbon isotope (DeNiro and Epstein, 1977). Thus the positive slope before the shift may in part reflect the progressive independence from maternal resources (Hobson and Sease, 1998; Martin, 1984; Polischuk *et al.*, 2001). Pups, which became early on independent from maternal resources, were able to forage on their own and adopted a very stable foraging strategy, lived longer than the other pups, suggesting thereby the potential importance of early life history for latter performances (Aubry *et al.*, 2011; Cam *et al.*, 2003; Lindström, 1999).

Given the pattern uncovered with blood stable isotopes (Figure 4.2), it was somewhat surprising that the Antarctic strategy was not associated with an increased life-span. There is some evidence suggesting that an Antarctic strategy yields higher fitness pay-offs, at least for females: breeding females with a blood $\delta^{13}\text{C}$ value reflective of an foraging in Antarctic waters had a larger probability of weaning a large pup (see Chapter3). Likewise, there is a latitudinal gradient in pup weaning mass with pups born in colonies closer to Antarctica having a larger weaning mass on average than pups born at lower latitude rookeries (Burton *et al.*, 1997). As weaning mass correlates with first-year survival (McMahon *et al.*, 2003), this suggests again that resources in Antarctic waters may be more profitable. Yet the pattern with males was mixed.

Unlike females which remained in the marginal sea-ice zone, juvenile male Southern Elephant Seals from îles Kerguelen readily foraged in the pack ice (Bailleul *et al.*, 2007*a*). This suggests that getting trapped in the ice is a potential cause of mortality that males foraging over the Kerguelen Plateau or in the Interfrontal Zone do not face (Bailleul *et al.*, 2010). Yet, the present analysis does not point to different foraging grounds influencing male life-span. The pattern uncovered is one of the benefit of a very stable foraging strategy from an early age in life. This pattern may lend support to a spatial familiarity hypothesis (Metzgar, 1967; Wolf *et al.*, 2009*a*), although a direct experimental test of such an hypothesis seems difficult with Southern Elephant Seals.

Changing its foraging strategy thus seemed costly in Southern Elephant Seals. Such costs may arise from unfamiliarity with novel environments, such as a greater susceptibility to predators, or increased travel costs. An alternative, non-exclusive, interpretation is that some individuals were more able to extract resources efficiently from the environment, either in Antarctic or Interfrontal waters. None of these interpretations suppose a strategy to be superior to the other in terms of fitness return. However, the second interpretation implies that seals which are less efficient to acquire resources may switch between foraging strategies while those which are efficient have no reason to do so. Under this latter interpretation, the $\delta^{13}\text{C}$ profile of seals may reflect their 'quality'.

A potential confounding factor in my data is that teeth were sampled from dead animals on beaches, thus I have to assume my sample is representative of the larger population of all males on Îles Kerguelen. Assuming otherwise would imply that males found dead on beaches were different than those dying at sea. The average longevity in my sample was 7 years, and only 5 males were older than 10 years (). In their study on reproduction costs on Sea Lion Island (52°26' S, 59°05' W), Galimberti et al. (2007) found only 4 males out of 78 (that is, $\approx 5\%$) that were older than 10 years old, while McCann (1980) reported a proportion of $\approx 22\%$ for South Georgia (54°15' S, 37°05' W). The observed proportion in my sample was 41.24%, compatible with both the Sea Lion Island and South Georgia estimates. Age in my study was estimated from teeth growth layers: there is thus an uncertainty associated with age (± 1 year). Yet it is very small (Martin et al., 2011), and cannot reverse the observed pattern. Defining a species' longevity as the time by which 99% of a cohort has died (Edney and Gill, 1968), the specific longevity of male Southern Elephant Seals is 13 years (Pistorius et al., 1999a). The oldest male in my sample was estimated to be 12 years old, which suggests that my sample does not seem atypical with respect to old age classes.

Another concern is the lack of fit of the AFT model to the data. Even my best model in terms of AIC_c did not provide an adequate fit to the data⁹. Yet it has been argued that the poor predictive ability is an intrinsic feature of survival models with realistic parameter values (Henderson et al., 2001). The joint model clearly captured some aspect of the data unaccounted for by the Null model given its large Akaike weight (Table 4.3). Further model checking revealed that this model was overparametrized, but still performed better than the Null model despite the penalty for the larger number of (unnecessary) parameters. The Mixture model also has a larger likelihood than the null model, although it is penalized by a larger number of parameters¹⁰, and in the end it is on a par with the Null model (similar Akaike weights). Thus the data suggest an effect of the foraging strategy, that I seemed to have picked up best with a change-point model.

⁹Adding a 'frailty' term did not improve the model.

¹⁰This was true with AIC_c but not with DIC.

In summary, the explicitly modelling of foraging strategy ontogeny in male Southern Elephant Seal via a change-point model of $\delta^{13}\text{C}$ values revealed how long-lived animals were those faithful to a foraging strategy from an early age, emphasizing the importance of early life in life-history trajectories. Studying of the life-span of wild animals is a difficult endeavour: ecological correlates can be uncovered but a large amount of variation usually remains unaccounted for (Gaillard *et al.*, 2003). This is unsurprising thinking of all the potential factors, related to fitness or accidental, that may affect an individual throughout its whole life (Kjellander *et al.*, 2004; Turner and Hanley, 2010).

Concluding Discussion

Contents

5.1	Indirect evidence	90
5.2	Mixture Models and Stable Isotopes	91
5.3	Some Limits of Indirect Evidence	94
5.4	Where to Next?	97

5.1 Indirect evidence

In this work I explored how stable isotopes of animal tissues could provide answers to some questions regarding the foraging ecology of Southern Elephant Seals on îles Kerguelen. In particular, the red thread of this work was to assess whether stable isotopes could help understanding the population decline of Southern Elephant Seals that happened during the 1970s (Chapter 2), before the development of satellite remote sensing of environmental conditions (Sea Surface Temperature, Sea Ice Extent, *etc*). Several causes have been put forward to explain this decline (McMahon *et al.*, 2005a). The two most plausible ones deal with a widespread decline in prey abundance either through an ecosystem regime shift (Weimerskirch *et al.*, 2003) or through an unprecedented overexploitation of the Southern Ocean by man (Ainley and Blight, 2009).

Because direct evidence is lacking, stable isotopes may fill a gap in our understanding. Yet it should also be kept in mind that any interpretation of indirect evidence is inherently more fragile than direct measures of the phenomenon of interest. Throughout this work, I endeavoured to privilege sophisticated modelling approaches, both to explicit most of the underlying assumptions and to take into account as many sources of variations as possible. This work focused more on inferring the latitudes at which seals were foraging rather than on what prey they may have consumed.

I first quantified the expected difference in $\delta^{13}\text{C}$ between seals foraging in Antarctic and Interfrontal waters (Chapter 3) to have a sense of how big should be the difference between the two $\delta^{13}\text{C}$ signature. In a previous study on the same population, Ducatez *et al.* (2008) validated how the blood $\delta^{13}\text{C}$ value of new-born and weaned pups reflected the blood $\delta^{13}\text{C}$ value of their mother. They expected a bimodal distribution in blood $\delta^{13}\text{C}$ values but found none () although the distribution was clearly skewed. This result was surprising compared to other species of pinnipeds (fur seals) or penguins (Cherel *et al.*, 2007), but may result from the large size of Southern Elephant Seals. Their large size and their ability to store reserves probably results in a smoothed isotopic signal compared to smaller species. In addition, recent biologging studies evidence the ability of Southern Elephant Seals to feed continuously along a foraging trip (Thums *et al.*, 2011). While Area Restricted Search behaviour is probably still associated with intense foraging, these seals are also able to eat while travelling in a more or less straight line. This behaviour is introducing measurement error for the purpose of inferring the foraging strategy of Southern Elephant Seals. While two clear modes were not easily visible in the distribution of blood $\delta^{13}\text{C}$ value of pups, a mixture model was nonetheless successfully fit to these data: the two modes are separated by an expected difference of only ≈ -2 or -1.5% (Chapter 3), which is rather modest and may explain why a clear camel-back shape was not recovered.

The expected isotopic difference in blood $\delta^{13}\text{C}$ value was ≈ -2 or -1.5‰ (Chapter 3), which is smaller than estimates from albatross $\delta^{13}\text{C}$ values (-3‰) (Jaeger et al., 2010). This discrepancy illustrates what I believe to be a broader problem within isotopic ecology about the effect size of estimates. Accurate estimation of isoscapes is paramount to assign correctly the location of foraging¹. Current practice in isotopic ecology emphasizes testing for differences in mean isotopic values (*t*-test, ANOVA, etc.). This type of analysis tends to lose sight of the problem we are really interested in: if given the isotopic value from a newly sampled individual, with how much certainty can we assign it to a foraging strategy or the other? This question deals explicitly with variation, while *t*-tests and the like tend to focus only on the mean response². Variability often matters more than the average: too much overlap between groups renders the use of a mean not very helpful.

5.2 Mixture Models and Stable Isotopes

This realization led me to mixture models as useful tools to classify seals into Antarctic or Subantarctic foragers. This kind of analysis explicitly deals with variation and allows to make *probabilistic statements* on individual observations. Focussing on females, a mixture modelling approach showed that there was no relationship between Snout-to-Tail Length and foraging strategy (Chapter 3). Using the blood carbon isotopic ratio of a pup, I used another mixture model approach to assess the fitness consequences of each female foraging strategy via the weaning mass of her pup. This analysis unveiled a bell-shaped relationship between $\delta^{13}\text{C}$ value and a pup's weaning mass. This was surprising as *a priori* a more simple relationship between latitude and weaning mass was expected given how much larger are weanlings born in colonies close to the Antarctic (Burton et al., 1997). This analysis showed that the few females with a very negative $\delta^{13}\text{C}$ value, a strong indicator of an Antarctic foraging strategy, weaned large pups with certainty. Yet, their scarce proportion among the large collected sample (≈ 700 individuals) points to the marginality of such unambiguous observations. For a large part of the sample, the uncertainty in classifying pups as either small or large weanlings was large. This analysis did not support a perfect mapping of foraging strategy onto fitness group: large weanlings could also be observed with a blood $\delta^{13}\text{C}$ value suggestive of Subantarctic maternal foraging (either Interfrontal or on the Kerguelen Plateau).

¹This problem belies the infamous scheme of the UK Border Agency to test with stable isotopes the country of origin of asylum seekers (Travis, 2009; Balding et al., 2010). Without a precise knowledge of all isoscapes, such an enterprise is not reliable. Hopefully this scheme which costed £190,000 ended in June this year (Travis, 2011).

²Additionally, these analyses are relying mainly on statistical significance, which is subject to the 'winner's curse': if an estimate is statistically significant, it is likely to be an overestimate (Lehrer, 2010).

The various analyses of stable isotopes data suggested that female were faithful to a foraging strategy as was found with track data on seals from Macquarie Island (Bradshaw et al., 2004). The analysis of pup weaning mass further suggested that foraging only in Subantarctic waters was more likely to yield smaller fitness gain than other foraging strategies. The uncovered non-linear relationship between pup weaning mass and their blood $\delta^{13}\text{C}$ values (Figure 3.9) argued against a perfect mapping between foraging strategy and fitness in female Southern Elephant Seals from îles Kerguelen. The group of large weanlings is more likely a composite group itself, an aggregate of pups whose mothers may differ in foraging strategy, in ingested preys or experience, although this last factor was somewhat less important than the others. This picture emphasized the importance of individual level characteristics, and maybe that of diet specialization (Chapter 4).

Unfortunately, this question could not be answered: is the population of Southern Elephant Seals made up a specialists or are every seals very opportunistic? The broadening in blood $\delta^{15}\text{N}$ values observed in the cross-sectional data on females suggested that older females may be feeding on a larger panels of preys, either from lower or upper trophic levels, than younger females. The isotopic longitudinal data collected from teeth were not able to resolve this question either: the recovered time-series were too short for females and may reflect a sampling bias due to young, possibly primiparous, females more likely to die during their first parturition on land. Yet, the analysis of pup weaning mass also pointed to preys from lower trophic levels being more profitable. If females were indeed specialists and preying consistently on the same preys, it could be possible for some females to wean only low fitness pups (for example, those females with nitrogen isotopic profile resembling ) and for others to have high fitness pups (). The data examined in the present thesis cannot bring a definite answer to this question.

As for males, the broadening in blood $\delta^{15}\text{N}$ values observed in the cross-sectional data is accompanied with a gradual, but systematic, elevation in trophic level. Longitudinal data confirmed this result, stressing also the widespread between-individual variability. This between-individual variability may be responsible for the increased dispersion of $\delta^{15}\text{N}$ observed in cross-sectional data. The gradual elevation in trophic level probably reflects the physiological needs of large individuals. Of course, not all males are expected to grow at the same rate, growth being itself very much dependent on foraging. While it is likely that males may broaden their prey panel as they age, the uncovered inter-individual variability is a confounding factor. The longitudinal data pointed to the importance of foraging stability from an early age as a predictor of longevity in males. However, a large amount of variation was still unaccounted for. The cross-sectional data strongly showed that bigger males were also more likely to forage in Antarctic waters than smaller ones. Teeth data also suggested an increased proportion of Antarctic feeders with age (inferred from the negative slope after the change-point, Table 4.1) and a cost (reduced longevity) in switching between strategies late in life.

One way to further resolve this matter would be to collect data on breeding males directly. Yet direct handling of such large animals is very difficult (Carlini et al., 2009). A solution may be to sample from a distance the skin of large breeding males (beach masters) and that of peripheric males to compare their isotopic values in carbon. Since moulting occurs after a post-breeding trip, skin $\delta^{13}\text{C}$ would reflect where breeding males have been foraging following the previous breeding season. The collected data would again be cross-sectional in nature, but here the exact status of males is known (beach masters, subordinates) and could resolve whether high fitness males are predominantly those foraging in Antarctic waters, given, as the teeth data showed, that adult males are faithful to a foraging strategy.

Studying Southern Elephant Seals with stable isotopes proved successful. The difficult question of assessing faithfulness of seals to a foraging strategy was tackled using isotopic measurement of blood and dentin tissues. The overall pattern is different between males and females. For females, most of the relevant data in this thesis are of cross-sectional nature and consistently suggest that female Southern Elephant Seals are faithful to their foraging grounds. The fitness consequences in terms of reproductive performance were explored with the analysis of pup weaning mass. I uncovered a small correlation between weaning mass of pups and Chlorophyll *a* concentration in Subantarctic waters (Chapter 3). This correlation was discussed in terms of plausibility: albeit the exact diet of Southern Elephant Seals is unknown (Cherel et al., 2008; Eder et al., 2010), we know for sure they don't feed on chlorophyll or phytoplankton. The link between Chlorophyll *a* concentration and female foraging success must be indirect. Recent evidence points to such an indirect role of phytoplankton: high phytoplankton concentrations were associated with decreased dive depths (Dragon et al., 2010). Higher phytoplankton concentrations may increase light attenuation into the water column and may 'fool' myctophid fish, which undertake nycthemeral migrations, to swim up the water column where they are more accessible to seals (Jaud, 2011).

For males, longitudinal data were also available. As males aged, most of them seemed to switch to foraging in Antarctic waters after a juvenile stage when their foraging strategy seemed more flexible. Thus the observed pattern with the cross-sectional data was not the result of an increased survival of animals that were foraging in the Antarctic Zone, but truly a shift in foraging grounds. However, the few males that were strongly committed to a foraging strategy from an early age were also the longest-lived ones. The fitness consequences in terms of survival were explored for males, but not in terms of reproductive output.

5.3 Some Limits of Indirect Evidence

I mentioned above the fragile nature of the evidence given by stable isotopes, but this does not mean that this evidence can be easily dismissed either. As argued in Chapter 1, stable isotopes are extremely relevant to the study of species with cryptic lifestages, species that are too small to be instrumented with electronic tags or endangered species. Yet the indirect nature of the evidence they provide demands an analysis tailored to the question at hand. The many-to-one mapping that results in an isotopic signature (for example, I was not able to distinguish between the Kerguelen Plateau and the Interfrontal Zone with blood stable isotopes in Chapter 3) means stable isotopes measure something, but they are not perfect instruments either. This was evident both in my analysis of pup blood data and adult dentin data. In both cases, the pattern recovered left a substantial amount of variability unaccounted for.

The dentin isotopic profiles for example showed a large variability which was puzzling compared to the *a priori* expectations of well-behaved cycles copying the two annual migrations (Figure 1.4). Such well-behaved patterns were found in Antarctic Fur Seals from îles Kerguelen (Cherel et al., 2009) or Southern Right Whales (Best and Schell, 1996). The discrepancy probably arose because both Antarctic Fur Seals and Southern Right Whales do not feed *en route*, and because the temporal resolution of the dentin data is low compared to that of whiskers (fur seal) or baleen plate (whale). Yet the strength of this data was that ageing the animal was possible. The hierarchical change-point model described in Chapter 4 was useful as an overarching model to extract a common pattern and reduce a longitudinal isotopic profile to just 4 parameters. This came at the price of ignoring for example the few cycles observed in the data. Nevertheless, this approach allowed to further correlate foraging location as inferred from $\delta^{13}\text{C}$ to longevity using a joint modelling approach developed in epidemiology (Guo and Carlin, 2004; Horrocks and van Den Heuvel, 2009; Liang et al., 2009; Gao et al., 2011). This joint model revealed that animals which were the long-lived were also those which I inferred to exhibit the highest fidelity to a foraging strategy.

The present work is indeed making use of a lot of statistical models, which is necessary given the many sources of variation that can affect stable isotopes. It may also have been the consequences of working on a large, capital-breeding species, for which the turn-over rate of blood for example was found to be larger than anticipated (Chapter 3). Yet, it is noteworthy that such model-based methods are on the rise in isotopic ecology. For example, [Hénaux et al. \(2011\)](#) and [Van Wilgenburg and Hobson \(2011\)](#) described Bayesian models to estimate the probable origin of migrating wild animals. [Parnell et al. \(2010\)](#) and [Semmens et al. \(2009\)](#) described Bayesian mixing models to estimate the probable diet of consumer from isotopic data only. Finally, [Jackson et al. \(2011\)](#) recently described a Bayesian framework to estimate isotopic niche width which outperforms existing methodology ([Layman et al., 2007](#)) and allows more quantitative tests of niche theory within community ecology.

Some of the problems associated with stable isotopes in the wild (for example, the many-to-one mapping issue) can be partially alleviated through the careful use of statistics. Issues about estimating small effects are, in my opinion, especially pressing. For example, in Chapter 1, I shortly described some isotopic gradients found in nature. These gradients are the results of several factors linked to fractionation of carbon isotopes. Quite notably, phytoplankton cellular growth rates have been advanced as a major cause of isotopic fractionation: more productive environment are enriched in ^{13}C ([France, 1995](#); [Schell, 2000](#)). This relationship has been used then to infer from $\delta^{13}\text{C}$ in archive tissues (baleen plates) the past productivity of whole ecosystem, for example the Bering Sea ([Schell, 2000](#)). [Schell \(2000\)](#) found a decrease of $\approx -2.7\%$ over time in the average $\delta^{13}\text{C}$ of baleen plates sampled from whales hunted for subsistence. For this figure, [Schell \(2000\)](#) estimated a decrease of between 30-40% in average seasonal primary productivity between the 1960s and the 1990s. Such a decrease is huge and is suspicious as such.

[Newsome et al. \(2007\)](#) also challenged this result using again stable isotopes from Northern Fur Seal (*Callorhinus ursinus*) teeth. While [Newsome et al. \(2007\)](#) also evidenced a decrease in the average $\delta^{13}\text{C}$ value of juvenile Northern Fur Seal teeth, the effect size was less than half of [Schell \(2000\)](#). The $\delta^{13}\text{C}$ evidence to infer past productivity relies on many *ceteris paribus* clauses such as no changes over the period considered in phytoplankton community composition, in dissolved CO_2 , etc.. This position may not be defensible: the Suess effect, which is an overall decline in $\delta^{13}\text{C}$ values due to the antropogenic combustion of large amount of fossil fuel in the atmosphere, flies in the face of the all-else-being-equal assumption. Finally, dissolved CO_2 which affect phytoplankton fractionation also depends on temperature, has also been rising in many large marine ecosystems, including the Bering Sea ([Belkin, 2009](#)).

The picture is thus one where many factors affect a $\delta^{13}\text{C}$ value, and these factors have opposite effects. Thus while it is possible to predict qualitatively the direction of change from any one factor, their interaction messes up the picture considerably (Rau et al., 2001). This situation creates predictive promiscuity³ and a causal conundrum as it becomes increasingly difficult to rely on all-else-being-equal arguments to infer *the causes of effect*, here a drop in $\delta^{13}\text{C}$ value. In addition, all these factors have arguably small effects which are difficult to estimate accurately (Gelman and Tuerlinckx, 2000): for example Hilton et al. (2006) estimated the maximum effect size of the Suess effect in the Southern Ocean to be of the order of -0.02‰ per year, which is smaller than the typical measurement error of a mass spectrophotometer! I took the party to avoid inferring past primary productivity from the data presented in this work, although this issue is very salient given the large population decrease in Southern Elephant Seals.

