Drivers and Fitness Consequences of
Individual and Sexual Foraging Specialisation in Fur Seals

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Submitted in fulfilment of the requirements for the degree of
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Deakin University
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I am the author of the thesis entitled

Drivers and Fitness Consequences of Individual and Sexual Foraging Specialisation in Fur Seals

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Abstract

Although sexual and individual specialisation is widespread with major implications in many ecological and evolutionary processes, its causes and consequences remain poorly understood. Therefore, using fur seals as model species, the overall aims of this thesis were to: (i) report the incidence of foraging segregation and critically access how the method/time-scale used to quantify resource partitioning affect our measurements; (ii) investigate its intrinsic and extrinsic drivers; and (iii) study the fitness consequences of individual specialisation.

Sexual niche segregation and individual specialisation were reported in Australian (Arctocephalus pusillus doriferus), Antarctic (A. gazella) and subantarctic (A. tropicalis) fur seals. The strength of niche differentiation greatly varied between species, but also populations and time, highlighting the fact that niche segregation is not a fixed characteristic of a species but is influenced by the local environment (extrinsic factors). In particular, resource diversity (ecological opportunity), inter- and intra-specific competition affected the level of resource partitioning at the sexual and individual levels. Estimations of the degree of individual specialisation in female Australian fur seals were also affected by the time-scale over which individuals were monitored. While short-term studies are prone to stochastic sampling errors, long-term studies face potential time averaging issues, leading to over- and under-estimation of the degree of specialisation, respectively.

Investigating the ontogeny of niche differentiation revealed at which life-stages sexual resource partitioning arises in the Antarctic fur seal, thus providing insights into the main intrinsic factors shaping niche segregation. Both sexes occupied distinct niches as soon as weaning, when size dimorphism is minimum and seals do not face any breeding constraints. While these two factors are assumed to be the main drivers explaining sexual niche segregation in fur seal species, results of the present thesis highlight the importance of testing the actual role factors play in driving niche differentiation.

Finally, fitness consequences of individual specialisation were investigated in territorial male Antarctic and Australian fur seals, two highly dimorphic and polygynous species where strong selective pressure toward foraging efficiency is
expected. In both species, foraging niche was not correlated to body size, condition or mating success. No foraging niche was predominant in either species, which would have indicated a substantial long-term fitness benefit of a particular foraging strategy via a higher survival rate. These results suggest that the fitness consequences of a foraging specialisation depends not only on the quality of prey and feeding habitat but also on an individual’s hunting efficiency and skills.
Preface

The ethical guidelines of Deakin University Animal Ethics Committee and Animal Welfare Committee, and the French Polar Institut IPEV ethics committee were followed during this present study. Protocols were approved by Deakin University Animal Ethics Committee and Animal Welfare Committee (Permit No. A16/2008, A14-2011, A71-2011 and B12-2013). The project was conducted in accordance with the regulations of Department of Environment, Land, Water and Planning (Wildlife Research Permits 10005362 and 10005848).

The core chapters of this thesis (Chapters 2 – 6) have been published or submitted for publication in peer-reviewed journals. Chapter 1 serves as an introduction to the main body of work while Chapter 7 discusses the main findings of the study.

I am the primary contributor to all aspects of the work presented in this study, with the exception of the data collection for Chapters 2 and 5, and the determination of seal diet from video footages in Chapter 2.

John P.Y Arnould and Yves Cherel are co-authors on all submitted publications for providing guidance and assistance in all aspects of my PhD.

Chapter 2 - Nicole Dorville processed all video footages and determined seal diets using video cameras; Daniel Ierodiaconou assisted with prey identification; Andrew J. Hoskins conducted the field work during multiple winters; Alastair M.M. Baylis provided fieldwork advices; Mark A. Hindell and Jayson Semmens provided financial and logistic support; Kyler Abernathy and Greg J. Marshall provided equipment for the study.

Chapter 3 - Christophe Guinet contributed to the study design and interpretation of the data; Bernard Cazelles provided assistance in the wavelet analyses; Pierre Richard provided laboratory assistance in the isotopic analyses.
Chapter 4 - Travis Knox assisted in conducting fieldwork and undertook the spatial analysis; Alastair M.M. Baylis assisted in conducting fieldwork.

Chapter 5 and 6 - Christophe Guinet contributed to the study design and interpretation of the data.

Publications arising from this thesis

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6
Kernaléguen L, Cherel Y, Guinet C, Arnould JPY Reproductive consequences of individual trophic specialisation: is it what you eat or how much? Open Science – in review
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This PhD would not have been possible without the precious help of my many fieldworkers. A huge thank you to Marion Fourquez, Nory El Ksabi, Cyrille Bouquinet, Matthieu Tetrel, Xavier Ignolin, Steph Bartissol, Nico Flenghi, Baptiste Picard, Pauline Vuaron, Susan Gallon, Camille Toscani, François Brignon, Elsa Day, Xavier Herlet, Seb Pennec, Adrien Mauss, Gégé Gaudin, Romain Thomas, Pierre Perrin, Pierre Chartier, Jemma Heritage, Travis Knox, Al Baylis, Nicole Dorville, Eric Hornung, Emma Tew; with a special thanks to Philippe Mistral, Damien Guillaume and Lova Randrianasolo. You all came to help me as volunteers, it means a lot to me. Thank you for sharing all these amazing moments in the field, while intimidating 300kg seals, body painting them and crossbowing them, during that storm, or all those amazing times putting the world to rights over a couple of drinks in front of the ocean… These have been the best moments of my PhD. Thanks for sharing with me my passion for Nature and the wild.
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Since I was a teenager I have had the hope to become, maybe, one day, a firefighter. And here I am today, a volunteer firefighter at the Belgrave Heights and South Brigade! And I found much more than the fulfilment of feeling useful for my community and the adrenaline rush in the truck on the way to a job. I also found you guys, friends, buddies, crew mates. I had never imagined that part of the job in my teenager hopes, but it is actually the best part of it.

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A chapter of my life ends today… to a new blank page waiting to be filled in. Let’s see what is on the other side!
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Within population resource segregation

The theory of natural selection predicts that a phenotypic trait (morphological, physiological, or behavioural) will be retained in a population if that particular trait provides individuals a survival and/or reproductive advantage (Darwin 1859). In this theoretical framework, selected behavioural strategies should maximize the balance between the costs and benefits in a given environment. When food is a limiting factor, individual fitness is strongly influenced by its foraging behaviour as it determines the quantity and quality of resources that can be allocated among competing fitness-related activities such as growth, reproduction and survival (Stearns 1989, Boggs 1992). Strong selective pressure should, thus, apply towards foraging efficiency (ratio of energy gained over energy spent while foraging per unit of time). Accordingly, the Optimal Foraging Theory, a model inspired by economical equations for optimisation of profit (MacArthur & Pianka 1966), has been successful in predicting the foraging behaviour of many free-ranging predators in patchy environments (Sih & Christensen 2001).

Most theories and models consider individuals within a population are ecologically equivalent, and most empirical studies make the assumption that the sampled individuals are representative of the whole population. However, conspecifics differ in many traits including their morphology, physiology, breeding status, experience and skills (Bolnick et al. 2003). These characteristics can potentially influence an individual’