The digression above illustrates why I also think that isotopic ecology is probably a young and burgeoning field. The exploration phase of the use of stable isotopes to answer long-standing ecological question of interest is ongoing. Yet, the field as a whole would probably benefit from a little more regard toward statistics. Published works in peer-reviewed journals sometimes betray confusion about concepts such as that of that of statistical independence or regression (for example, Auerswald et al. (2010) or Robbins et al. (2010)), or conflation of statistical significance with effect size (for example MacKenzie et al. (2011)). The occasional debate about the use of phenomenological versus mechanistical models also betrays that this issue is sensitive (see for example Carleton et al. (2008); Caut et al. (2009); Auerswald et al. (2010); Perga and Grey (2010)).

In closing this discussion, I should add that sophisticated statistical approaches for the sake of it is not desirable either (Achen, 2002). The question of interest is paramount is determining both the data collecting design and the analysis of data. The attractiveness of the stable isotope technique in ecology lies in its inexpensiveness, in the ability to analyze museum specimens and the possibility of multi-layers design exploiting the different turn-over times of different tissues (Jaeger, 2009). This should not distract from the fact that the technique still need more laboratory experiments to remedy some of its blind spots (Gannes et al., 1997; Wolf et al., 2009b), in particular the accurate quantification of enrichment factors to estimate the probable diet of species (Bond and Diamond, 2011). It is currently hard to think of a laboratory that could accommodate Southern Elephant Seals. Thus, working on Southern Elephant Seals and stable isotopes naturally led to sophisticated statistical methods to alleviate some problems.

³I owe the expression to Freese (2008).

5.4 Where to Next?

This work gave some answers to the initial questions about the foraging ecology of Southern Elephant Seals on Îles Kerguelen. Questions relating to the cause of the large population decline observed in the 1970s motivated much of the present work, but the stable isotopic evidence is here mixed both because no differences were found between seals that lived before and after the population crash (Chapter 4). However, this work focused for a large part on carbon isotopes. The analysis of pup weaning mass nevertheless highlighted that food quality may be very important (Chapter 3). Since female Southern Elephant Seals showed an increased in the spread of their $\delta^{15}\text{N}$ with age, the question of whether there are individual specialization is very relevant as it may influence pup weaning mass, and ultimately, survival. Further work may elaborate on the use of mixing model to infer the individual diet of seals (Semmens et al., 2009) and to relate it to life-history traits. The question of what these seals are eating is simple yet vexing as there is no clear answer. Stomach content (Rodhouse et al., 1992; Field et al., 2007b), stable isotopes (Cherel et al., 2008; Eder et al., 2010) or fatty acids analyses (Bradshaw et al., 2003; Newland et al., 2009) all show Southern Elephant Seals can prey on a large panel of species. Accurate quantification of this diet has been so far elusive but current evidence points to the importance of myctophid fish (Cherel et al., 2008; Newland et al., 2009). Knowledge on these fish within the Southern Ocean is sparse (Catul et al., 2011) despite their importance in the food web (Figure 3.2). Current mixing models which accommodate many sources of variations in isotopic data have a great potential to help resolve this question (Parnell et al., 2010).

The use of mixing models was in fact touched upon during this *Ph.D.* thesis with the help of a Master Student, Adrien Chaigne. However I ran into the issue of the large number of potential preys (> 20) which renders mixing models less useful because of the small precision of posterior estimates. To remedy this, I considered using clustering methods jointly with a mixing model (Ward et al., 2011). The approach taken made use of a Dirichlet Process (Dunson, 2009; Ghosh et al., 2010) to cluster together preys with similar proportion in the diet of Southern Elephant Seals⁴. The model has the virtue of side-stepping the issue of determining meaningful isotopic clusters (how big is a big enough difference in isotopic values?), but has also convergence problems. Sweeping aside issues about eliciting enrichment factors⁵ (Bond and Diamond, 2011), the coherence of results in light of prior knowledge about the diet of these seals was also questionable. This work is still largely in progress. Yet successful convergence would be highly relevant to identify relevant preys of Southern Elephant Seals, and then to evaluate the hypothesis of Ainley and Blight (2009) that the population decline was largely due to anthropogenic depletion of Southern Ocean resources.

⁴This modelling choice betrays again my belief in a greater need for sophisticated models with the analysis of stable isotopes.

⁵See Caut et al. (2011) for an impressive attempt at estimating these factors in large cetaceans.

Finally, the analysis of the dentin isotopic data underscored the importance of foraging stability from an early age on male longevity (Chapter 4). The longitudinal data were more limited for females, but cross-sectional data suggested that females were faithful to a foraging strategy from an early age too, with potential far-reaching consequences on the weaning mass of the pup they will subsequently wean. The next question is then to understand how newly weaned pups develop their foraging skills and routes. [Field et al. \(2005\)](#) investigated the spatial distribution of Macquarie Island seals for their first trip at sea and evidenced how seals foraged further from the island as they grew. Newly weaned pups already have impressive diving capacities: like adults, they dived continuously while at sea and average dive duration was already half that of adult females ([Irvine et al., 2000](#)). [Irvine et al. \(2000\)](#) also reported that there was considerable between-individual variation in dive duration, with some underyearlings performing dives of comparable duration to some adult females. This may betray individual quality ([Bergeron et al., 2011](#)). Studying the development of foraging routes in these animals would be a challenge but an interesting question is the interplay between chance events and fitness in its determination ([Hays et al., 2010](#)). The correlation between foraging stability and male longevity reflects that both foraging strategies may be equivalent in terms of survival, but does not answer why some individuals find the Antarctic and others don't, or whether some sire more pups than others.

Bayesian Statistics

Statistical analysis is the art of separating the wheat from the chaff with a mathematical rake¹; that is the process of separating systematic effects from mere random flukes inherent in any set of observations (Gill, 2009). Statistical methods provide means 'to make inference from data using probability models for quantities we observe and for quantities we wish to learn' (Gelman et al., 2003). Some data, y , are observed, and a deterministic model plus a stochastic component (random errors) is posited to give rise to these data. This statistical model (deterministic relationships plus random noise) is parametrized in terms of unknown quantities of scientific interest θ . The likelihood function, $p(y|\theta)$, is then the probability of observing the data as a function of the unknown θ .

Maximum Likelihood estimation proceeds by finding the values $\hat{\theta}$ that maximizes the probability of observing the data given the posited statistical models. As the sample size of the data tends to infinity, $\hat{\theta}$ becomes an unbiased estimator of θ ; that is the expectation of $\hat{\theta}$, $E(\hat{\theta})$, equals the true values of θ . Maximum Likelihood thus relies on an asymptotic justification, but in practice, it is not always clear how large is large enough for the asymptotic justification to reliably hold².

In contrast, with Bayesian statistical analysis, assertions about θ are not made in terms of single point estimates; rather one attempts to find out the whole probability distribution of θ . That is Bayesian methods do not seek out to find a point estimate that maximizes a likelihood function, but rather is concerned with mapping out the whole distribution of the unknown parameters. This mapping out means in practice that in addition to specify a distribution for the observed data (the likelihood), one has to specify a distribution on the unknowns, unconditionally on the observed data $p(\theta)$; that is unknowns are treated as random rather than fixed quantities (Gelman et al., 2003; Gill, 2009). These unconditional distributions are called the prior distributions of the unknown parameters, and should ideally encapsulate prior knowledge about the θ .

¹I took the rake metaphor from Neal Stephenson's delightful novel 'Anathem' (2008).

²See the blog post of statistician Radford Neal on this topic:

<http://radfordneal.wordpress.com/2008/08/09/inconsistent-maximum-likelihood-estimation-an-ordinary-example/>

Priors and the likelihood of the data are then combined to update our knowledge on the scientific parameters of interest, yielding the posterior distribution of θ given the observed data:

$$p(\theta|y) \propto p(\theta) \times p(y|\theta) \quad (\text{A.1})$$

$$\text{where } \begin{cases} p(\theta) : & \text{prior distribution (unconditional of the currently observed data } y); \\ p(y|\theta) : & \text{likelihood of the data given the posited statistical model; and} \\ p(\theta|y) : & \text{posterior distribution of the parameters of interest.} \end{cases} \quad (\text{A.2})$$

The Bayesian approach directly estimates the whole probability distribution of θ , that is it yields a distributional summary of how the observed data y has updated our knowledge about θ . It does not rely on any asymptotic justifications. However the price to pay is to formulate a prior, an act which may be viewed as a direct violation of the scientific ideal of objectivity ('Tobacco science' as Dennis (2004) puts it) and which has led to the 'Balkanization' of statistics throughout the last century (Shafer, 1990). It is noteworthy that Dennis (2004) later put Bayesian water in his likelihood wine, and eventually teamed up with a patented Bayesian (Ellison, 2004a,b; Ellison and Dennis, 2010; Dennis and Ellison, 2010). This exemplifies the current 'détente' within statistical practice between frequentism, likelihood-ism and Bayesianism (Efron, 2010; Kass, 2011).

The view adopted throughout this thesis work was mostly a pragmatic one, but with an emphasis on quantifying uncertainty, hence the adoption of the Bayesian framework. The exact filiation comes from my weariness of finding ways to obtain approximate confidence intervals for functions of parameters, and the discovery that the wonderful BUGS language (Lunn et al., 2000) could do that easily, provided one was willing to break the Bayesian eggs (Figure A.1).

Finally, I tried to privilege the use of robust priors, that is priors obeying 'Cromwell's Rule': 'I beseech you, in the bowels of Christ, think it possible that you may be mistaken' (Gelman, 2006; Gelman et al., 2008; Fúquene et al., 2009; Fúquene, 2011). This meant avoiding using conjugate priors in some cases and resulted in an increased computational burden, which hopefully is shrinking with modern computers. The advantage of such priors lies in their ability to accommodate outlying observations and to avoid assigning 0 probability to surprising values. Bayesian inference is sometimes railed for this: if one rules out *a priori* some values for a parameter of interest, then no amount of data can overturn this prior (see Equation A.1). Cromwell's Rule thus invite to elicit priors that don't silence the data.



Figure A.1: 'Break the eggs (prior) and enjoy the Bayesian omelette' (Jimmy Savage).

Methods for Chapter 2

Contents

B.1 Priors	103
B.2 Alternatives to the Inverse Wishart Prior	103

B.1 Priors

All models were fitted with `winBUGS` (Lunn et al., 2000; Spiegelhalter et al., 2003) called from R (R Development Core Team, 2009) with the package `R2WinBUGS` (Sturtz et al., 2005). Weakly informative priors (Half-Cauchy and Cauchy priors for variance and other parameters respectively) were used (Gelman, 2006; Gelman et al., 2008; Fúquene et al., 2009). An Inverse Wishart prior was used for the variance-covariance matrix.

For each model, three chains were initialized with overdispersed starting values. After appropriate burn-in and thinning of the chains (1 value every 100 or 200 iterations stored) to reduce autocorrelation, convergence was assessed using the Gelman-Rubin convergence diagnostic (Cowles and Carlin, 1996) with the `coda` package (Plummer et al., 2008). Unless stated otherwise, posterior mean and standard error of the mean ($\bar{\theta} \pm se$) are reported, along with 95% Highest Probability Density (HPD) credible intervals: lower bound $\bar{\theta}$ upper bound (Louis and Zeger, 2009).

B.2 Alternatives to the Inverse Wishart Prior

The Inverse Wishart prior for modelling a covariance matrix Σ of dimension k is commonly used for its desirable conjugacy properties that substantially speed up computation. However, this prior is also controversial as it imposes rather stiff constraints on the correlation parameters (Gelman and Hill, 2007). Practically, estimating a covariance matrix of size greater than 2 is a challenge: in addition to the usual restriction to lie between -1 and 1 , correlations are jointly constrained. For example, with a 3×3 covariance matrix, $\rho_{1,2}$ and $\rho_{1,3}$ can take any value between -1 and 1 , but $\rho_{2,3}$ must then conform to the following constraints for the matrix to be positive-definite and invertible (Budden et al., 2007):

$$\rho_{1,2}\rho_{1,3} - \sqrt{(1 - \rho_{1,2}^2)(1 - \rho_{1,3}^2)} \leq \rho_{2,3} \leq \rho_{1,2}\rho_{1,3} + \sqrt{(1 - \rho_{1,2}^2)(1 - \rho_{1,3}^2)}$$

Yet there are alternative priors like using a Cholesky decomposition of Σ into a diagonal matrix Γ and a lower triangular matrix L with 1s on the diagonal:

$$\Sigma = \Gamma L L^T \Gamma \quad (\text{B.1})$$

There are several Cholesky decompositions, all of which guarantee positive-definiteness (Pourahmadi, 2007), but equation B.1 neatly separates variance (Γ) and correlation (LL^T) parameters (Barnard et al., 2000; Chen and Dunson, 2003).

Tokuda et al. (2011) recently proposed another prior based on another decomposition of Σ :

$$\Sigma = \text{diag}(\sigma_1, \dots, \sigma_k) \Lambda D \Lambda^T \text{diag}(\sigma_1, \dots, \sigma_k) \quad (\text{B.2})$$

where σ_i are standard deviation on the folded standardized normal distribution, Λ is a randomly generated $k \times k$ orthogonal matrix ¹ and D is a diagonal matrix of eigenvalues (Tokuda et al., 2011).

The Cholesky decomposition and Tokuda et al. (2011)'s prior were implemented in winBUGS to compare results with those from the Inverse Wishart Prior on the hierarchical model describing the haul-out process of breeding Southern Elephant Seal females. Note that for this exercise, a logarithmic scale was used for N_{max} in contrast to Authier et al. (2011b). This was used to avoid working with large variances. Prior-Posteriors plots are represented below.

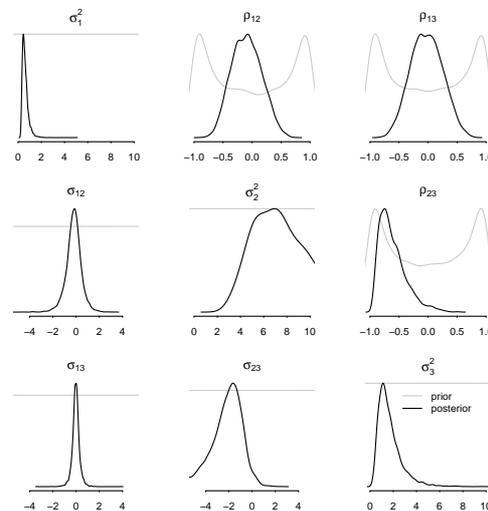


Figure B.1: Inference on Σ with an Inverse Wishart Prior. Variance parameters are depicted on the diagonal, while covariance and correlation parameters are depicted below and above the diagonal respectively.

¹see Anderson et al. (1987) for implementation details.

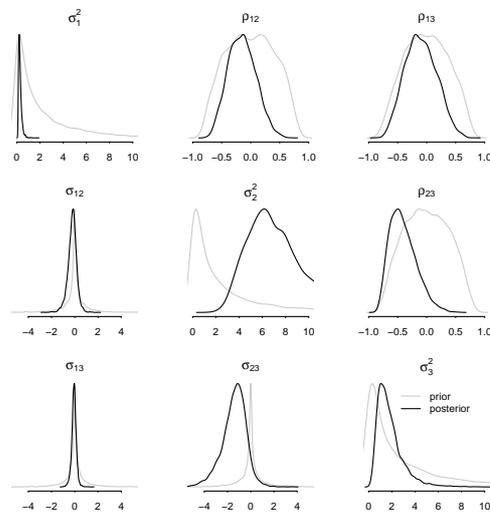


Figure B.2: Inference on Σ with a Cholesky Decomposition. Variance parameters are depicted on the diagonal, while covariance and correlation parameters are depicted below and above the diagonal respectively.

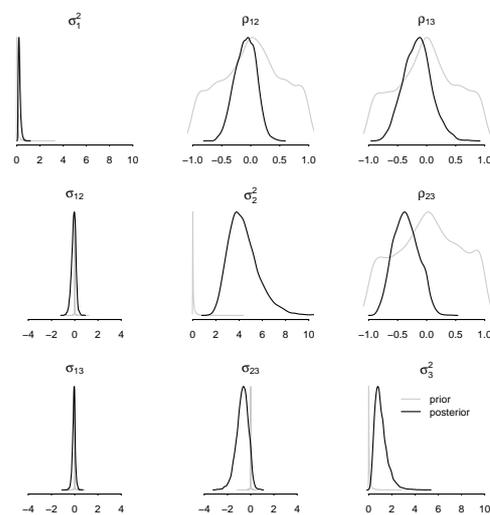


Figure B.3: Inference on Σ with Tokuda et al. (2011)'s prior. Variance parameters are depicted on the diagonal, while covariance and correlation parameters are depicted below and above the diagonal respectively.

From Figures B.1, B.2 and B.3, it is clear that the different prior induces different correlation structures on the prior Σ . In particular, marginal distributions for ρ are bimodal with the Inverse-Wishart prior with modes on -1 and 1 . Although the distributions for the variances are flat, this is hardly a non-informative distribution! In contrast, the other two priors are less informative on the correlations, but more informative on the variance parameters. The impact on the posterior of Σ are summarized on Figure B.4.

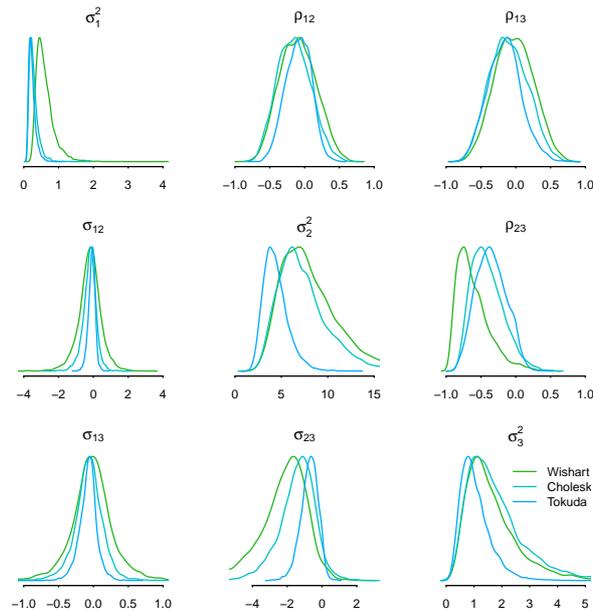


Figure B.4: Impact of the prior on posterior inferences on Σ . Variance parameters are depicted on the diagonal, while covariance and correlation parameters are depicted below and above the diagonal respectively.

The Inverse-Wishart prior seems to overestimate small variance components while Tokuda et al. (2011)'s prior may overshrink large ones. The Cholesky decomposition seems to provide a trade-off between the two other priors. Compared to the results presented in Authier et al. (2011b), it thus seems that the variation associated with the number of breeding females and synchrony has been overestimated, meaning that confidence intervals for the corrected censuses are too wide. The correlation between peak haul-out date and synchrony reported in Authier et al. (2011b) is also an overestimate (being more likely around -0.4 than -0.6), although it is clearly negative. Importantly though, all other parameters were not affected by the choice of the covariance matrix prior.

BUGS code for the Cholesky decomposition of 3×3 covariance matrix

```

for ( i in 1:n.levels ) {
  a[i,1:3] ~ dnorm(a.hat[i,1:3],InvSigma2.a[1:3,1:3])
  for ( j in 1:3 ) { a.hat[i,j] <- 0 }
}
# Construct the covariance matrix as V=D%*%L%*%t(L)%*%D
for ( j in 1:3 ) {
  sd.a[j] <- sqrt(Sigma2.a[j,j])
  D[j,j] ~ dnorm(0,0.45)I(0,)
  L[j,j] <- 1
  for ( k in 1:3 ) {
    C[j,k] <- inprod(D[j,1:3],L[1:3,k]) # this is C=D%*%L
    Sigma2.a[j,k] <- inprod(C[j,1:3],C[k,1:3]) # this is V=C%*%t(C)
  }
}
for ( j in 2:3 ) {
  for ( k in 1:(j-1) ) {
    D[j,k] <- 0 ; D[k,j] <- 0
    L[j,k] ~ dnorm(0,4) ; L[k,j] <- 0
  }
}
InvSigma2.a[1:3,1:3] <- inverse(Sigma2.a[1:3,1:3])
rho.a[1] <- Sigma2.a[1,2]/sqrt(Sigma2.a[1,1]*Sigma2.a[2,2])
rho.a[2] <- Sigma2.a[1,3]/sqrt(Sigma2.a[1,1]*Sigma2.a[3,3])
rho.a[3] <- Sigma2.a[2,3]/sqrt(Sigma2.a[2,2]*Sigma2.a[3,3])

```

BUGS code for Tokuda et al. (2011)'s prior for a 3×3 covariance matrix

```

for ( i in 1:n.levels ) {
  b[i,1:3] ~ dnorm(b.hat[i,1:3],InvSigma2.b[1:3,1:3])
  for ( j in 1:3 ) { b.hat[i,j] <- 0 }
}
# Construct a orthogonal matrix
m[1] ~ dbeta(0.5,0.5)
m[2] ~ dbeta(1,0.5)
m[3] ~ dbeta(1,0.5)
L[1,1] <- eps[1]*sqrt(m[1]*m[2])
L[1,2] <- eps[2]*(-sqrt(m[3]*(1-m[1])) - sqrt(m[1]*(1-m[2])*(1-m[3])))
L[1,3] <- eps[3]*(sqrt((1-m[1])*(1-m[2])) - sqrt(m[1]*m[3]*(1-m[2])))
L[2,1] <- eps[1]*sqrt(m[2]*(1-m[1]))
L[2,2] <- eps[2]*(sqrt(m[1]*m[3]) - sqrt((1-m[1])*(1-m[2])*(1-m[3])))
L[2,3] <- eps[3]*(-sqrt(m[1]*(1-m[3])) - sqrt(m[3]*(1-m[1])*(1-m[2])))
L[3,1] <- eps[1]*sqrt(1-m[2])
L[3,2] <- eps[2]*sqrt(m[2]*(1-m[3]))
L[3,3] <- eps[3]*sqrt(m[2]*m[3])

# Construct the covariance matrix as V=S%*%L%*%D%*%t(L)%*%S
# where S is diagonal, D is diagonal and
# L is orthogonal (ie L%*%t(L) = Identity)
for ( i in 1:3 ) {
  eps[i] <- 2*X[i] - 1
  X[i] ~ dbern(0.5)
  D[i,i] ~ dbeta(0.5,5)
  S[i,i] ~ dnorm(0,1)I(0,)
  sd.b[i] <- sqrt(Sigma2.b[i,i])
}
for ( j in 2:3 ) {
  for ( k in 1:(j-1) ) {
    D[j,k] <- 0 ; D[k,j] <- 0
    S[j,k] <- 0 ; S[k,j] <- 0
  }
}
for ( j in 1:3 ) {
  for ( k in 1:3 ) {
    C[j,k,1] <- inprod(S[j,1:3],L[1:3,k]) # S%*%L
    C[j,k,2] <- inprod(C[j,1:3,1],D[1:3,k]) # S%*%L%*%D
    Sigma2.b[j,k] <- inprod(C[j,1:3,2],C[k,1:3,1]) # S%*%L%*%D%*%t(S%*%L)
  }
}
InvSigma2.b[1:3,1:3] <- inverse(Sigma2.b[1:3,1:3])
rho.b[1] <- Sigma2.b[1,2]/sqrt(Sigma2.b[1,1]*Sigma2.b[2,2])
rho.b[2] <- Sigma2.b[1,3]/sqrt(Sigma2.b[1,1]*Sigma2.b[3,3])
rho.b[3] <- Sigma2.b[2,3]/sqrt(Sigma2.b[2,2]*Sigma2.b[3,3])

```

BUGS code for fitting the Hierarchical Model exposed in Equation 2.1

```

model{
  for ( i in 1 : N ) {
    n[i] ~ dt( mu[i],tau,nu )
    mu[i] <- Nmax[ Site[i] ]*p[i] + manipeur[ who[i] ]
    p[i] <- Arrival[i] - Departure[i]
    Arrival[i] <- phi((t[i]-peak.return[ Site[i] ])/synchrony[ Site[i] ])
    Departure[i] <- phi((t[i]-S.cut-peak.return[ Site[i] ])/synchrony[ Site[i] ])
  }
  # Priors
  tau <- pow(sd.res,-2) ;
  sd.res ~ dunif(0,100) ;
  nu ~ dunif(2,50) ;
  for ( i in 1 : N.site ) {
    peak.haulout[i] <- peak.return[i]+S.cut/2 ;
    Max.at.peak[i] <- 100*(2*phi(S.cut/(2*synchrony[i])) - 1)
  }
  S.cut <- cut(S)
  S ~ dnorm(28,0.20)
  beta[1] ~ dt(0,0.01,7)
  beta[2] ~ dt(0,0.01,7)
  beta[3] ~ dt(0,0.01,7)
  for ( i in 1 : (N.site+1) ) {
    Nmax[i] <- exp(a[ i,1 ]) ; a.hat[ i,1 ] <- beta[1]
    peak.return[i] <- a[ i,2 ] ; a.hat[ i,2 ] <- beta[2]
    synchrony[i] <- a[ i,3 ] ; a.hat[ i,3 ] <- beta[3]
    a[ i,1:3 ] ~ dnorm( a.hat[ i, ],InvSigma2.a[, ] )
  }
  InvSigma2.a[ 1:3,1:3 ] ~ dwish( W[, ],3 ) ;
  W[1,1] <- 5 ; W[1,2] <- 0 ; W[1,3] <- 0 ;
  W[2,1] <- 0 ; W[2,2] <- 4 ; W[2,3] <- 0 ;
  W[3,1] <- 0 ; W[3,2] <- 0 ; W[3,3] <- 1 ;
  Sigma2.a[ 1:3,1:3 ] <- inverse( InvSigma2.a[, ] )
  for ( j in 1 : 3 ) { sd.a[j] <- sqrt(Sigma2.a[ j,j ] ) }
  rho.a[1] <- Sigma2.a[ 1,2 ] / sqrt( Sigma2.a[1,1]*Sigma2.a[2,2] )
  rho.a[2] <- Sigma2.a[ 1,3 ] / sqrt( Sigma2.a[1,1]*Sigma2.a[3,3] )
  rho.a[3] <- Sigma2.a[ 2,3 ] / sqrt( Sigma2.a[2,2]*Sigma2.a[3,3] )
  # Half-Cauchy Priors for variance parameters
  for ( i in 1:N.who ) { manipeur[i] <- x*U[i] ; U[i] ~ dnorm( 0,tau.U ) }
  x ~ dnorm(0,tau.x) ; tau.x <- pow(prior.scale.who,-2) ; tau.U ~ dgamma(0.5,0.5)
  sd.manipeur <- abs(x)/sqrt(tau.U)
}

```


Methods for Chapter 3

Contents

C.1 Laboratory Analyses	111
C.2 Statistical Analyses	111
C.2.1 Temporal Resolution	111
C.2.2 Southern Ocean Isoscapes	112
C.2.3 Inferring Foraging Strategy	113
C.2.4 Mixture Model Selection	113
C.2.5 Robust Link Function: the Robit	114

C.1 Laboratory Analyses

Before isotopic analysis, whole blood was oven-dried for 48 hours at 50-60° Celsius. Samples were weighted (range: 3-5 mg) into tin cups prior to combustion in an elemental analyser (Euro Vector EA 3024) coupled to a continuous flow mass spectrometer (Micromass Isoprime). Carbon to Nitrogen ($\frac{C}{N}$) ratios were checked, and when above 3.7, lipids were extracted using cyclohexane. Lipids are depleted in ^{13}C relative to proteins and carbohydrates (DeNiro and Epstein, 1977), but lipid extraction is usually unnecessary due to the typically small lipid content of blood. Replicate measurements of internal laboratory standards (acetanilide, $\delta^{13}C = -27.5\text{‰}$ and $\delta^{15}N = 10.3\text{‰}$, 2 every 23 samples) indicated precisions of 0.15 ‰ and 0.20 ‰ for carbon and nitrogen respectively.

C.2 Statistical Analyses

C.2.1 Temporal Resolution

All models for evaluating the temporal resolution of blood turn-over were fitted in R version 12.0 (R Development Core Team, 2009) using the `arm` package (Gelman et al., 2011). The threshold for statistical significance was set to 5%. Values for parameter θ are reported as $\bar{\theta}_{se}$ where *se* is the standard error (Louis and Zeger, 2009).

C.2.2 Southern Ocean Isoscapes

Spike-and-slab variable selection for linear models is implemented in the R package `spikeslab` (Ishwaran et al., 2010). Figure C.1 depicts a spike-and-slab prior. This package also implements a cross-validation procedure (function `cv.spikeslab`). For all computations, a burn-in of 10,000 iterations was adopted. Posterior means are computed from an additional 10,000 iterations. The package `spikeslab` does not allow to run multiple chains in parallel: computations were done several times with different seeds to check the stability of the results.

The use of a prior here is highly desirable as potentially small effects are to be estimated, which is challenging and susceptible to type-M (magnitude) and type-S (sign) errors (Gelman and Tuerlinckx, 2000). In particular, two sign reversals occur in Table 3.2 between the OLS and the Posterior Mean estimates. The stability analysis further suggests that these two parameters are not improving on the predictive power of the model. Finally, the OLS estimate for the effect size of the interaction between sex and body length seems too large and influenced by a single datum with high leverage. The Posterior Mean effect size in contrast is half that of the OLS.

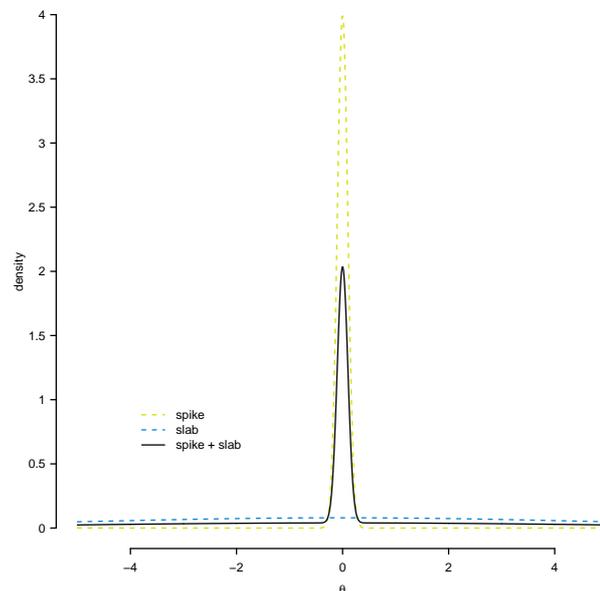


Figure C.1: A graphical example of a spike-and-slab prior. The spike correspond to a sharp density around zero, which effectively shrink the posterior estimate towards zero. The slab is a diffuse density over a wide interval, which gives a small, but non-zero, weight to other values than zero.

C.2.3 Inferring Foraging Strategy

Hierarchical models were fitted with `winBUGS` (Spiegelhalter et al., 2003) called from R (R Development Core Team, 2009) with the package `R2WinBUGS` (Sturtz et al., 2005). The `sn` package (Azzalini, 2009) was used to back-transform estimates on the robit scale to a probability scale. Weakly informative priors were used (Gelman, 2006; Gelman et al., 2008): Half-Cauchy or Uniform priors for variance parameters; Normal priors for regression parameter on the natural scale and Student priors with 7 degrees of freedom for regression parameters on the robit scale. Continuous and categorical covariates were standardized following Gelman (2008). Three chains were initialized with overdispersed starting values. After appropriate burn-in (40,000 iterations) and thinning of the chains (1 value every 100 iterations stored), convergence was assessed using the Gelman-Rubin convergence diagnostic (Cowles and Carlin, 1996) with the `coda` package (Plummer et al., 2008). Unless stated otherwise, posterior mean and standard error of the mean ($\bar{\theta} \pm se$) are reported, along with 95% Highest Probability Density (HPD) credible intervals: lower bound $\bar{\theta}_{\text{lower}}$ upper bound (Louis and Zeger, 2009).

C.2.4 Mixture Model Selection

The Deviance Information Criterion (Spiegelhalter et al., 2002) is a popular tool for Bayesian model selection (Barnett et al., 2010). Yet its use with mixture models is problematic (Celeux et al., 2006), and the criterion itself is somewhat controversial (see the discussion of Spiegelhalter et al. (2002)). Here, I selected a model with Posterior Predictive Checks (Gelman et al., 1996; Gelman, 2003; Berkhof et al., 2003) wherein the posterior distributions are used to predict (hypothetical) repetitions of the data set under a fitted model. From these hypothetical datasets, I compared an observed summary statistics (\mathbf{T}_{obs}) to its predicted values (\mathbf{T}_{rep}) and compute a p_{value} :

$$p_{\text{value}} = Pr(\mathbf{T}_{\text{rep}} > \mathbf{T}_{\text{obs}}) \quad (\text{C.1})$$

A p_{value} close to 0.5 tells us of a good fit ($\mathbf{T}_{\text{rep}} \approx \mathbf{T}_{\text{obs}}$), while an extreme p_{value} (0 or 1) betrays a major model misfit. Thus, with an appropriate summary statistics \mathbf{T} , I investigated which regularities of the original dataset was captured by the model. We chose three test-statistics: minimum, maximum and kurtosis of the weaning mass distribution. My data span a large range (Table 3.3) and has negative kurtosis, which can betray bimodality (Darlington, 1970; Hilderbrand, 1971). We simulated 1,000 repetitions of the dataset, and for each repetition recorded whether the predicted test-statistic exceeded the observed one.

C.2.5 Robust Link Function: the Robit

The robit link is a robust link function corresponding to the Cumulative Distribution Function (CDF) of a Student-t distribution with 7 degrees of freedom and scale set to 1.5484 (Liu, 2004). The CDF of a standard logistic distribution and the robit are largely indistinguishable (Figure C.2), but a closer look on the distribution tails reveals that tail probabilities of the robit regression model are heavier, which confer robustness against outliers to the robit (Liu, 2004; Gelman and Hill, 2007).

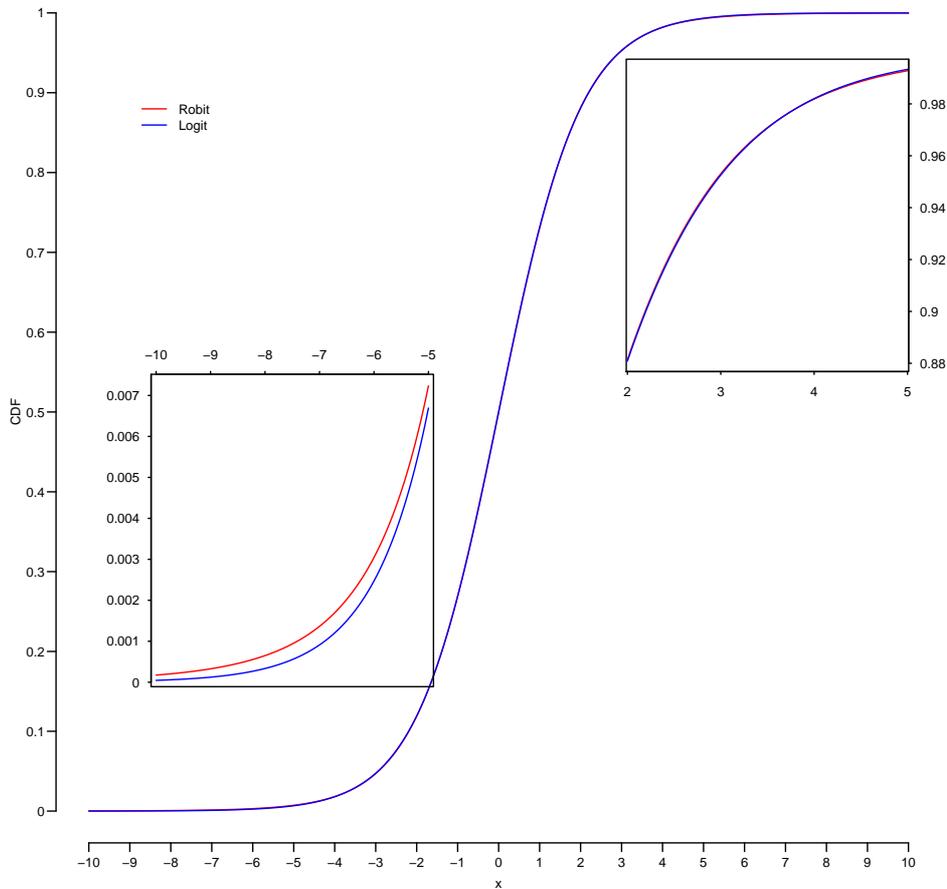


Figure C.2: Cumulative Distribution Function (CDF) of a standard logistic distribution and a Student-t distribution with 7 degrees of freedom and scale set to 1.5484.

BUGS code for 2-component mixture model with a robit link

```

model{
  # Likelihood
  for ( i in 1 : n.obs ) {
    MASS[i] ~ dnorm( mu[i],tau )
    mu[i] <- alpha[ R[i] ]

    # latent variable for group membership
    # if R[i]=2, pup i belongs to a group with large weaning mass
    # if R[i]=1, pup i belongs to a group with small weaning mass
    R[i] <- step(Z[i])+1

    # Student distribution coded as a scale mixture of a normal
    # if Z[i]>0, pup belongs to a group with large weaning mass
    # if Z[i]<0, pup belongs to a group with small weaning mass
    Z[i] ~ dnorm(nu[i],tau2[i])

    # fix the scale of the Student distribution with 7 df
    # to approximate a logistic distribution
    tau2[i] <- lambda[i]*pow(1.5484,-2)
    lambda[i] ~ dgamma(3.5,3.5)

    # Robit regression for predicting group membership

    nu[i] <- beta[1] +
      beta[2]*std.d13C[i] + beta[3]*pow(std.d13C[i],2) +
      beta[4]*std.d15N[i] + beta[5]*pow(std.d15N[i],2) +
      beta[6]*std.Mid.October[i]
  }

  # End of likelihood

  # Priors
  ## Residual Variance
  tau <- pow(sd.res,-2)
  sd.res ~ dunif(0,100)

  # Regression Parameters, robit scale
  # Student-t priors with 7 degrees of freedom
  for ( i in 1:6 ) {
    beta[i] ~ dt(0,prior.tau.beta[i],7)
    prior.tau.beta[i] <- pow(prior.scale.beta[i],-2)
  }

  # Mixture Components, same scale as data
  # Normal priors
  alpha[1] ~ dnorm(0,0.00001)
  # identifiability constraint
  # alpha[2] > alpha[1]

```

```
alpha[2] <- alpha[1] + abs(delta)
delta ~ dnorm(0,0.00001)

# end of prior specification
}

#### DATA
## n.obs = number of data points
## MASS[] = weaning mass of pups
## std.d13C[] = standardized carbon isotopic signature
## std.d15N[] = standardized nitrogen isotopic signature
## std.MiOctobre[] = standardized weaning date.
##                               Zero is October 15th
## prior.scale.beta[] = c(5,2.5,2.5,2.5,2.5,2.5)
## NB: standardized means centered and scaled by 2 standard deviations

#### PARAMETERS
## R[] = latent indicator variable
## Z[] = latent student-t variable (robit)
## beta[1] = intercept of the robit regression
## beta[2] = d13C effect for predicting group membership
## beta[3] = d13C^2 effect for predicting group membership
## beta[4] = d15N effect for predicting group membership
## beta[5] = d15N^2 effect for predicting group membership
## beta[6] = weaning date effect for predicting group membership
## alpha[1] = mean weaning mass of small pups
## alpha[2] = mean weaning mass of large pups
```

Methods for Chapter 4

Contents

D.1 Laboratory Analyses	117
D.1.1 Blood Data	117
D.1.2 Tooth Data	118
D.2 Cross Sectional Data	120
D.3 Hierarchical Change-Point Model	120
D.3.1 Priors	120
D.3.2 Model Selection and Fit	121
D.4 Joint Longitudinal-Survival Model	125
D.4.1 Priors	125
D.4.2 Model Checking	125
D.4.3 Stochastic Search Variable Selection	126

D.1 Laboratory Analyses

D.1.1 Blood Data

Before isotopic analysis, whole blood was oven-dried for 48 hours at 50-60° Celsius. Samples were weighted (range: 3-5 mg) into tin cups prior to combustion in an elemental analyser (Euro Vector EA 3024) coupled to a continuous flow mass spectrometer (Micromass Isoprime). Carbon to Nitrogen ($\frac{C}{N}$) ratios were checked, and when above 3.7, lipids were extracted using cyclohexane. Lipids are depleted in ^{13}C relative to proteins and carbohydrates (DeNiro and Epstein, 1977), but lipid extraction is usually unnecessary due to the typically small lipid content of blood. Replicate measurements of internal laboratory standards (acetanilide, $\delta^{13}C = -27.5$ ‰ and $\delta^{15}N = 10.3$ ‰, 2 every 23 samples) indicated precisions of 0.15 ‰ and 0.20 ‰ for carbon and nitrogen respectively.

D.1.2 Tooth Data

Each growth layer was sampled for 1 mg of bulk dentin using a MicromillTM sampler (Institut des Sciences de l'Évolution de Montpellier, Université de Montpellier 2). Thus each growth layer was assumed to correspond to one fourth of a year. Organic matter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the bulk dentine were measured with an elemental analyzer (EA-IRMS, Euro-Vector EA 3000) coupled to a continuous flow mass spectrometer (Optima-Micromass) at the Université de Montpellier 2. Typical precisions for isotopic measurement were 0.20 ‰ for both carbon and nitrogen.

Bulk dentin was analyzed because of the small amount of drilled material for each layer. To test the impact of the inorganic fraction, [Martin et al. \(2011\)](#) compared acid-treated and untreated samples but found no differences ($\pm 0.02\text{‰}$). Measured $\delta^{13}\text{C}$ is a mixture of organic carbon with a small amount of inorganic carbon. [Schulting et al. \(2008\)](#) found similar $\frac{\text{C}}{\text{N}}$ ratios between bulk dentin and collagen, with a lower carbon and nitrogen contents in bulk dentin most likely due to the mineral fraction. The impact of the mineral fraction was thus assumed negligible. As a recent study raised concerns about non-linear offsets of organic ‰C, ‰N and $\frac{\text{C}}{\text{N}}$ after acid treatment ([Brodie et al., 2011](#)), no acid (or demineralization) treatment were performed prior to isotopic measurement.

I used $\frac{\text{C}}{\text{N}}$ ratio thresholds of bone and tooth collagen (2.9 to 3.6) as criteria for the identification of diagenetic alteration ([Ambrose, 1990](#)); assuming that total dentin, whose organic phase is mainly collagen and water ([Moyes and Doidge, 1984](#)), has the same $\frac{\text{C}}{\text{N}}$ ratio than bone and tooth collagen. Thus, 1,590 samples were analyzed, but 176 were discarded because of anomalous $\frac{\text{C}}{\text{N}}$ ratios, yielding a final sample size of 1,414 (1,115 from males and 299 from females) isotopic values from 67 individuals (47 males and 20 females). The first $\delta^{15}\text{N}$ value of each time-series was also removed as it is clearly a reflection of maternal diet ([Hobson and Sease, 1998](#); [Martin et al., 2011](#)): during lactation, pups 'feed' on their mother and have a larger $\delta^{15}\text{N}$ value because of fractionation. Summary statistics of the data are depicted on Figure D.1.

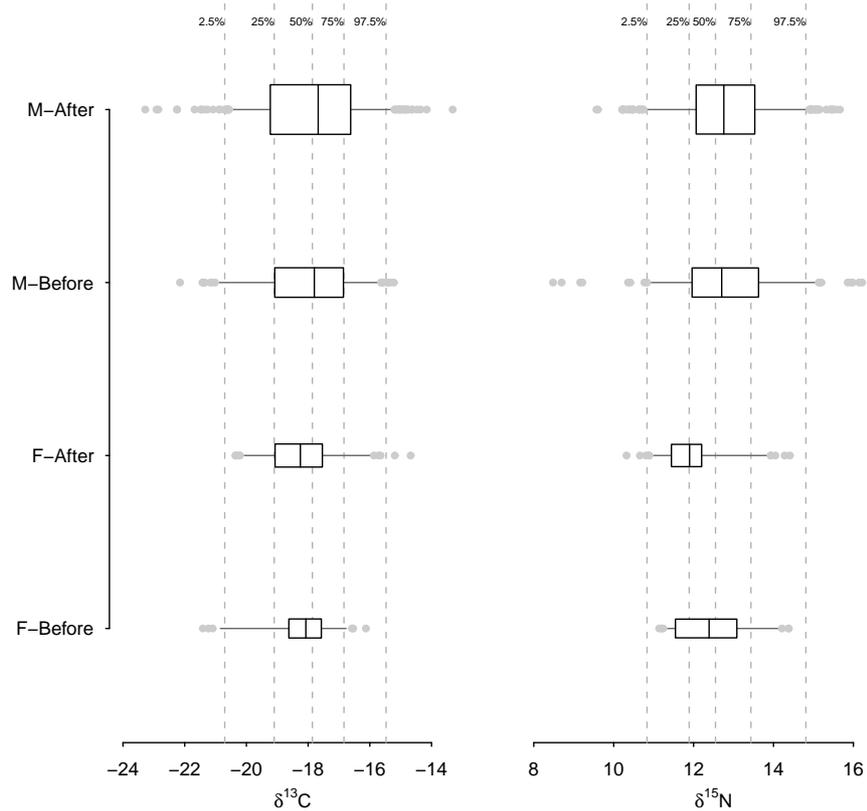


Figure D.1: Tukey plots of the distributions of dentin carbon and nitrogen isotopic values of Southern Elephant Seals from îles Kerguelen. Box-plots for males (M-) and females (F-) *after* and *before* the population crash are depicted. Box sizes are proportional to the square root of sample size and represent 50% of the data for a given category. Black points within each box symbolize the mean isotopic signature for a given year. Grey points highlight outliers which were defined as in [Dümgen and Riedwyl \(2007\)](#). Dotted lines in the background show percentiles of the whole data set.

D.2 Cross Sectional Data

Models were fitted with `winBUGS` (Spiegelhalter et al., 2003) called from `R` (R Development Core Team, 2009) with the package `R2WinBUGS` (Sturtz et al., 2005). Weakly informative priors were used (Gelman, 2006; Gelman et al., 2008): Uniform priors for variance parameters; Normal priors for regression parameter on the natural scale and Student priors with 7 degrees of freedom for regression parameters on a logit scale. Snout-to-Tail Length was standardized following Gelman (2008). Three chains were initialized with overdispersed starting values. After appropriate burn-in (40,000 iterations) and thinning of the chains (1 value every 10 iterations stored), convergence was assessed using the Gelman-Rubin convergence diagnostic (Cowles and Carlin, 1996) with the `coda` package (Plummer et al., 2008). Unless stated otherwise, posterior mean and standard error of the mean ($\bar{\theta} \pm se$) are reported, along with 95% Highest Probability Density (HPD) credible intervals: lower bound $\bar{\theta}_{\text{lower bound}}$ (Louis and Zeger, 2009).

D.3 Hierarchical Change-Point Model

D.3.1 Priors

I used weakly-informative priors: for parameters on the same scale as the data (α_1 , α_2 and α_4) I used normal priors with a large variance. For the parameter α_3 , I used a Student- t prior (Gelman et al., 2008). For the covariance matrix Σ , I used a Cholesky decomposition (see Appendix B) and priors similar to those of Chen and Dunson (2003): independent Half-Normal priors of mean 0 and standard deviation 1.5 for the elements, $\gamma_{p \in [1:8]}$, of the diagonal matrix Γ , and independent normal priors of mean 0 and standard deviation 0.5 for the elements, $\lambda_{p \in [2:8]; q < p}$, of L . This prior gives reasonable values (that is between 0 and 10) for the variances of the $a_{i,j}$ (see Figure B.2). It is also somewhat conservative as most of the probability mass for variance parameters is put on values less than 5. This prior thus reflects skepticism for large differences between individuals. Uniform priors were put on the residual standard deviations (Gelman, 2006).

All models were fitted with `winBUGS` (Spiegelhalter et al., 2003) called from `R` (R Development Core Team, 2009) with the package `R2WinBUGS` (Sturtz et al., 2005). Three chains were initialized with overdispersed starting values. After appropriate burn-in (200,000 iterations) and thinning of the chains (1 value every 200 iterations stored), convergence was assessed using the Gelman-Rubin convergence diagnostic (Cowles and Carlin, 1996) with the `coda` package (Plummer et al., 2008). Posterior mean (or median when posterior distributions were asymmetric) with 95% Highest Probability Density (HPD) intervals are reported as $2.5\% \bar{\theta}_{97.5\%}$ following Louis and Zeger (2009).

D.3.2 Model Selection and Fit

With hierarchical models, model selection is a challenge and several methods have been suggested, such as the Deviance Information Criterion (Spiegelhalter et al., 2002; Barnett et al., 2010); but there is currently no consensus (Jordan, 2011). I choose to avoid using DIC because of drawbacks such as lack of invariance to reparametrization (Spiegelhalter et al. (2002) and the following discussion). In fact, DIC was computed but yielded non-sensical results¹ for the estimated number of parameters when the Cholesky decomposition was used (see Table D.1).

Model	\bar{D}	\hat{D}	pD	DIC
8x8	3645	3662	-18	3627
2x4x4	3633	3591	41	3675
Null	4913	4671	242	5155

Table D.1: Deviance Information Criterion (DIC). \bar{D} is the posterior mean of the deviance, \hat{D} is the deviance evaluated at the posterior mean of the parameters; and pD is the estimated number of parameters in the model. DIC is calculated as $DIC = 2 \times \bar{D} - \hat{D}$. The estimated number of parameters is too small for the model 2x4x4, and nonsensical for the model 8x8. See Spiegelhalter et al. (2002); Plummer (2008); Celeux et al. (2006) for discussions about DIC.

To select an appropriate model, I used Posterior Predictive Checks (Gelman et al., 1996; Berkhof et al., 2003) wherein each fitted model is used to predict (hypothetical) repetitions of the data set. From this hypothetical dataset, I compared an observed summary statistic (\mathbf{T}_{obs}) to its predicted values (\mathbf{T}_{rep}) and compute a p_{value} :

$$p_{\text{value}} = Pr(\mathbf{T}_{\text{rep}} > \mathbf{T}_{\text{obs}}) \quad (\text{D.1})$$

A p_{value} close to 0.5 tells us of a good fit ($\mathbf{T}_{\text{rep}} \approx \mathbf{T}_{\text{obs}}$), while an extreme p_{value} (0 or 1) betrays a major model misfit. I chose the range of observed isotopic values as discrepancy statistics to assess model fit. The rationale for choosing the range as a test statistic is the following: if a change-point is necessary to describe the time-series of isotopic measurement, the range of predicted value is likely to be underestimated when fitting a model with no change-point. The tip of the broken-stick will be missed by a simple linear regression, hence an underestimation of the range. Posterior Predictive Checks can be used to test whether a broken-stick model is justified or to select a covariance structure.

¹DIC is reported to be valid with priors of the exponential family (Spiegelhalter et al., 2002). Here I used Student-t priors which do not belong to the exponential family.

We tested 3 models: a (hierarchical) null model (labeled `Null`) which had no change-point and only varying intercepts and slopes for a linear trend, a hierarchical random change-point model for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ but with no correlation between the two elements (labeled `2x4x4`); and hierarchical random change-point model where $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were correlated (labeled `8x8`).

Model	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
8x8	0.85	0.73
2x4x4	0.84	0.69
Null	0.69	0.58

Table D.2: Posterior Predictive Checks. The statistic considered is the range of isotopic values and the reported *p-values* are the probability that the predicted range exceeds the observed one. The percentage of individuals with a $0.1 < p_{value} < 0.9$ is reported for both carbon and nitrogen isotopic time-series. Broken-stick models decreased the proportion of individuals with extreme *p-values*: a broken-stick model was appropriate for most individuals. There was however little support for an increase in covariance complexity: overall changes in $\delta^{13}\text{C}$ were not correlated with changes in $\delta^{15}\text{N}$.

A hierarchical change-point model provided an adequate fit to the Southern Elephant Seal isotopic data (Figures D.2 & D.3). The model effectively smoothed over a lot of the variation that is visible on Figure D.2. In doing so, it actually ignored the few cyclic time-series, and lumped these cycles into a residual variance. While this is not satisfactory at the level of these specific time-series, the hierarchical model is still usefull as an overarching model to investigate some aspects of the biology of Southern Elephant Seals on îles Kerguelen.

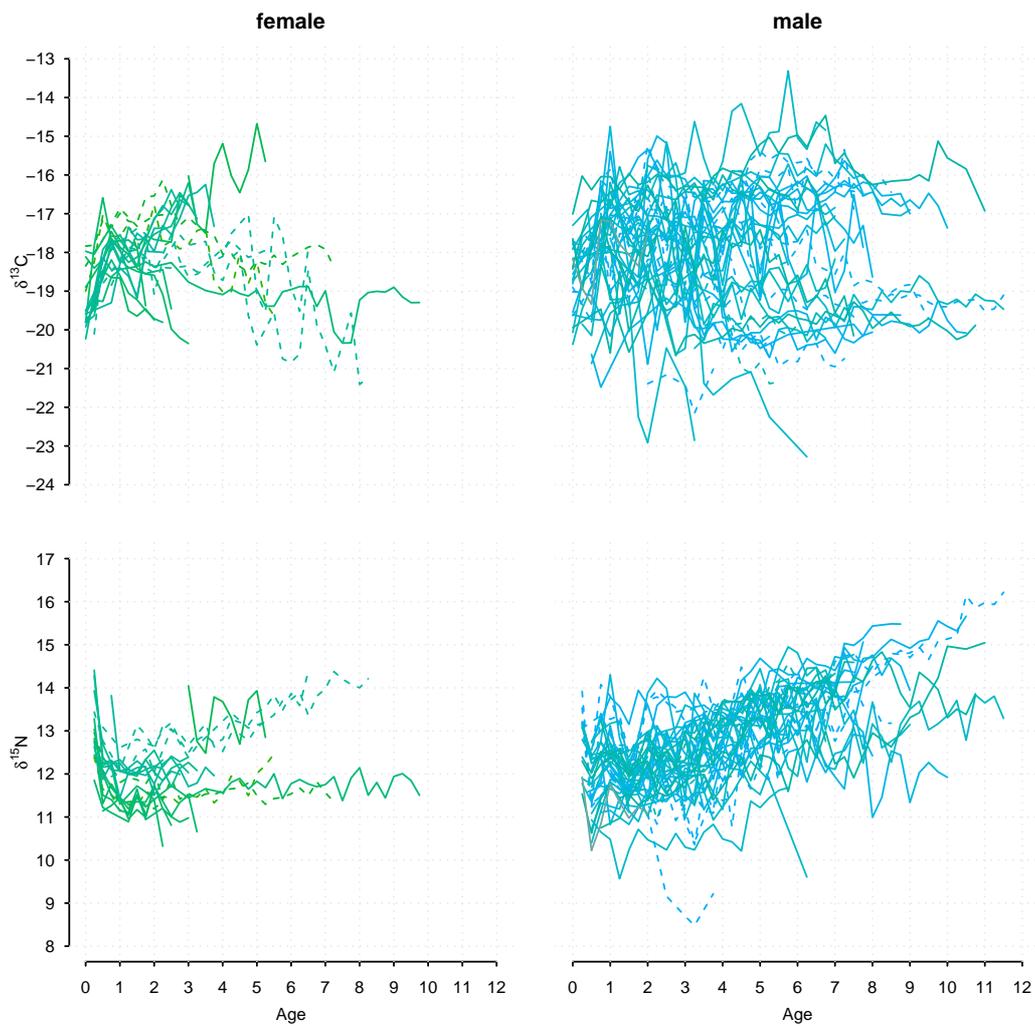


Figure D.2: Spaghetti plots of the raw data for the Southern Elephant Seal data. Dotted lines represent animals that died before the population crash in the 1970s, while continuous lines are for animals sampled in the 2000s.

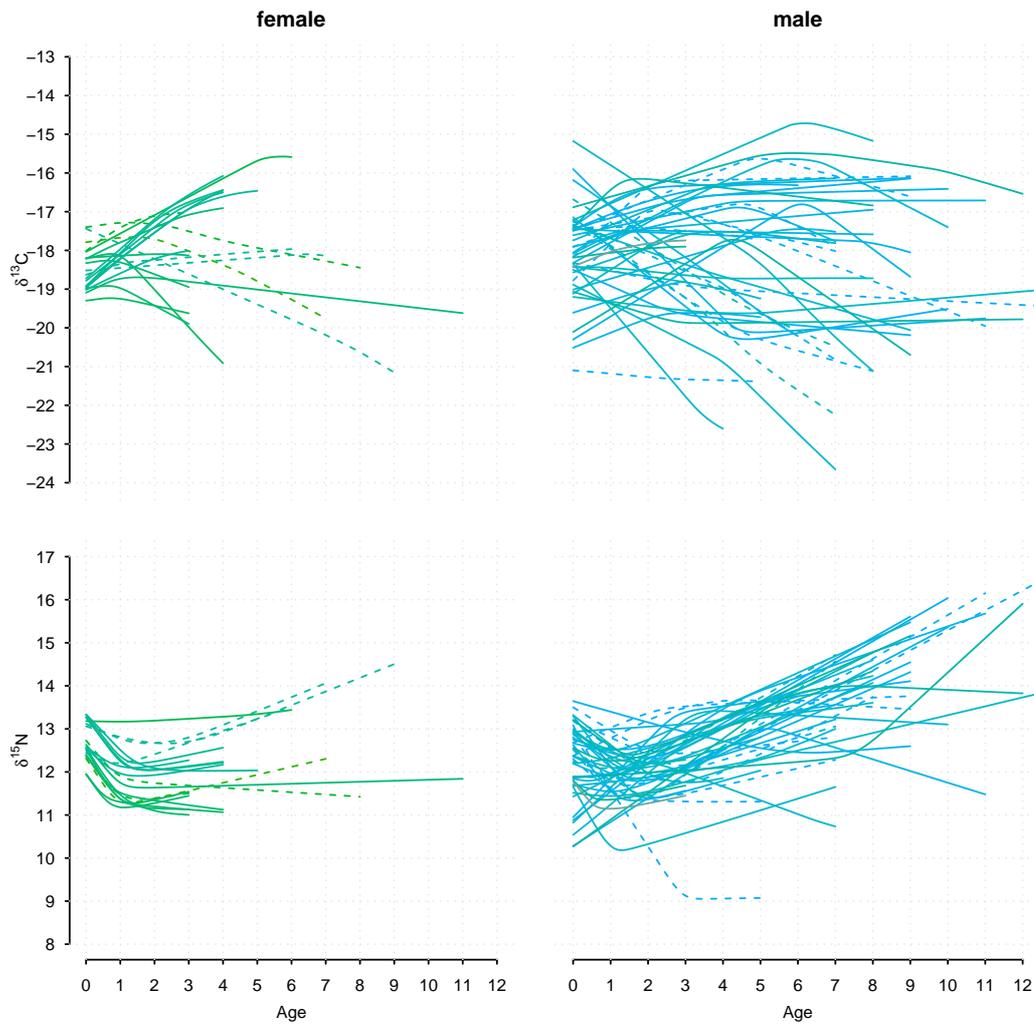


Figure D.3: Spaghetti plots of the random change-point model fitted to the Southern Elephant Seal data. Dotted lines represent animals that died before the population crash in the 1970s, while continuous lines are for animals sampled in the 2000s.

D.4 Joint Longitudinal-Survival Model

D.4.1 Priors

All models were run with `winBUGS` (Spiegelhalter et al., 2003) called from `R` (R Development Core Team, 2009) with the package `R2WinBUGS` (Sturtz et al., 2005). We used for the AFT model the default Student- t prior of Gelman et al. (2008) for the parameter $\beta_{k \in [1:4]}$, and a uniform prior bounded between 0 and 10 for r . Three chains were initialized with overdispersed starting values. After appropriate burn-in (200,000 iterations) and thinning of the chains (1 value every 200 iterations stored), convergence was assessed using the Gelman-Rubin convergence diagnostic (Cowles and Carlin, 1996) with the `coda` package (Plummer et al., 2008). Unless stated otherwise, posterior mean and standard error of the mean are reported, either with its standard error ($\pm se$) or with 95% Highest Probability Density (HPD) intervals ($2.5\% \text{Mean} 97.5\%$) following Louis and Zeger (2009). Inferences are based on a posterior sample of 3,000 iterations.

D.4.2 Model Checking

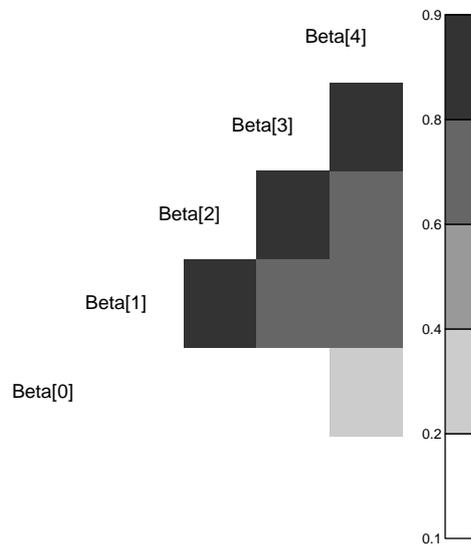


Figure D.4: Correlations between the predictors of the Accelerated Failure Time survival model. The large correlations means that these parameters are not independent. Further model checking revealed that only β_4 covaried with longevity.

D.4.3 Stochastic Search Variable Selection

Because of the large correlations between the $\beta_{k \in [1:4]}$ in the joint change-point/AFT model (Figure D.4), I used Stochastic Search Variable Selection (O'Hara and Sillanpää, 2009) to evaluate which covariate(s) was (were) the most important. Stochastic Search Variable Selection is related to the Spike-and-Slab approach detailed in Appendix C. Namely, I assign a sharp mixture prior for each β : for each iteration of the Gibbs Sampler, a β was either included or not in the model with probability $p_{\text{prior inclusion}}$. The percentage of iterations a β was in fact included approximates its posterior probability of inclusion. If this latter probability was above 0.80, I concluded the variable to be important. Given the large support for the joint change-point/AFT model, I considered two cases with $p_{\text{prior inclusion}}$ equals to 0.5 and 0.8. In the first case, the prior probability of including at least one covariate is $1 - (1 - 0.5)^4 = 0.9375$, while it is $1 - (1 - 0.8)^4 = 0.9984$ in the second case. Thus the prior is strongly in favor of including at least on covariate. Results are summarized in Table D.3.

Covariate	$p_{\text{prior inclusion}}$		Interpretation
	0.5	0.8	
a_1	0.06	0.30	Value at Shift
a_2	0.15	0.46	Slope before
a_3	0.41	0.75	Age at Shift
a_4	0.83	0.96	Slope after

Table D.3: Stochastic Search Variable Selection to identify which parameter of the change-point model correlates with longevity.

This analysis shows that the only parameter to truly covary with longevity was a_4 , the slope after the ontogenetic shift. It is the only parameter whose posterior probability of inclusion is larger than that of the prior. As a final check, I also computed the AIC_c of a joint model with only a_4 as a covariate and found it to equals 214.3 (for the full model, ($\text{AIC}_c = 215.6$)), which confirms that the slope after the ontogenetic shift is the only important covariate.

BUGS code to fit the Hierarchical Change-Point Model 8x8

```

model {
# Likelihood
for ( i in 1:N ) {
  d13C[i] ~ dnorm(mu[i,1],tau[i,1])
  tau[i,1] <- X[ 1,i,1 ]*pow(sd.res[ 1,1 ],-2) +
             X[ 1,i,2 ]*pow(sd.res[ 1,2 ],-2)
  mu[i,1] <- a[ ind[i],1 ] + (Age[i] - K[ 1,ind[i] ]) *
             (a[ ind[i],2 ]*X[ 1,i,1 ] + a[ ind[i],4 ]*X[ 1,i,2 ])
  X[1,i,1] <- step(K[ 1,ind[i] ] - Age[i])
  X[1,i,2] <- step(Age[i] - K[ 1,ind[i] ])
  d15N[i] ~ dnorm(mu[ i,2 ],tau[ i,2 ])
  tau[i,2] <- X[ 2,i,1 ]*pow(sd.res[ 2,1 ],-2) +
             X[ 2,i,2 ]*pow(sd.res[ 2,2 ],-2)
  mu[i,2] <- a[ ind[i],5 ] + (Age[i] - K[ 2,ind[i] ]) *
             (a[ ind[i],6 ]*X[ 2,i,1 ] + a[ ind[i],8 ]*X[ 2,i,2 ])
  X[2,i,1] <- step(K[ 2,ind[i] ] - Age[i])
  X[2,i,2] <- step(Age[i] - K[ 2,ind[i] ])
}
# Priors
for ( i in 1:n.ind ) {
  K[1,i] <- exp(a[i,3])
  K[2,i] <- exp(a[i,7])
  for ( j in 1:8 ) {
    epsilon.a[i,j] ~ dnorm(0,1)
    a[i,j] <- alpha[j] + a.hat[i,j]
  }
  a.hat[i,1] <- sd.a[1]*epsilon.a[i,1]
  a.hat[i,2] <- sd.a[2]*(L.a[2,1]*epsilon.a[i,1] +
                    epsilon.a[i,2])
  a.hat[i,3] <- sd.a[3]*(L.a[3,1]*epsilon.a[i,1] +
                    L.a[3,2]*epsilon.a[i,2] + epsilon.a[i,3])
  a.hat[i,4] <- sd.a[4]*(L.a[4,1]*epsilon.a[i,1] +
                    L.a[4,2]*epsilon.a[i,2] + L.a[4,3]*epsilon.a[i,3] +
                    epsilon.a[i,4])
  a.hat[i,5] <- sd.a[5]*(L.a[5,1]*epsilon.a[i,1] +
                    L.a[5,2]*epsilon.a[i,2] + L.a[5,3]*epsilon.a[i,3] +
                    L.a[5,4]*epsilon.a[i,4] + epsilon.a[i,5])
  a.hat[i,6] <- sd.a[6]*(L.a[6,1]*epsilon.a[i,1] +
                    L.a[6,2]*epsilon.a[i,2] + L.a[6,3]*epsilon.a[i,3] +
                    L.a[6,4]*epsilon.a[i,4] + L.a[6,5]*epsilon.a[i,5] +
                    epsilon.a[i,6])
  a.hat[i,7] <- sd.a[7]*(L.a[7,1]*epsilon.a[i,1] +
                    L.a[7,2]*epsilon.a[i,2] + L.a[7,3]*epsilon.a[i,3] +
                    L.a[7,4]*epsilon.a[i,4] + L.a[7,5]*epsilon.a[i,5] +
                    L.a[7,6]*epsilon.a[i,6] + epsilon.a[i,7])
  a.hat[i,8] <- sd.a[8]*(L.a[8,1]*epsilon.a[i,1] +
                    L.a[8,2]*epsilon.a[i,2] + L.a[8,3]*epsilon.a[i,3] +

```

```

        L.a[8,4]*epsilon.a[i,4] + L.a[8,5]*epsilon.a[i,5] +
        L.a[8,6]*epsilon.a[i,6] + L.a[8,7]*epsilon.a[i,7] +
        epsilon.a[i,8])
    }
# Hyperpriors
L.a[2,1] ~ dnorm(0,4)
L.a[3,1] ~ dnorm(0,4)
L.a[3,2] ~ dnorm(0,4)
L.a[4,1] ~ dnorm(0,4)
L.a[4,2] ~ dnorm(0,4)
L.a[4,3] ~ dnorm(0,4)
L.a[5,1] ~ dnorm(0,4)
L.a[5,2] <- -L.a[2,1]*L.a[5,1]
L.a[5,3] <- -L.a[3,2]*L.a[5,2] - L.a[3,1]*L.a[5,1]
L.a[5,4] <- -L.a[4,3]*L.a[5,3] - L.a[4,2]*L.a[5,2] - L.a[4,1]*L.a[5,1]
L.a[6,1] <- 0
L.a[6,2] ~ dnorm(0,4)
L.a[6,3] <- -L.a[3,2]*L.a[6,2]
L.a[6,4] <- -L.a[4,3]*L.a[6,3] - L.a[4,2]*L.a[6,2]
L.a[6,5] ~ dnorm(0,4)
L.a[7,1] <- 0
L.a[7,2] <- 0
L.a[7,3] ~ dnorm(0,4)
L.a[7,4] <- -L.a[4,3]*L.a[7,3]
L.a[7,5] ~ dnorm(0,4)
L.a[7,6] ~ dnorm(0,4)
L.a[8,1] <- 0
L.a[8,2] <- 0
L.a[8,3] <- 0
L.a[8,4] ~ dnorm(0,4)
L.a[8,5] ~ dnorm(0,4)
L.a[8,6] ~ dnorm(0,4)
L.a[8,7] ~ dnorm(0,4)

for ( j in 1:2 ) {
  alpha[j] ~ dnorm(0,0.001) ; alpha[j+4] ~ dnorm(0,0.001) ;
  for ( i in 1:2 ) { sd.res[j,i] ~ dunif(0,10) }
}
alpha[3] ~ dt(0,0.01,7) ; alpha[7] ~ dt(0,0.01,7) ;
alpha[4] ~ dnorm(0,0.001) ; alpha[8] ~ dnorm(0,0.001) ;
for ( j in 1:8 ) { sd.a[j] ~ dnorm(0,0.45)I(0,) }
}

```

BUGS code to fit the joint Accelerated Failure Time\Change-point Model

```

model {
  # Likelihood: Change Point
  for ( i in 1:N ) {
    d13C[i] ~ dnorm(mu[i],tau[i])
    tau[i] <- X[i,1]*pow(sd.res[1],-2) + X[i,2]*pow(sd.res[2],-2)
    mu[i] <- a[ ind[i],1 ] + (Age[i] - K[ind[i]]) * slope[i]
    slope[i] <- (a[ ind[i],2 ]*X[i,1] + a[ind[i],4]*X[i,2])
    X[i,1] <- step(K[ind[i]] - Age[i])
    X[i,2] <- step(Age[i] - K[ind[i]])
  }

  # Likelihood: Accelerated Failure Time model
  for ( i in 1:n.ind ) {
    Longevity[i] ~ dweib(r,nu[i])
    log(nu[i]) <- beta[1] + beta[2]*a.hat[i,1] + beta[3]*a.hat[i,2]
      + beta[4]*a.hat[i,3] + beta[5]*a.hat[i,4]
  }

  # Priors: Change-Point model
  sd.res[1] ~ dunif(0,10) ; sd.res[2] ~ dunif(0,10)
  alpha[1] ~ dnorm(0,0.001) ; alpha[2] ~ dnorm(0,0.001)
  alpha[3] ~ dt(0,0.01,7) ; alpha[4] ~ dnorm(0,0.001)
  for ( i in 1:n.ind ) {
    K[i] <- exp(a[i,3])
    for ( j in 1:4 ) {
      epsilon.a[i,j] ~ dnorm(0,1)
      a[i,j] <- alpha[j] + a.hat[i,j]
    }
    a.hat[i,1] <- sd.a[1]*epsilon.a[i,1]
    a.hat[i,2] <- sd.a[2]*(L.a[2,1]*epsilon.a[i,1] + epsilon.a[i,2])
    a.hat[i,3] <- sd.a[3]*(L.a[3,1]*epsilon.a[i,1] + L.a[3,2]*epsilon.a[i,2]
      + epsilon.a[i,3])
    a.hat[i,4] <- sd.a[4]*(L.a[4,1]*epsilon.a[i,1] + L.a[4,2]*epsilon.a[i,2]
      + L.a[4,3]*epsilon.a[i,3] + epsilon.a[i,4])
  }

  # Hyperpriors for the Choleski Decomposition of the Covariance Matrix
  L.a[2,1] ~ dnorm(0,4)
  L.a[3,1] ~ dnorm(0,4) ; L.a[3,2] ~ dnorm(0,4)
  L.a[4,1] ~ dnorm(0,4) ; L.a[4,2] ~ dnorm(0,4) ; L.a[4,3] ~ dnorm(0,4)
  for ( j in 1:4 ) { sd.a[j] ~ dnorm(0,0.45)I(0,) }

  # Priors: Accelerated Failure Time model
  beta[1] ~ dt(0,0.01,7)
  beta[2] ~ dt(0,0.04,7) ; beta[3] ~ dt(0,0.04,7)
  beta[4] ~ dt(0,0.04,7) ; beta[5] ~ dt(0,0.04,7)
  r ~ dunif(0,10) # shape parameter of the Weibull
} # End

```


Bibliography

- Aarestrup, K., F. Økland, M. Hansen, D. Righton, P. Gargan, M. Castonguay, L. Bernatchez, P. Howey, H. Sparholt, M. Pedersen, and R. McKinley. 2009. Oceanic Spawning Migration of the European Eel *Anguilla anguilla*. *Science* **325**:1660. (Cited on page 4.)
- Achen, C. 2002. Toward a New Political Methodology: Microfoundations and ART. *Annual Review of Political Science* **5**:423–450. (Cited on pages 46 and 96.)
- Ainley, D., and L. Blight. 2009. Ecological Repercussions of Historical Fish Extraction from the Southern Ocean. *Fish and Fisheries* **10**:13–38. (Cited on pages 11, 27, 58, 67, 90 and 97.)
- Ainley, D., and D. DeMaster, 1990. Polar Oceanography Part B. Chemistry, Biology and Geology, Chapter upper Trophic Levels in Polar Marine Ecosystems, pages 599–630 . Academic Press. (Cited on page 50.)
- Ambrose, S. 1990. Preparation and Characterization of Bone and Tooth Collagen for Isotopic Analysis. *Journal of Archaeological Science* **17**:431–451. (Cited on page 118.)
- An, L., and E. Ahmed. 2008. Improving the Performance of the Kurtosis Estimator. *Computational Statistics and Data Analysis* **52**:2669–2681. (Cited on page 44.)
- Anderson, T., I. Olkin, and L. Underhill. 1987. Generation of Random Orthogonal Matrices. *SIAM Journal on Scientific and Statistical Computing* **8**:625–629. URL <http://statistics.stanford.edu/~ckirby/techreports/NSF/ANDNSF06.pdf>. (Cited on page 104.)
- Ariew, A., and R. Lewontin. 2004. The Confusions of Fitness. *British Journal of Philosophy of Science* pages 347–363. (Cited on page 43.)
- Arnomb, T., M. Fedak, and I. Boyd. 1997. Factors Affecting Maternal Expenditure in Southern Elephant Seals during Lactation. *Ecology* **78**:471–483. (Cited on pages 11, 25, 40, 43 and 48.)
- Aubry, L., E. Cam, D. Koons, J. Monnat, and S. Parvard. 2011. Drivers of Age-Specific Survival in a Long-Lived Seabird: Contributions of Observed and Hidden Sources of Heterogeneity. *Journal of Animal Ecology* **80**:375–383. (Cited on page 85.)
- Auerswald, K., M. Wittmer, A. Zazzo, R. Schäufole, and H. Schnyder. 2010. Biases in the Analysis of Stable Isotope Discrimination in Food Webs. *Journal of Applied Ecology* **47**:936–941. (Cited on pages 7 and 96.)

- Authier, M., E. Cam, and C. Guinet. 2011*a*. Selection for Increased Body Length in Subantarctic Fur Seals Amsterdam Island. *Journal of Evolutionary Biology* **24**:607–616. (Cited on page 8.)
- Authier, M., K. Delord, and C. Guinet. 2011*b*. Population Trends of Female Elephant Seals Breeding on the Courbet Peninsula, îles Kerguelen. *Polar Biology* **34**:319–328. (Cited on pages 104 and 106.)
- Azzalini, A., 2009. *sn: the Skew-Normal and Skew-t Distributions*. (Cited on page 113.)
- Bailleul, F., M. Authier, S. Ducatez, F. Roquet, J.-B. Charassin, Y. Cherel, and C. Guinet. 2010. Looking at the Unseen: Combining Bio-logging and Stable Isotopes to Reveal a Shift in the Ecological Niche of a Deep-Diving Predator. *Ecography* **33**:709–719. (Cited on pages 13, 29, 34, 37, 46, 51, 57, 76, 77 and 85.)
- Bailleul, F., J.-B. Charassin, R. Ezraty, F. Girard-Ardhuin, C. McMahon, I. Field, and C. Guinet. 2007*a*. Southern Elephant Seals from Kerguelen Islands Confronted by Antarctic Sea Ice. Changes in Movements and in Diving Behaviour. *Deep Sea Research Part II* **54**:343–355. (Cited on pages 13, 34, 37, 51, 53, 56 and 85.)
- Bailleul, F., J.-B. Charassin, P. Monestiez, F. Roquet, M. Biuw, and C. Guinet. 2007*b*. Successful Foraging Zones of Southern Elephant Seals from the Kerguelen Islands in Relation to Oceanographic Conditions. *Philosophical Transactions of the Royal Society of London series B* **362**:2169–2181. (Cited on page 13.)
- Bakun, A. 2006. Fronts and Eddies as Key Structures in the Habitat of Marine Fish Larvae: Opportunity, Adaptive Response and Competitive Advantage. *Scientia Marina* **70**:105–122. (Cited on page 29.)
- Balding, D., M. Weale, M. Richards, and M. Thomas. 2010. Genetic and Isotopic Analysis and the UK Border Agency. *Significance* **7**:58–61. (Cited on page 91.)
- Barnard, J., R. McCulloch, and X. Meng. 2000. Modeling Covariance Matrices in Terms of Standard Deviations and Correlations, with Application to Shrinkage. *Statistica Sinica* **10**:1281–1311. (Cited on page 104.)
- Barnett, A., N. Koper, A. Dobson, F. Schmiegelow, and M. Manseau. 2010. Using Information Criteria to Select the Correct Variance-Covariance Structure for Longitudinal Data in Ecology. *Methods in Ecology and Evolution* **1**:15–24. (Cited on pages 113 and 121.)
- Beauplet, G., C. Barbraud, W. Dabin, C. Küssener, and C. Guinet. 2006. Age-Specific Survival and Reproductive Performances in Fur Seals: Evidence of Senescence and Individual Quality. *Oikos* **112**:430–441. (Cited on page 66.)

- Beauplet, G., and C. Guinet. 2007. Phenotypic Determinants of Individual Fitness in Female Fur Seals: Larger is Better. *Proceedings of the Royal Society of London series B* **274**:1877–1883. (Cited on page 79.)
- Beckage, B., L. Joseph, P. Belisle, D. B. Wolfson, and W. J. Platt. 2007. Bayesian Change-Point Analyses in Ecology. *New Phytologist* **174**:456–467. (Cited on page 69.)
- Beeton, M., and K. Pearson. 1901. On the Inheritance of the Duration of Life, and on the Intensity of Natural Selection in Man. *Biometrika* **1**:50–89. URL <http://www.jstor.org/stable/2331672>. (Cited on page 79.)
- Belkin, I. 2009. Rapid Warming of Large Marine Ecosystems. *Progress in Oceanography* **81**:207–213. (Cited on page 95.)
- Bell, C., H. Burton, M.-A. Lea, and M. Hindell. 2005. Growth of Female Elephant Seals *Mirounga leonina*. *Polar Biology* **28**:395–401. (Cited on page 40.)
- Bellera, C., J. Hanley, L. Joseph, and P. Albertsen. 2008. Hierarchical Change-point Models for Biochemical Markers Illustrated by Tracking Postradiotherapy Prostate-Specific Antigen Series in Men with Prostate Cancer. *Annals of Epidemiology* **18**:270–282. (Cited on page 69.)
- Bentaleb, I., M. Fontugne, C. Descolas-Gros, C. Girardin, A. Mariotti, C. Pierre, C. Brunet, and A. Poisson. 1998. Carbon Isotopic Fractionation by Phytoplankton in the Southern Indian Ocean: Relationship between $\delta^{13}\text{C}$ of Particulate Organic Carbon and Dissolved Carbon Dioxide. *Journal of Marine Systems* **17**:39–58. (Cited on pages 31 and 41.)
- Bergeron, P., R. Baeta, F. Pelletier, D. Réale, and D. Garant. 2011. Individual Quality : Tautology or Biological Reality? *Journal of Animal Ecology* **80**:361–364. (Cited on pages 2 and 98.)
- Berkhof, J., I. van Mechelen, and A. Gelman. 2003. A Bayesian Approach to the Selection and Testing of Mixture Models. *Statistica Sinica* **13**:423–442. (Cited on pages 113 and 121.)
- Berubé, C., M. Festa-Bianchet, and J. Jorgenson. 1999. Individual Differences, Longevity, and Reproductive Senescence in Big Horn Ewes. *Ecology* **80**:2554–2565. (Cited on page 79.)
- Best, P., and D. Schell. 1996. Stable Isotopes in Southern Right Whale (*Eubalaena australis*) Baleen as Indicators of Seasonal Movements, Feeding and Growth. *Marine Biology* **124**:483–494. (Cited on pages 69 and 94.)
- Biuw, M., L. Boehme, C. Guinet, M. Hindell, D. Costa, J.-B. Charassin, F. Roquet, M. Meredith, S. Thorpe, Y. Tremblay, B. McDonald, Y.-H. Park, S. Rintoul, N. Bindoff, M. Goebel, D. Crocker, P. Lovell, J. Nicholson, F. Monks, and

- M. Fedak. 2007. Variations in Behaviour and Condition of a Southern Ocean Top Predator in Relation to *in situ* Oceanographic Conditions. Proceedings of the National Academy of Sciences **104**:13705–13710. (Cited on pages 11 and 40.)
- Blain, S., P. Tréguer, S. Belviso, E. Bucciarelli, M. Denis, S. Desabre, M. Fiala, V. Jézéquel, J. Le Fèvre, P. Mayzaud, J.-M. Marty, and S. Razouls. 2001. A Biogeographical Study of the Island Mass Effect in the Context of the Iron Hypothesis: Kerguelen Islands, Southern Ocean. Deep-Sea Research Part I **48**:163–187. (Cited on pages 32, 40, 42, 51 and 53.)
- Boggs, C. 1992. Resource Allocation: Exploring Connections between Foraging and Life History. Functional Ecology **6**:508–518. (Cited on pages 2 and 3.)
- Bolnick, D., R. Svänback, J. Fordyce, L. Yang, C. Hulsey, and M. Forister. 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. American Naturalist **161**:1–28. (Cited on page 65.)
- Bond, A., and A. Diamond. 2011. Recent Bayesian Stable-Isotope Mixing Models are highly Sensitive to Variation in Discrimination Factors. Ecological Applications **21**:1017–1023. (Cited on pages 7, 96 and 97.)
- Bost, C.-A., C. Cotté, F. Bailleul, B. Charassin, C. Guinet, D. Ainley, and H. Weimerskirch. 2009a. The Importance of Oceanographic Fronts to Marine Birds and Mammals of the Southern Oceans. Journal of Marine Systems **78**:363–376. (Cited on page 53.)
- Bost, C.-A., J.-B. Thiebot, D. Pinaud, Y. Cherel, and P. Trathan. 2009b. Where Do Penguins Go During the Inter-Breeding Period? Using Geolocation to Track the Winter Dispersion of the Macaroni Penguin. Biology Letters **5**:473–476. (Cited on page 29.)
- Box, G. 1990. Comment. Statistical Science **5**:448–449. (Cited on page 9.)
- Boyd, I., T. Walker, and J. Poncet. 1996. Status of Southern Elephant Seals at South Georgia. Antarctic Science **8**:237–244. (Cited on page 25.)
- Bradburn, M., T. Clark, and D. Altman. 2003a. Survival Analysis Part II: Multivariate Data Analysis - an Introduction to Concept and Methods. British Journal of Cancer **89**:431–436. (Cited on page 80.)
- Bradburn, M., T. Clark, and D. Altman. 2003b. Survival Analysis Part III: Choosing a Model and Assessing its Adequacy and Fit. British Journal of Cancer **89**:605–611. (Cited on pages 80 and 82.)
- Bradshaw, C., M. Hindell, N. Best, K. Phillips, G. Wilson, and P. Nichols. 2003. You Are what You Eat: Describing the Foraging Ecology of Southern Elephant Seals (*Mirounga leonina*) using Blubber Fatty Acids. Proceedings of the Royal Statistical Society of London series B **270**:1283–1292. (Cited on page 97.)

- Bradshaw, C., M. Hindell, M. Sumner, and K. Michael. 2004. Loyalty Pays: Potential Life History Consequences of Fidelity to Marine Foraging Regions by Southern Elephant Seals. *Animal Behaviour* **68**:1349–1360. (Cited on pages 58, 60, 65, 71, 76 and 92.)
- Brodie, C., M. Leng, J. Casford, C. Kendrick, J. Lloyd, Z. Yongqiang, and M. Bird. 2011. Evidence for Bias in C and N Concentrations and $\delta^{13}\text{C}$ Composition of Terrestrial and Aquatic Organic Materials Due to Pre-Analysis Acid Preparation Methods. *Chemical Geology* **282**:67–83. URL <http://www.sciencedirect.com/science/article/pii/S0009254111000222>. (Cited on page 118.)
- Brommer, J., L. Gustafsson, H. Pietiäinen, and J. Merilä. 2004. Single-Generation Estimates of Individual Fitness as Proxies for Long-Term Genetic Contribution. *American Naturalist* **163**:505–517. (Cited on page 43.)
- Brommer, J., J. Merilä, and H. Kokko. 2002. Reproductive Timing and Individual Fitness. *Ecology Letters* **5**:802–810. (Cited on page 43.)
- Browne, W., R. McCleery, B. Sheldon, and R. Pettifor. 2007. Using Cross-Classified Multivariate Mixed Response Models with Application to Life-History Traits in Great Tits (*Parus major*). *Statistical Modelling* **7**:217–238. (Cited on page 8.)
- Budden, M., P. Havadas, L. Hoffman, and C. Pretz. 2007. Generating Valid 4×4 Correlation Matrices. *Applied Mathematics E-Notes* **7**:53–59. (Cited on page 103.)
- Burnham, K., and D. Anderson. 2002. *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach*. 2nd edition. Springer. (Cited on page 8.)
- Burnham, K., and D. Anderson. 2004. Understanding AIC and BIC in Model Selection. *Sociological Methods and Research* **33**:261–304. (Cited on pages 82 and 83.)
- Burton, R., T. Arnbohm, M. Bester, D. Vergani, and I. Wilkinson, 1997. *Antarctic Communities - Species Structure and Survival*, Chapter significant Differences in Weaning Mass of Southern Elephant Seals from Five sub-Antarctic Islands in Relation to Population Declines, pages 335–338. Cambridge University Press. (Cited on pages 43, 50, 85 and 91.)
- Cam, E., W. Link, E. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual Covariation in Life-History Traits: Seeing the Trees Despite the Forests. *American Naturalist* **159**:96–105. (Cited on page 2.)
- Cam, E., J.-Y. Monnat, and J. Hines. 2003. Long-Term Fitness Consequences of Early Conditions in the Kittiwake. *Journal of Animal Ecology* **72**:411–424. (Cited on page 85.)

- Carleton, S., L. Kelly, R. Anderson-Sprecher, and C. Martínez del Río. 2008. Should We Use One-, or Multi-Compartment Models to Describe ^{13}C Incorporation Into Animal Tissues? *Rapid Communications in Mass Spectrometry* **22**:3008–3014. (Cited on page 96.)
- Carleton, S., and C. Martínez del Río. 2005. The Effect of Cold-Induced Increased Metabolic Rate on the Rate of ^{13}C and ^{15}N Incorporation in House Sparrows (*Passer domesticus*). *Oecologia* **144**:226–232. (Cited on page 35.)
- Carlini, A., M. Márquez, G. Soave, V. Vergani, and P. Ronayne de Ferrer. 1994. Southern Elephant Seals, *Mirounga leonina*: Composition of Milk during Lactation. *Polar Biology* **14**:37–42. (Cited on page 85.)
- Carlini, A., J. Negrete, G. Daneri, T. Rogers, M. Márquez, M. Ciaglia, and J. Mennucci. 2009. Immobilization of Adult Male Southern Elephant Seals (*Mirounga leonina*) during the Breeding and Molting Periods using a Tiletamine/Zolazepam Mixture and Ketamine. *Polar Biology* **32**:915–921. (Cited on page 93.)
- Catul, V., M. Gauns, and P. Karappasamy. 2011. A Review on Mesopelagic Fishes belonging to Family Myctophidae. *Reviews in Fish Biology and Fisheries* **21**:339–354. (Cited on pages 52 and 97.)
- Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in Discrimination Factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the Effect of Diet Isotopic Values and Applications for Diet Reconstruction. *Journal of Applied Ecology* **46**:443–453. (Cited on pages 7, 31 and 96.)
- Caut, S., E. Angulo, F. Courchamp, and J. Figuerola. 2010. Trophic Experiment to Estimate Isotope Discrimination Factors. *Journal of Applied Ecology* **47**:948–954. (Cited on page 7.)
- Caut, S., S. Laran, E. Garcia-Hartmann, and K. Das. 2011. Stable Isotopes of Captive Cetaceans (Killer Whales and Bottlenose Dolphins). *Journal of Experimental Biology* **214**:538–545. (Cited on page 97.)
- Celeux, G., F. Forbes, C. Robert, and D. Titterton. 2006. Deviance Information Criteria for Missing Data Models. *Bayesian Analysis* **1**:651–674. (Cited on pages 113 and 121.)
- Chalmers, A. 2006. *What is This Thing Called Science?* 3rd edition. Open University Press. (Cited on page 9.)
- Chen, Z., and D. Dunson. 2003. Random Effects Selection in Linear Mixed Models. *Biometrics* **59**:762–769. (Cited on pages 104 and 120.)
- Cherel, Y., S. Ducatez, C. Fontaine, P. Richard, and C. Guinet. 2008. Stable Isotopes Reveals the Trophic Position and Mesopelagic Diet of Female Southern Elephant Seals Breeding on the Kerguelen Islands. *Marine Ecology Progress Series* **370**:239–247. (Cited on pages 52, 78, 93 and 97.)

- Cherel, Y., C. Fontaine, P. Richard, and J. Labat. 2010. Isotopic Niches and Trophic Levels of Myctophid Fishes and their Predators in the Southern Ocean. *Limnology and Oceanography* **55**:324–332. (Cited on page 52.)
- Cherel, Y., and K. Hobson. 2007. Geographical Variation in the Carbon Stable Isotope Signatures of Marine Predators: a Tool to Investigate Their Foraging Areas in the Southern Ocean. *Marine Ecology Progress Series* **329**:281–287. (Cited on pages 32 and 52.)
- Cherel, Y., K. Hobson, C. Guinet, and C. Vanpe. 2007. Stable Isotopes Document Seasonal Changes in Trophic Niches and Winter Foraging Individual Specialization in Diving Predators from the Southern Ocean. *Journal of Animal Ecology* **76**:826–836. (Cited on pages 32 and 90.)
- Cherel, Y., L. Kernaléguen, P. Richard, and C. Guinet. 2009. Whisker Isotopic Signature Depicts Migration Patterns and Multi-Year Intra- and Inter-Individual Foraging Strategies in Fur Seals. *Biology Letters* **5**:830–832. (Cited on pages 66, 69 and 94.)
- Choquet, R., A. Viallefont, L. Rouan, K. Gaanoun, and J. Gaillard. 2011. A Semi-Markov Model to Assess Reliably Survival Patterns from Birth to Death in Free-Ranging Populations. *Methods in Ecology and Evolution* **in press**:–. (Cited on page 80.)
- Clark, T., M. Bradburn, S. Love, and D. Altman. 2003. Survival Analysis Part IV: Basic Concepts and First Analyses. *British Journal of Cancer* **89**:232–238. (Cited on page 80.)
- Cole, L. 1954. The Population Consequences of Life-History Phenomena. *The Quarterly Review of Biology* **29**:103–137. (Cited on page 2.)
- Condit, R., B. Le Boeuf, P. Morris, and M. Sylvan. 2007. Estimating Population Size in Asynchronous Aggregations: a Bayesian Approach and Test with Elephant Seal Censuses. *Marine Mammal Science* **23**:834–855. (Cited on pages 17, 22 and 24.)
- Cooch, E., E. Cam, and W. Link. 2002. Occam's Shadow: Levels of Analysis in Evolutionary-Ecology – Where to Next? *Journal of Applied Statistics* **29**:19–48. (Cited on page 2.)
- Correia, A., F. Barros, and A. Sial. 2011. Stock Discrimination of European Conger Eel (*Conger conger* L.) using Otolith Stable Isotope Ratios. *Fisheries Research* **108**:88–94. (Cited on page 66.)
- Cowles, M., and B. Carlin. 1996. Markov Chain Monte Carlo Convergence Diagnostics: a Comparative Review. *Journal of the American Statistical Association* **91**:883–904. (Cited on pages 103, 113, 120 and 125.)
- Cox, D. 1972. Regression Models and Life Tables. *Journal of the Royal Statistical Society of London Serie B* **34**:187–220. (Cited on page 80.)

- Da-Silva, C., A. Gomes, E. Martins, V. Bonato, and S. dos Reis. 2008. A Bayesian Change-Point Model for Describing Partial Semelparity of a Neotropical Didelphid Marsupial. *Review of Brazilian Biometry* **26**:31–44. (Cited on page 69.)
- Darlington, R. 1970. Is Kurtosis Really "Peakedness"? *American Statistician* **24**:19–22. URL <http://www.jstor.org/stable/2681925>. (Cited on pages 46, 54 and 113.)
- Davis, R., L. Fuiman, T. Williams, S. Collier, W. Hagey, S. Kanatous, S. Kohin, and M. Horning. 1999. Hunting Behavior of a Marine Mammal Beneath the Antarctic Fast Ice. *Science* **283**:993–996. (Cited on page 4.)
- de Bruyn, P., C. Tosh, M. Bester, E. Cameron, T. McIntyre, and I. Wilkinson. 2011. Sex at Sea: Alternative Mating System in an Extremely Polygynous Mammal. *Animal Behaviour* **82**:445–451. (Cited on page 57.)
- DeNiro, M., and S. Epstein. 1977. Mechanism of Carbon Isotope Fractionation associated with Lipid-Synthesis. *Science* **197**:261–263. (Cited on pages 85, 111 and 117.)
- DeNiro, M., and S. Epstein. 1978. Influence of Diet on the Distribution of Carbon Isotopes in Animals. *Geochimica et Cosmochimica Acta* **42**:495–506. (Cited on page 5.)
- DeNiro, M., and S. Epstein. 1981. Influence of Diet on the Distribution of Carbon Isotopes in Animals. *Geochimica et Cosmochimica Acta* **45**:341–351. (Cited on page 5.)
- Dennis, B., 2004. *The Nature of Scientific Evidence*, Chapter 11 - Statistics and the Scientific Method in Ecology, pages 327–360 . The University of Chicago Press. (Cited on page 100.)
- Dennis, B., and A. Ellison. 2010. A Reply to Millsaugh and Gitzen. *Frontiers in Ecology and the Environment* **8**:515–516. (Cited on page 100.)
- Depew, D. 2010. Is Evolutionary Biology Infected with Invalid Teleological Reasoning? *Philosophy and Theory in Biology* **2**:e105. URL <http://hdl.handle.net/2027/spo.6959004.0002.005>. (Cited on page 4.)
- Descamps, S., S. Boutin, D. Berteaux, and J.-M. Gaillard. 2006. Best Squirrels Trade a long Life for an early Reproduction. *Proceedings of the Royal Statistical Society London Series B* **273**:2369–2374. (Cited on page 79.)
- Doniol-Valcroze, T., V. Lesage, J. Giard, and R. Michaud. 2011. Optimal Foraging Theory Predicts Diving and Feeding Strategies of the Largest Marine Predator. *Behavioral Ecology* **22**:880–888. (Cited on page 4.)

- Dragon, A., A. Bar-Hen, P. Monestiez, and C. Guinet, 2011*a*. Comparative Analysis of Methods for Inferring Successful Foraging Areas from Argos and GPS Tracking Data. unpublished manuscript, Centre d'Études Biologiques de Chizé. (Cited on page 33.)
- Dragon, A., S. Marchand, M. Authier, C. Cotté, S. Blain, and C. Guinet, 2011*b*. The Kerguelen Plateau - Marine Ecosystem and Fisheries, Chapter insights of the Spatio-Temporal Productivity Distribution in the Indian Southern Ocean Provided by Satellite Observations, pages 57–67 . Société Française d'Ichtyologie. (Cited on page 53.)
- Dragon, A., P. Monestiez, A. Bar-Hen, and C. Guinet. 2010. Linking Foraging Behaviour to Physical Oceanographic Structures: Southern Elephant Seals and Mesoscale Eddies East of Kerguelen Islands. *Progress in Oceanography* **87**:61–71. (Cited on pages 51 and 93.)
- Ducatez, S., S. Dalloyau, P. Richard, C. Guinet, and Y. Cherel. 2008. Stable Isotopes Document Winter Trophic Ecology and Maternal Investment of Adult Female Southern Elephant Seals (*Mirounga leonina*) Breeding at the Kerguelen Islands. *Marine Biology* **155**:413–420. (Cited on pages 13, 43, 45, 48, 50, 57 and 90.)
- Dümgen, L., and H. Riedwyl. 2007. On Fences and Asymmetry in Box-and-Whiskers Plots. *American Statistician* **61**:356–359. (Cited on pages 45 and 119.)
- Dunson, D., 2009. Bayesian Nonparametrics, Chapter 7 - Nonparametric Bayes Applications to Biostatistics, pages 223–273 . Cambridge University Press. (Cited on page 97.)
- Eder, E., M. Lewis, C. Campagna, and P. Koch. 2010. Evidence of Demersal Foraging from Stable Isotope Analysis of Juvenile Elephant Seals from Patagonia. *Marine Mammal Science* **26**:430–442. (Cited on pages 93 and 97.)
- Edmonds, J., and W. Fletcher. 1997. Stock Discrimination of Pilchards *Sardinops sagax* by Stable Isotope Ratio Analysis of Otolith Carbonate. *Marine Ecology Progress Series* **152**:241–247. (Cited on page 66.)
- Edney, E., and R. Gill. 1968. Evolution of Senescence and Specific Longevity. *Nature* **220**:281–282. (Cited on page 86.)
- Efron, B. 1979. Bootstrap Methods: Another Look at the Jackknife. *Annals of Statistics* **7**:1–26. URL <http://projecteuclid.org/euclid.aos/1176344552>. (Cited on page 9.)
- Efron, B. 2010. The Future of Indirect Evidence. *Statistical Science* **25**:145–157. (Cited on page 100.)
- Ellison, A. 2004*a*. Bayesian Inference in Ecology. *Ecology Letters* **7**:509–520. (Cited on page 100.)

- Ellison, A., 2004*b*. The Nature of Scientific Evidence, Chapter 11 - Statistics and the Scientific Method in Ecology (commentary), pages 362–367 . The University of Chicago Press. (Cited on pages 8 and 100.)
- Ellison, A., and B. Dennis. 2010. Paths to Statistical Fluency for Ecologists. *Frontiers in Ecology and the Environment* **8**:362–370. (Cited on pages 7, 8 and 100.)
- Estrada, J., A. Rice, L. Natanson, and G. Skomal. 2006. Use of Isotopic Analysis of Vertebrae in Reconstructing Ontogenetic Feeding Ecology in White Sharks. *Ecology* **87**:829–834. (Cited on page 67.)
- Fagerland, M., and L. Sandvik. 2009. The Wilcoxon-Mann-Whitney Test under Scrutiny. *Statistics in Medicine* **28**:1487–1497. (Cited on page 9.)
- Field, I., C. Bradshaw, H. Burton, and M. Hindell. 2007*a*. Differential Resource Allocation Strategies in Juvenile Elephant Seals in the Highly Seasonal Southern Ocean. *Marine Ecology Progress Series* **331**:281–290. (Cited on page 53.)
- Field, I., C. Bradshaw, H. Burton, M. Sumner, and M. Hindell. 2005. Resource Partitioning through Oceanic Segregation of Foraging Juvenile Southern Elephant Seals. *Oecologia* **142**:127–135. (Cited on page 98.)
- Field, I., C. Bradshaw, J. van den Hoff, H. Burton, and M. Hindell. 2007*b*. Age-Related Shifts in the Diet Composition of Southern Elephant Seals Expand Overall Foraging Niche. *Marine Biology* **150**:1441–1452. (Cited on pages 77 and 97.)
- France, R. 1995. ^{13}C Carbon Enrichment in Benthic Compared to Planktonic Algae: Foodweb Implications. *Marine Ecology Progress Series* **124**:307–312. (Cited on pages 6 and 95.)
- Francois, R., M. A. Altabet, R. Goericke, D. McCorkle, C. Brunet, and A. Poisson. 1993. Changes in the $\delta^{13}\text{C}$ of Surface Water Particulate Organic Matter across the Subtropical Convergence in the SW Indian Ocean. *Global Geochemical Cycles* **7**:627–644. (Cited on page 41.)
- Freese, J., 2008. Intergenerational Caregiving, Chapter the Problem of Predictive Promiscuity in Deductive Applications of Evolutionary Reasoning to Intergenerational Transfers: Three Cautionary Tales, pages 45–78 . Urban Institute Press. (Cited on page 96.)
- Fry, B. 2006. *Stable Isotope Ecology*. 1st edition. Springer. (Cited on pages 5 and 7.)
- Fry, B., W. Jeng, R. Scalan, P. Parker, and J. Baccus. 1978. $\delta^{13}\text{C}$ Food Web Analysis of a Texas Sand Dune Community. *Geochimica et Cosmochimica Acta* **42**:1299–1302. (Cited on page 5.)

- Fúquene, J., 2011. Heavy Tailed Prior: an Alternative to the Non-Informative Priors in the Estimation of Proportions on Small Areas. Article, University of California Santa Cruz. URL http://arxiv.org/PS_cache/arxiv/pdf/1107/1107.2724v1.pdf. (Cited on page 100.)
- Fúquene, J., J. Cook, and L. Pericchi. 2009. A Case for Robust Bayesian Priors with Applications to Clinical Trials. *Bayesian Analysis* **4**:817–846. URL ba.stat.cmu.edu/journal/2009/vol04/issue04/fuquene.pdf. (Cited on pages 100 and 103.)
- Gaillard, J.-M., , A. Loison, M. Festa-Bianchet, N. Yoccoz, and E. Solberg, 2003. Life Span: Evolutionary, Ecological, and Demographic Perspectives, Chapter ecological correlates of life span in populations of large herbivorous mammals, pages 39–56 . The Population Council. (Cited on page 87.)
- Gaillard, J.-M., M. Festa-Bianchet, D. Delorme, and J. Jorgensen. 2000. Body Mass and Individual Fitness in Female Ungulates: Bigger is not always Better. *Proceedings of the Royal Society of London Series B* **267**:471–477. (Cited on page 79.)
- Galimberti, F., and L. Boitani. 1999. Demography and Breeding Biology of a Small, Localized Population of Southern Elephant Seals (*Mirounga Leonina*). *Marine Mammal Science* **15**:159–178. (Cited on page 25.)
- Galimberti, F., L. Boitani, and I. Sanvito. 2002. Measure of reeding Inequality: a Case Study in Southern Elephant Seals. *Canadian Journal of Zoology* **80**:1240–1249. (Cited on page 79.)
- Galimberti, F., and S. Sanvito. 2001. Modelling Female Haul-Out in Southern Elephant Seal *Mirounga leonina*. *Aquatic Mammals* **27**:92–104. (Cited on pages 17, 22, 24 and 25.)
- Galimberti, F., S. Sanvito, C. Braschi, and L. Boitani. 2007. The Costs of Success: Reproductive Effort in Male Southern Elephant Seals (*Mirounga leonina*). *Behavioural Ecology and Sociobiology* **62**:159–171. (Cited on pages 79 and 86.)
- Gannes, L., D. O'Brien, and C. Martinez del Rio. 1997. Stable Isotopes in Animal Ecology: Assumptions, Caveats and a Call for Laboratory Experiments. *Ecology* **78**:71–76. (Cited on pages 7 and 96.)
- Gao, F., J. Miller, C. Xiong, J. Beiser, M. Gordon, and The Ocular Hypertension Treatment Study (OHTS) Group. 2011. A Joint-Modelling Approach to Assess the Impact of Biomarker Variability on the Risk of Developing Clinical Outcome. *Statistical Methods and Applications* **20**:83–100. (Cited on page 94.)
- Gelman, A. 2003. A Bayesian Formulation of Exploratory Data Analysis and Goodness-of-Fit Testing. *International Statistical Review* **71**:369–382. (Cited on page 113.)

- Gelman, A. 2006. Prior Distributions for Variance Parameters in Hierarchical Models (Comment on Article by Browne and Draper). *Bayesian Analysis* **1**:515–534. (Cited on pages 100, 103, 113 and 120.)
- Gelman, A. 2008. Scaling Regression Inputs by Dividing by Two Standard Deviations. *Statistics in Medicine* **27**:2865–2873. (Cited on pages 38, 113 and 120.)
- Gelman, A. 2010. Bayesian Statistics Then and Now. *Statistical Science* **25**:162–165. (Cited on page 8.)
- Gelman, A., J. Carlin, H. Stern, and D. Rubin. 2003. *Bayesian Data Analysis*. 2nd edition. Chapman & Hall\CRC. (Cited on pages 9 and 99.)
- Gelman, A., and J. Hill. 2007. *Data Analysis Using Regression and Multilevel-Hierarchical Models*. 1st edition. Cambridge University Press. (Cited on pages 9, 19, 57, 103 and 114.)
- Gelman, A., A. Jakulin, M. Grazia Pittau, and Y.-S. Su. 2008. A Weakly Informative Default Prior Distribution for Logistic and Other Regression Models. *The Annals of Applied Statistics* **2**:1360–1383. (Cited on pages 100, 103, 113, 120 and 125.)
- Gelman, A., X.-L. Meng, and H. Stern. 1996. Posterior Predictive Assessment of Model Fitness via Realized Discrepancies. *Statistica Sinica* **6**:733–807. (Cited on pages 113 and 121.)
- Gelman, A., and I. Pardoe. 2006. Bayesian Measures of Explained Variance and Pooling in Multilevel (Hierarchical) Models. *Technometrics* **48**:241–251. (Cited on page 54.)
- Gelman, A., and C. Shalizi, 2010. *Philosophy and the Practice of Bayesian Statistics*. Working paper, Department of Statistics and Department of Political Science, Columbia University. URL <http://www.stat.columbia.edu/~gelman/research/unpublished/philosophy.pdf>. (Cited on page 9.)
- Gelman, A., Y. Su, M. Yajima, J. Hill, M. Pittau, J. Kerman, and T. Zheng, 2011. *arm: Data Analysis Using Regression and Multilevel-Hierarchical Models*. URL <http://cran.r-project.org/web/packages/arm>. (Cited on page 111.)
- Gelman, A., and F. Tuerlinckx. 2000. Type-S Error Rates for Classical and Bayesian Single and Multiple Comparison Procedures. *Computational Statistics* **15**:373–390. (Cited on pages 41, 96 and 112.)
- Ghosh, P., P. Gill, S. Muthukumarana, and T. Swartz. 2010. A Semi-Parametric Bayesian Approach to Network Modelling using Dirichlet Process Prior Distributions. *Australian and New Zealand Journal of Statistics* **52**:289–302. (Cited on page 97.)

- Ghosh, P., and F. Vaida. 2007. Random Change-point Modelling of HIV Immunologic Responses. *Statistics in Medicine* **26**:2074–2087. (Cited on page 69.)
- Gill, J. 2009. *Bayesian Methods. A Social and Behavioural Sciences Approach*. 2nd edition. Chapman & Hall/CRC. (Cited on pages 9 and 99.)
- Glymour, C. 1998. What Went Wrong? Reflections on Science by Observation and the Bell Curve. *Philosophy of Science* **65**:1–32. (Cited on page 27.)
- Gompertz, B. 1825. On the Nature of the Function Expressive of the Law of Human Mortality, and on a New Mode of Determining the Value of Life Contingencies. *Philosophical Transactions of the Royal Society of London* **115**:513–583. URL <http://www.jstor.org/stable/107756>. (Cited on page 79.)
- Gould, S., and R. Lewontin. 1979. The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Programme. *Proceedings of the Royal Society of London series B* **205**:581–598. (Cited on page 4.)
- Green, A. 2001. Mass \Length Residuals: Measures of Body Condition or Generators of Spurious Results. *Ecology* **82**:1473–1483. (Cited on page 48.)
- Guinet, C. 1992. Comportement de Chasse des Orques *Orcinus orca* autour des Îles Crozet. *Canadian Journal of Zoology* **70**:1656–1667. (Cited on page 51.)
- Guinet, C., P. Jouventin, and H. Weimerskirch. 1999. Recent Population Change of the Southern Elephant Seal at Îles Crozet and Îles Kerguelen: the End of the Decrease? *Antarctic Science* **11**:193–197. (Cited on pages 11, 13, 16, 24, 27, 67 and 82.)
- Guo, X., and B. Carlin. 2004. Separate and Joint Modeling of Longitudinal and Event Time Data Using Standard Computer Packages. *The American Statistician* **58**:1–9. (Cited on pages 80 and 94.)
- Gurrin, L., K. Scurrah, and M. Hazelton. 2005. Tutorial in Biostatistics: Spline Smoothing with Linear Mixed Models. *Statistics in Medicine* **24**:3361–3381. (Cited on page 24.)
- Hall, C., R. Lipton, M. Sliwinski, and W. Stewart. 2000. A Change Point Model for Estimating the Onset of Cognitive Decline in Preclinical Alzheimer's Disease. *Statistics in Medicine* **19**:1555–1566. (Cited on page 69.)
- Hamel, S., S. Côté, J. Gaillard, and M. Festa-Bianchet. 2009. Individual Variation in Reproductive Costs of Reproduction: High-Quality Females Always Do Better. *Journal of Animal Ecology* **78**:143–151. (Cited on page 79.)
- Hamel, S., J. Gaillard, N. Yoccoz, A. Loison, C. Bonenfant, and S. Descamps. 2010. Fitness Costs of Reproduction Depend on Life Speed: Empirical Evidence from Mammalian Populations. *Ecology Letters* **13**:915–935. (Cited on page 79.)

- Hart, K., and I. Fujisaki. 2010. Satellite Tracking Reveals Habitat Use by Juvenile Green Sea Turtle *Chelonia mydas* in the Everglades, Florida, USA. *Endangered Species Research* **11**:221–232. (Cited on page 4.)
- Hays, G., S. Fossette, K. Katselidis, P. Mariani, and G. Schofield. 2010. Ontogenetic Development of Migration: Lagrangian Drift Trajectories Suggest a New Paradigm for Sea Turtles. *Interface* **7**:1319–1327. (Cited on page 98.)
- Hebblewhite, M., and D. Haydon. 2010. Distinguishing Technology from Biology: a Critical Review of the Use of GPS Telemetry Data in Ecology. *Philosophical Transactions of the Royal Society London series B* **365**:2303–2312. (Cited on page 4.)
- Hénaux, V., L. Powell, K. Hobson, C. Nielsen, and M. LaRue. 2011. Tracking Large Carnivore Dispersal using Isotopic Clues in Claws: an Application to Cougars across the Great Plains. *Methods in Ecology and Evolution* . (Cited on pages 8 and 95.)
- Henderson, R., P. Diggle, and A. Dobson. 2000. Joint Modelling of Longitudinal Measurements and Event-Time Data. *Biostatistics* **1**:465–480. (Cited on page 80.)
- Henderson, R., M. Jones, and J. Stare. 2001. Accuracy of Point Predictions in Survival Analysis. *Statistics in Medicine* **20**:3083–3096. (Cited on page 86.)
- Higgins, J., and D. Spiegelhalter. 2002. Being Skeptical about Meta-Analyses: a Bayesian Perspective on Magnesium Trials in Myocardial Infarction. *International Journal of Epidemiology* **31**:96–104. (Cited on page 19.)
- Hilderbrand, D. 1971. Kurtosis Measures Bimodality? *American Statistician* **25**:42–43. URL <http://www.jstor.org/stable/2682213>. (Cited on pages 46, 54 and 113.)
- Hilton, G., D. Thompson, P. Sagar, R. Cuthbert, Y. Cherel, and S. Bury. 2006. A Stable Isotopic Investigation into the Causes of Decline in a Sub-Antarctic Predator, the Rockhopper Penguin *Eudyptes chrysocome*. *Global Change Biology* **12**:611–625. (Cited on pages 67 and 96.)
- Hindell, M., M. Bryden, and H. Burton. 1994. Early Growth and Milk-Composition in Southern Elephant Seals (*Mirounga-Leonina*). *Australian Journal of Zoology* **14**:723–732. (Cited on page 85.)
- Hindell, M., and H. Burton. 1988. Seasonal Haul-Out Patterns of the Southern Elephant Seal (*Mirounga leonina* L.) at Macquarie Island. *Journal of Mammalogy* **69**:81–88. (Cited on page 25.)
- Hindell, M., D. Slip, and H. Burton. 1991. The Diving behaviour of dult ale and emale outhern lephant eals, *Mirounga leonina* (Pinnipedia: Phocidae). *Australian Journal of Zoology* **39**:595–619. (Cited on page 10.)

- Hobson, K., J. Piatt, and J. Pitocchelli. 1994. Using Stable Isotopes to Determine Seabird Trophic Relationships. *Journal of Animal Ecology* **63**:786–798. (Cited on page 6.)
- Hobson, K., and J. Sease. 1998. Stable Isotope Analyses of Tooth Annuli Reveal Temporal Dietary Records: an Example Using Steller Sea Lions. *Marine Mammal Science* **14**:116–129. (Cited on pages 66, 67, 76, 77, 85 and 118.)
- Hobson, K., L. Wassenaar, and O. Taylor. 1999. Stable Isotope (δD and $\delta^{13}C$) are Geographic Indicators of Natal Origins of Monarch Butterflies in Eastern North America. *Oecologia* **120**:397–404. (Cited on page 31.)
- Hodges, J., and M. Clayton. 2011. Random Effects: Old and New. *Statistical Science* **XX**:XX–XX. URL <http://www.biostat.umn.edu/~hodges/Hodges-ClaytonREONsubToStatSci.pdf>. (Cited on page 19.)
- Horrocks, J., and M. van Den Heuvel. 2009. Prediction of Pregnancy: a Joint Model for Longitudinal and Binary Data. *Bayesian Analysis* **4**:523–538. (Cited on page 94.)
- Hovestadt, T., and P. Nowicki. 2008. Process and Measurement Errors in Population Size: their Mutual Effects on Precision and Bias of Estimates for Demographic Parameters. *Biodiversity and Conservation* **17**:3417–3429. (Cited on page 16.)
- Irvine, L., M. Hindell, J. van den Hoff, and H. Burton. 2000. The Influence of Body Size on Duration of Underyearling Southern Elephant Seals (*Mirounga leonina*). *Journal of Zoology London* **251**:463–471. (Cited on page 98.)
- Ishwaran, H., U. Logalur, and J. Rao. 2010. spikeslab: Prediction and Variable Selection using Spike and Slab Regression. *The R Journal* **2**:68–73. (Cited on pages 38 and 112.)
- Ishwaran, H., and J. Rao. 2005. Spike and Slab Variable Selection: Bayesian and Frequentist Strategies. *Annals of Statistics* **33**:730–773. (Cited on page 38.)
- Jackson, A., R. Inger, A. Parnell, and S. Bearhop. 2011. Comparing Isotopic Niche Widths among and within Communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* **80**:595–602. (Cited on pages 8 and 95.)
- Jaeger, A., 2009. Étude isotopique des variations saisonnière et à long term de l'écologie alimentaire des oiseaux marins de l'océan austral. Phd thesis, Centre d'Études Biologiques de Chizè - Université de Paris 6. (Cited on pages 6 and 96.)
- Jaeger, A., V. Lecomte, H. Weimerskirch, P. Richard, and Y. Cherel. 2010. Seabird Satellite Tracking Validates the Use of Latitudinal Isoscapes to Depict Predators' Foraging Areas in the Southern Ocean. *Rapid Communication in Mass Spectrometry* **24**:3456–3460. (Cited on pages 31, 41, 52 and 91.)

- Jaud, T., 2011. Relation entre Chlorophylle a, Absorption de la Lumière, et Profondeur de Plongée chez l'Éléphant de Mer Austral. Master of sciences thesis, Centre d'Études Biologiques de Chizé. (Cited on page 93.)
- Johnson, D. 1995. Statistical Sirens: The Allure of Nonparametrics. *Ecology* **76**:1998–2000. (Cited on page 9.)
- Jones, E. 1981. Age in Relation to Breeding Status of the Male Southern Elephant Seal, *Mirounga leonina* (L.), at Macquarie Island. *Australina Wildlife Research* **8**:327–334. (Cited on pages 16 and 79.)
- Jonsen, I., R. Myers, and J. Flemming. 2003. Meta-Analysis of Animal Movement Data using State-Space Models. *Ecology* **84**:3055–3063. (Cited on pages 8 and 33.)
- Jonsen, I., R. Myers, and M. James. 2007. Identifying Leatherback Turtle Foraging Behaviour from Satellite Telemetry using a Switching State-Space Model. *Marine Ecology Progress Series* **337**:255–64. (Cited on page 4.)
- Jönsson, K. 1997. Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction. *Oikos* **78**:57–66. (Cited on page 43.)
- Jordan, M. 2011. What Are the Open Problems in Bayesian Statistics? The ISBA Bulletin **18**:1–4. URL www.bayesian.org. (Cited on pages 9 and 121.)
- Kass, R. 2011. Statistical Inference: the Big Picture. *Statistical Science* **26**:1–9. (Cited on pages 9 and 100.)
- Kelly, J. 2000. Stable Isotopes of Carbon and Nitrogen in the Study of Avian and Mammalian Trophic Ecology. *Canadian Journal of Zoology* **78**:1–27. (Cited on pages 5, 6 and 31.)
- Kim, T.-H., and H. White, 2003. On More Robust Estimation of Skewness and Kurtosis: Simulation and Application to S& P500 Index. Working paper. URL http://www.cirano.qc.ca/realisations/grandes_conferences/methodes_econometriques/white.pdf. (Cited on page 44.)
- Kirkman, S., M. Bester, P. Pistorius, G. Hofmeyr, F. Jonker, R. Owen, and N. Strydom. 2004. Variation in the Timing of the Breeding Haulout in Female Southern Elephant Seals at Marion Island. *Australian Journal of Zoology* **52**:379–388. (Cited on page 48.)
- Kjellander, P., J. Gaillard, M. Hewison, and O. Liberg. 2004. Predation Risk and Longevity Influence Variation in Fitness of Female Roe Deer (*Capreolus capreolus* L.). *Proceedings of the Royal Society of London B* **271**:S338–S340. (Cited on pages 79 and 87.)
- Kruuk, L. 2004. Estimating Genetic Parameters in Natural Populations Using the "Animal Model". *Philosophical Transactions of the Royal Society of London series B* **359**:873–890. (Cited on page 8.)

- Kruuk, L., T. Clutton-Brock, J. Slate, J. Penderton, S. Brotherstone, and F. Guinness. 2000. Heritability of Fitness in a wild Mammal Population. *Proceedings of the National Academy of Sciences of the USA* **97**:698–703. (Cited on page 79.)
- Kuhn, T. 1996. *The Structure of Scientific Revolutions*. 3rd edition. Chicago University Press. (Cited on pages 7 and 9.)
- Laws, R. 1952. A New Method of Age Determination for Mammals. *Nature* **169**:972–974. (Cited on pages 66 and 67.)
- Laws, R., 1953. The Elephant Seal (*Mirounga leonina* Linn.). I. Growth and Age. Falkland islands dependencies survey scientific report n°8. (Cited on pages 11 and 40.)
- Laws, R. 1960. The Southern Elephant Seal (*Mirounga leonina*) at South Georgia. *Norsk Hvalfangstlid* **466-476**:520–542. (Cited on pages 11, 12 and 25.)
- Laws, R., 1993. Antarctic Seals. *Research Methods and Techniques*, Chapter 11 - Age Determination, pages 199–227 . Cambridge University Press. (Cited on page 67.)
- Layman, C., D. Arrington, C. Montaña, and D. Post. 2007. Can Stable Isotope Ratios Provide for Community-wide Measures of Trophic Structure? *Ecology* **88**:42–48. (Cited on page 95.)
- Lehrer, J. 2010. The Truth Wears Off. *The New Yorker* **December 13**:52–57. (Cited on page 91.)
- Lenglart, P., and M. Bester. 1982. Post-Weaning Dispersion of Southern Elephant Seal *Mirounga leonina* Underyearlings at Kerguelen. *Revue d'Écologie (Terre Vie)* **36**:175–185. (Cited on page 22.)
- Liang, L., D. Huang, M. Brecht, and Y. Hser. 2009. Differences in Mortality among Heroin, Cocaine, and Methamphetamine Users: a Hierarchical Bayesian Approach. *Journal of Drug Issues* **40**:121–140. (Cited on page 94.)
- Lindström, J. 1999. Early Development and Fitness in Birds and Mammals. *Trends in Ecology and Evolution* **14**:343–348. (Cited on page 85.)
- Ling, J., and M. Bryden, 1981. *Handbook of Marine Mammals - Volume 2: Seals*, Chapter 13 - Southern Elephant Seals, pages 297–327 . Academic Press. (Cited on page 11.)
- Link, W., and R. Barker, 2009. *Bayesian Inference with Ecological Applications*, Chapter individual Fitness, pages 271–286 . Associated Press. (Cited on pages 2 and 9.)
- Link, W., E. Cooch, and E. Cam. 2002. Model-Based Estimation of Individual Fitness. *Journal of Applied Statistics* **29**:207–224. (Cited on pages 2 and 43.)

- Liu, C., 2004. Applied Bayesian Modeling and Causal Inference from Incomplete Data Perspectives, Chapter 21 - robit regression: A simple robust alternative to logistic and probit regression, pages 227–238 . John Wiley and Sons Ltds. (Cited on pages 46 and 114.)
- Loeb, V., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece, and S. Trivelpiece. 1997. Effects of Sea-Ice Extent and Krill or Salp Dominance on the Antarctic Food Web. *Nature* **387**:897–900. (Cited on page 29.)
- Louis, T., and S. Zeger. 2009. Effective Communication of Standard Error and Confidence Interval. *Biostatistics* **10**:1–2. (Cited on pages 20, 103, 111, 113, 120 and 125.)
- Lunn, W., T. A., N. Best, and D. Spiegelhalter. 2000. *WinBUGS* - A Bayesian Modelling Framework: Concept, Structure, and Extensibility. *Statistics and Computing* **10**:325–337. (Cited on pages 19, 100 and 103.)
- Lynch, M., and B. Walsh. 1998. *Genetics and Analysis of Quantitative Traits*. 1st edition. Sinauer Associates. (Cited on page 8.)
- MacArthur, R., and E. Pianka. 1966. On Optimal Use of a Patchy Environment. *American Naturalist* **100**:603–609. (Cited on page 4.)
- MacCarthy, M. 2007. *Bayesian Methods for Ecology*. 1st edition. Cambridge University Press. (Cited on page 9.)
- MacKenzie, K., R. Palmer, A. Moore, A. Ibbotson, W. Beaumont, D. Poulter, and C. Trueman. 2011. Locations of Marine Animals Revealed by Carbon Isotopes. *Nature Scientific Reports* **1**:1–6. (Cited on page 96.)
- Martin, C., I. Bentaleb, S. Steedlandt, and C. Guinet. 2011. Stable Carbon and Nitrogen Isotope Variations in Canine Dentin Growth Layers of Kerguelen Southern Elephant Seals. *Marine Ecology Progress Series* **XX**:accepted. (Cited on pages 67, 68, 86 and 118.)
- Martin, P. 1984. The Meaning of Weaning. *Animal Behaviour* **32**:1257–1259. (Cited on page 85.)
- Martinez del Rio, C., N. Wolf, S. Carleton, and L. Gannes. 2009. Isotopic Ecology ten Years after a Call for more Laboratory Experiments. *Biological Reviews* **84**:91–111. (Cited on page 7.)
- Matthen, M., and A. Ariew. 2002. Two Ways of Thinking about Fitness and Natural Selection. *The Journal of Philosophy* **99**:55–83. (Cited on page 43.)
- Matthews, B., and A. Mazunder. 2004. A Critical Evaluation of Intrapopulation Variation of $\delta^{13}C$ and Isotopic Evidence of Individual Specialization. *Oecologia* **140**:361–371. (Cited on page 71.)

- McCann, T. 1980. Population Structure and Social Organisation of Southern Elephant Seals, *Mirounga leonina* (L.). *Biological Journal of the Linnean Society* **14**:133–150. (Cited on page 86.)
- McConnell, B., C. Chambers, and M. Fedak. 1992. Foraging Ecology of Southern Elephant Seals in Relation to the Bathymetry and Productivity of the Southern Ocean. *Antarctic Science* **4**:393–398. (Cited on page 11.)
- McIntyre, T., P. de Bruyn, I. Ansorge, M. Bester, H. Bornemann, J. Plötz, and C. Tosh. 2010. A Lifetime at Depth: Vertical Distribution of Southern Elephant Seals in the Water Column. *Polar Biology* **33**:1037–1048. (Cited on pages 10 and 79.)
- McLaren, I. 1993. Growth in Pinnipeds. *Biological Reviews* **68**:1–79. (Cited on pages 40, 77 and 79.)
- McMahon, C., M. Bester, H. Burton, M. Hindell, and C. Bradshaw. 2005a. Population Status, Trends and a re-Examination of the Hypotheses Explaining the Recent Declines in the Southern Elephant Seal *Mirounga leonina*. *Mammal Review* **35**:82–100. (Cited on pages 11, 16, 27, 58, 67 and 90.)
- McMahon, C., and H. Burton. 2005. Climate Change and Seal Survival: Evidence for Environmentally Mediated Changes in Elephant Seal, *Mirounga leonina*, Pup Survival. *Proceedings of the Royal Society of London series B* **272**:923–928. (Cited on page 66.)
- McMahon, C., H. Burton, and M. Bester. 2000a. Weaning Mass and the Future Survival of Juvenile Southern Elephant Seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science* **12**:149–153. (Cited on pages 13, 43 and 48.)
- McMahon, C., H. Burton, and M. Bester. 2003. A Demographic Comparison of two Southern Elephant Seal Populations. *Journal of Animal Ecology* **72**:61–74. (Cited on pages 16 and 85.)
- McMahon, C., H. Burton, S. McLean, D. Slip, and M. Bester. 2000b. Field Immobilisation of Southern Elephant Seals with Intravenous Tiletamine and Zolazepam. *The Veterinary Record* **146**:251–254. (Cited on page 33.)
- McMahon, C., M. Hindell, H. Burton, and M. Bester. 2005b. Comparison of Southern Elephant Seal Populations, and Observations of a Population on a Demographic Knife-Edge. *Marine Ecology Progress Series* **288**:273–283. (Cited on pages 13, 58 and 85.)
- Mendes, S., J. Newton, R. Reid, A. Zuur, and G. Pierce. 2007. Stable Carbon and Nitrogen Isotope Ratio Profiling of Sperm Whale Teeth Reveals Ontogenetic Movements and Trophic Ecology. *Oecologia* **151**:605–615. (Cited on page 67.)

- Meng, X.-L. 2000. Missing Data: Dial M for ??? Journal of the American Statistical Association **95**:1325–1330. URL <http://www.jstor.org/stable/2669781>. (Cited on page 8.)
- Metcalf, J., and S. Parvard. 2006. Why Evolutionary Biologists Should Be Demographers. Trends in Ecology and Evolution **22**:205–212. (Cited on pages 2 and 43.)
- Metzgar, L. 1967. An Experimental Comparison of Screech Owl Predation on Resident and Transient White-Footed Mice (*Peromyscus leucopus*). Journal of Mammalogy **48**:387–391. (Cited on page 85.)
- Michener, R., and L. Kaufman, 2007. Stable Isotope Ratios as Tracers in Marine Food Webs: an Update, Chapter 9, pages 238–282 . Blackwell Publishing. (Cited on page 32.)
- Mongin, M., E. Molina, and T. Trull. 2008. Seasonality and Scale of Kerguelen Plateau Phytoplakton Bloom: a Remote Sensing and Modeling Analysis of the Influence of Natural Iron Fertilization in the Southern Ocean. Deep-Sea Research II **55**:880–892. (Cited on page 53.)
- Moore, J., and M. Abbott. 2000. Phytoplankton Chlorophyll Distribution and Primary Production in the Southern Ocean. Journal of Geophysical Research **105**:709–722. (Cited on page 53.)
- Moyes, A., and D. Doidge. 1984. Composition of the Mineral Phase of Dentin in Southern Elephant Seal and Antarctic Fur Seal Teeth. British Antarctic Survey Bulletin **64**:81–84. (Cited on page 118.)
- Muniz-Terrera, G., A. van den Hout, and F. Matthews. 2011. Random Change Point Models: Investigating Cognitive Decline in the Presence of Missing Data. Statistics in Medicine **30**:599–610. (Cited on page 69.)
- Nelder, J. 1996. An Applied Statistician's Creed. Applied Statistician **45**:401–410. (Cited on page 8.)
- Newland, C., I. Field, P. Nichols, C. Bradshaw, and M. Hindell. 2009. Blubber Fatty Acid Profiles Indicate Dietary Resource Partitioning between Adult and Juvenile Elephant Seals. Marine Ecology Progress Series **384**:303–312. (Cited on pages 52 and 97.)
- Newsome, S., M. Clementz, and P. Koch. 2010. Using Stable Isotope Biogeochemistry to Study Marine Mammal Ecology. Marine Mammal Science **26**:509–572. (Cited on page 66.)
- Newsome, S., C. Martinìnez del Rio, S. Bearhop, and D. Phillips. 2007. Historic Decline in Primary Productivity in Western Gulf of Alaska and Eastern Bering Sea: Isotopic Analysis of Northern Fur Seal Teeth. Marine Ecology Progress Series **332**:211–224. (Cited on page 95.)

- Norman, A., M. Wilmot, D. Thomas, D. Masters, and D. Revell. 2009. Stable Carbon Isotopes Accurately Predict Diet Selection by Sheep Fed Mixtures of C₃ Annual Pastures and Saltbush or C₄ Perennial Grasses. *Livestock Science* **121**:162–172. (Cited on page 5.)
- O’Hara, R., and M. Sillanpää. 2009. A Review of Bayesian Variable Selection Methods: What, How and Which. *Bayesian Analysis* **4**:85–118. (Cited on page 126.)
- Orsi, A., T. Whitworth III, and J. W. Nowlin. 1995. On the Meridional Extent and Fronts of the Antarctic Circumpolar Current. *Deep-Sea Research I* **42**:641–673. (Cited on pages 30 and 34.)
- Parnell, A., R. Inger, S. Bearhop, and A. Jackson. 2010. Source Partitioning Using Stable Isotopes: Coping with Too Much Variation. *PLoS One* **5**:e9672. (Cited on pages 6, 7, 8, 95 and 97.)
- Pascal, M., 1981. Évolution Numérique de la Population d’Éléphants de Mer (*Mirounga leonina* (L.)) de l’Archipel des Kerguelen au Cours des 30 Dernières Années. Publications 51, CNFRA. (Cited on pages 17 and 24.)
- Patterson, T., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-Space Models of Individual Animal Movement. *Trends in Ecology and Evolution* **23**:87–94. (Cited on pages 4, 8 and 33.)
- Perga, M., and J. Grey. 2010. Laboratory Measures of Isotope Discrimination Factors: Comments on Caut, Angulo & Courchamp (2008,2009). *Journal of Applied Ecology* **47**:942–947. (Cited on pages 7 and 96.)
- Péron, C., 2011. Impacts des Changements Climatiques et Distribution spatiale des oiseaux marins de l’océan austral. Phd thesis, Centre d’Études Biologiques de Chizè - Université de Paris 6. (Cited on page 31.)
- Péron, C., K. Delord, R. Phillips, Y. Charbonnier, C. Marteau, M. Louzao, and H. Weimerskirch. 2010. Seasonal Variation in Oceanographic Habitat and Behaviour of White-Chinned Petrel *Procellaria aequinoctialis* from Kerguelen Island. *Marine Ecology Progress Series* **416**:267–284. (Cited on page 4.)
- Peterson, P., and B. Fry. 1987. Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics* **18**:293–320. (Cited on pages 5 and 6.)
- Pettorelli, N., and S. Durant. 2007. Longevity in Chettahs: the Key to Success. *Oikos* **116**:1879–1886. (Cited on page 79.)
- Pianka, E. 1976. Natural Selection of Optimal Reproductive Tactics. *American Zoologist* **16**:775–784. (Cited on page 2.)
- Pistorius, P., M. Bester, and S. Kirkman. 1999a. Dynamic Age-Distributions in a Declining Population of Southern Elephant Seals. *Antarctic Science* **11**:445–450. (Cited on page 86.)

- Pistorius, P., M. Bester, and S. Kirkman. 1999b. Survivorship of a Declining Population of Southern Elephant Seals, *Mirounga leonina*, in relation to Age, Sex and Cohort. *Oecologia* **121**:201–211. (Cited on pages 66 and 79.)
- Plummer, M. 2008. Penalized Loss Functions for Bayesian Model Comparison. *Biostatistics* **9**:523–539. (Cited on page 121.)
- Plummer, M., N. Best, K. Cowles, and K. Vines, 2008. coda: Output Analysis and Diagnostics for MCMC. (Cited on pages 103, 113, 120 and 125.)
- Polischuk, S., K. Hobson, and M. Ramsay. 2001. Use of Stable-Carbon and -Nitrogen Isotopes to Assess Weaning and Fasting in Female Polar Bears and their Cubs. *Canadian Journal of Zoology* **79**:499–511. (Cited on pages 76 and 85.)
- Popa-Lisseanu, A., A. Delgado-Huertas, M. Forero, A. Rodríguez, R. Arlettaz, and C. Ibáñez. 2007. Bats' Conquest of a Formidable Foraging Niche: the Myriads of Nocturnally Migrating Songbirds. *PLoS One* **2**:e205. (Cited on page 6.)
- Post, D. 2002. Using Stable Isotopes to Estimate Trophic Position: Models, Methods and Assumptions. *Ecology* **83**:703–718. (Cited on page 5.)
- Pourahmadi, M. 2007. Choleski Decompositions and Estimation of a Covariance Matrix: Orthogonality of Variance-Correlation Parameters. *Biometrika* **94**:1006–1013. (Cited on page 104.)
- R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>. (Cited on pages 8, 103, 111, 113, 120 and 125.)
- Rau, G., F. Chavez, and G. Friederich. 2001. Plankton $\frac{^{13}\text{C}}{^{12}\text{C}}$ Variations in Monterey Bay, California: Evidence of Non-Diffusive Inorganic Carbon Uptake by Phytoplankton in an Upwelling Environment. *Deep Sea Research Part I* **48**:79–94. (Cited on page 96.)
- Rau, G., A. Mearns, D. Young, R. Olson, H. Schafer, and I. Kaplan. 1984. Animal $\frac{^{13}\text{C}}{^{12}\text{C}}$ Correlates with Trophic Level in Pelagic Food Webs. *Ecology* **64**:1314–1318. (Cited on page 31.)
- Rau, G., R. Sweeney, and I. Kaplan. 1982. Plankton $\frac{^{13}\text{C}}{^{12}\text{C}}$ ratio Changes with Latitude: Differences between Northern and Southern Oceans. *Deep Sea Research Part I* **29**:1035–1039. (Cited on pages 6 and 32.)
- Rau, G., T. Takahashi, and D. Des Marais. 1989. Latitudinal Variation in Plankton $\delta^{13}\text{C}$: Implications for CO_2 and Productivity in Past Oceans. *Nature* **341**:516–518. (Cited on page 6.)
- Reich, K., K. Bjorndal, and A. Bolten. 2007. The "Lost Years" of Green Turtles: using Stable Isotopes to Study Cryptic Lifestages. *Biology Letters* **3**:712–714. (Cited on pages 6, 66 and 67.)

- Robbins, C., L. Felicetti, and S. Florin. 2010. The Impact of Protein Quality on Stable Nitrogen Isotope Ratio Discrimination and Assimilated Diet Estimation. *Oecologia* **162**:571–579. (Cited on page 96.)
- Robinson, W. 2009. Reprint: Ecological Correlations and the Behavior of Individuals. *International Journal of Epidemiology* **38**:337–341. (Cited on page 2.)
- Rodhouse, P., T. Arnbom, M. Fedak, J. Yeatman, and A. Murray. 1992. Cephalopod Prey of the Southern Elephant Seal, *Mirounga leonina* L. *Canadian Journal of Zoology* **70**:1007–1015. (Cited on pages 52, 78 and 97.)
- Ropert-Coudert, Y., and R. Wilson. 2005. Trends and Perspectives in Animal-Attached Remote Sensing. *Frontiers in Ecology and the Environment* **3**:437–444. (Cited on page 4.)
- Rosenberg, A., and F. Bouchard, 2010. Fitness. *in* E. N. Zalta, editor. *The Stanford Encyclopedia of Philosophy*. Fall 2010 edition. (Cited on page 43.)
- Rothery, P., and T. McCann. 1987. Estimating Pup Production of Elephant Seals at South Georgia. *Symposia of the Zoological Society of London* **58**:211–223. (Cited on pages 17, 22 and 25.)
- Rubin, D. 1981. The Bayesian Bootstrap. *The Annals of Statistics* **9**:130–134. (Cited on page 9.)
- Sagarin, R., and A. Pauchard. 2010. Observational Approaches in Ecology Open New Ground in a Changing World. *Frontiers in Ecology and the Environment* **8**:379–386. (Cited on page 7.)
- Sakar, S. 2005. Maynard Smith, Optimization, and Evolution. *Biology and Philosophy* **20**:951–966. (Cited on page 4.)
- Schell, D. 2000. Declining Carrying Capacity in the Bering Sea: Isotopic Evidence from Whale Baleen. *Limnology and Oceanography* **45**:459–462. (Cited on page 95.)
- Schoeninger, M., and M. DeNiro. 1984. Nitrogen and Carbon Isotopic Composition of Bone Collagen from Marine and Terrestrial Animals. *Geochimica et Cosmochimica Acta* **48**:625–639. (Cited on page 6.)
- Schulting, R., S. Blockley, H. Bocherens, D. Drucker, and M. Richards. 2008. Stable Carbon and Nitrogen Isotope Analysis on Human Remains from the Early Mesolithic Site of La Vergne (Charente-Maritime, France). *Journal of Archeological Science* **35**:763–772. URL [10.1016/j.jas.2007.06.008](https://doi.org/10.1016/j.jas.2007.06.008). (Cited on page 118.)
- Semmens, B., E. Ward, J. Moore, and C. Darimont. 2009. Quantifying Inter- and Intra-Population Niche Variability using Bayesian Hierarchical Stable Isotope Mixing Models. *PLoS One* **4**:e6187. (Cited on pages 6, 8, 95 and 97.)

- Shafer, G. 1990. The Unity and Diversity of Probability. *Statistical Science* **5**:435–444. (Cited on page 100.)
- Slade, R., C. Moritz, A. Hoelzel, and H. Burton. 1998. Molecular Population Genetics of the Southern Elephant Seal *Mirounga leonina*. *Genetics* **149**:1945–1957. (Cited on page 25.)
- Slip, D., and H. Burton. 1999. Population Status and Seasonal Haulout Patterns of the Southern Elephant Seals (*Mirounga leonina*) at Heard Island. *Antarctic Science* **11**:38–47. (Cited on page 25.)
- Spiegelhalter, D., T. Best, N. Best, and D. Lunn, 2003. WinBUGS User Manual version 1.4. URL <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>. (Cited on pages 19, 103, 113, 120 and 125.)
- Spiegelhalter, D., T. Best, B. Carlin, and A. van der Linde. 2002. Bayesian Measures of Model Complexity and Fit (with Discussion). *Journal of the Royal Statistical Society Series B* **64**:583–640. (Cited on pages 19, 113 and 121.)
- Stanford, P. 2006. Exceeding our Grasp: Science, History and the Problem of Unconceived Alternatives. 1st edition. Oxford University Press. (Cited on page 7.)
- Stearns, S. 1989. Trade-offs in Life History Evolution. *Functional Ecology* **3**:259–268. (Cited on page 2.)
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a Package for Running *WinBUGS* from *R*. *Journal of Statistical Software* **12**:1–16. URL <http://www.jstatsoft.org>. (Cited on pages 103, 113, 120 and 125.)
- Swindell, W. 2009. Accelerated Failure Time Models Provide a Useful Statistical Framework for Aging Research. *Experimental Gerontology* **44**:190–200. (Cited on page 80.)
- Thiebot, J., 2011. Déplacements et sélection d’habitat chez les animaux non contraints par la reproduction : une étude de l’écologie en mer des Manchots durant les phases d’immaturité et inter-nuptiale. Phd thesis, Centre d’Études Biologiques de Chizè - Université de Paris 6. (Cited on pages 4 and 6.)
- Thums, M., C. Bradshaw, and M. Hindell. 2011. *In-Situ* Measures of Foraging Success and Prey Encounter Reveals Marine Habitat-Dependent Search Strategies. *Ecology* **92**:1258–1270. (Cited on pages 51, 57, 76 and 90.)
- Tokuda, T., B. Goodrich, I. Van Mechelen, A. Gelman, and F. Tuerlinckx, 2011. Visualizing Distributions of Covariance Matrices. Technical report, University of Leuven, Belgium and Columbia University, USA. URL <http://www.stat.columbia.edu/~gelman/research/unpublished/Visualization.pdf>. (Cited on pages 104, 105, 106 and 108.)

- Travis, J. 2009. Scientists Decry 'Flawed' and 'Horrifying' Nationality Tests. *Science Insider* **29 September 2009**. URL <http://news.sciencemag.org/scienceinsider/2009/09/border-agencys.html>. (Cited on page 91.)
- Travis, J. 2011. U.K. Abandons Study of Nationality Testing Using DNA and Isotopes. *Science Insider* **17 June 2011**. URL <http://news.sciencemag.org/scienceinsider/2011/06/uk-abandons-study-of-nationality.html>. (Cited on page 91.)
- Trull, T., and L. Armand. 2001. Insight into Southern Ocean Carbon Export from the $\delta^{13}C$ of Particles and Dissolved Inorganic Carbon using the SOIREE Iron Release Experiment. *Deep-Sea Research Part II* **48**:2655–2680. (Cited on page 31.)
- Tufte, E. 2006. *Beautiful Evidence*. 1st edition. Graphic Press. URL www.edwardtufte.com. (Cited on page 69.)
- Turner, E., and J. Hanley. 2010. Cultural Imagery and Statistical Models of the Force of Mortality: Addison, Gompertz and Pearson. *Journal of the Royal Statistical Society series A* **173**:483–499. (Cited on page 87.)
- Van Aarde, R. 1980. Fluctuations in the Population of Southern Elephant Seals *Mirounga leonina* at Kerguelen Island. *South African Journal of Zoology* **15**:99–106. (Cited on pages 16 and 17.)
- van den Hoff, J., and M. Morrice. 2008. Sleeper Sharks (*Somniosus antarcticus*) and other Bite Wounds Observed on Southern Elephant Seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science* **24**:239–247. (Cited on page 51.)
- van Noordwijk, A., and G. de Jong. 1986. Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. *American Naturalist* **128**:137–142. (Cited on page 2.)
- Van Wilgenburg, S., and K. Hobson. 2011. Combining Stable-Isotope (δD) and Band Recovery Data to Improve Probabilistic Assignment of Migratory Birds to Origin. *Ecological Applications* **21**:1340–1351. (Cited on pages 8, 31 and 95.)
- Vanderklift, M., and S. Ponsard. 2003. Sources of Variation in Consumer-Diet $\delta^{15}N$ Enrichment: a Meta-Analysis. *Oecologia* **136**:169–182. (Cited on pages 5 and 7.)
- Wakefield, E., R. Phillips, P. Trathan, J. Arata, R. Gales, N. Huin, G. Robertson, S. Waugh, H. Weimerskirch, and J. Matthiopoulos. 2011. Habitat Preference, Accessibility, and Competition Limit the Global Distribution of Breeding Black-Browed Albatrosses. *Ecological Monographs* **81**:141–167. (Cited on page 4.)
- Ward, E., B. Semmens, D. Phillips, J. Moore, and N. Bouwes. 2011. A Quantitative Approach to Combine Source in Stable Isotope Mixing Models. *Ecosphere* **2**. (Cited on pages 8 and 97.)

- Weimerskirch, H., P. Inchausti, C. Guinet, and C. Barbraud. 2003. Trends in Birds and Seal Populations as Indicators of a System Shift in the Southern Ocean. *Antarctic Science* **15**:249–256. (Cited on pages 27, 58 and 90.)
- Weladji, R., J. Gaillard, N. Yoccoz, O. Holland, A. Mysterud, A. Loison, M. Nieminen, and N. Stenseth. 2006. Good Reindeer Mother Live Longer and Become Better in Raising Offspring. *Proceedings of the Royal Society London Series B* **273**:1239–1244. (Cited on page 79.)
- Werner, E., and J. Gilliam. 1984. The Ontogenetic Niche and Species Interactions in Size Structured Populations. *Annual Review of Ecology and Systematics* **15**:393–425. (Cited on page 67.)
- West, J., G. Bowen, T. Cerling, and J. Ehleringer. 2006. Stable Isotopes as One of Nature’s Ecological Recorders. *Trends in Ecology and Evolution* **21**:408–414. (Cited on pages 5 and 6.)
- Whittingham, M., P. Stephens, R. Bradbury, and R. Freckleton. 2006. Why Do We Still Use Stepwise Modelling in Ecology and Behaviour? *Journal of Animal Ecology* **75**:1182–1189. (Cited on page 41.)
- Wilske, J., and T. Arnbom. 1996. Seasonal Variation in Vitamin D Metabolites in Southern Elephant Seals (*Mirounga leonina*) Females at South Georgia. *Comparative Biochemistry and Physiology A* **114**:9–14. (Cited on pages 67 and 68.)
- Wolf, M., J. Frair, E. Merrill, and P. Turchin. 2009a. The Attraction of the Known: the Importance of Spatial Familiarity in Habitat Selection in Wapiti *Cervus elaphus*. *Ecography* **32**:401–401. (Cited on page 85.)
- Wolf, N., S. Carleton, and C. Martinez del Rio. 2009b. Ten Years of Experimental Animal Isotopic Ecology. *Functional Ecology* **23**:17–26. (Cited on pages 7 and 96.)

Unveiling the At-Sea Ecology of Southern Elephant Seals From Indirect Evidence

Abstract: How can we study the foraging of organisms with a cryptic lifestyle? For many species, including marine ones, direct observations may not be logistically feasible. To circumvent these problems, indirect approaches, which aim at tracking the flux of molecules within ecosystems, have been on the rise in ecology since the 1970s. One indirect approach relies on measuring stable isotopes in various organic tissues, including those from museum specimens, to study the trophic ecology of wild animals.

Using the indirect evidence stable isotopes can provide, this Ph.D. thesis endeavoured to study the at-sea ecology of a large predator: the Southern Elephant Seal (*Mirounga leonina*) breeding on îles Kerguelen in the Southern Ocean. This seal spends less than one fifth of its lifetime on land where it may be directly observed, and only forages at sea.

By taking advantage of the existence of a latitudinal gradient in carbon isotopes within the Southern Ocean, I investigated the relationship between foraging strategy and fitness in this capital breeder, through the use of Bayesian models. I favoured a Bayesian approach in order to accommodate the indirect nature of the evidence provided by stable isotopes.

Inferences on foraging locations from stable isotopic data were in broad agreement with 'biologging' results: Southern Elephant Seals from îles Kerguelen were mainly foraging at the Polar Front or in Antarctic waters.

Using mixture models, I studied how breeding females foraging in Antarctic waters were more likely to wean a large pup compared to females foraging in Subantarctic waters. Stable isotopes also suggested that females were faithful to a foraging strategy and were broadening their panel of prey as they aged.

I used a joint modelling approach to study longevity in males, a fitness-related trait that is hard to study in wild populations, and its relationship with foraging as inferred from repeated isotopic sampling of teeth. This approach revealed males that had a very stable and constant foraging from an early age to be the most long-lived ones.

Keywords: Pinnipeds, Foraging, Stable Isotopes, Hierarchical Models
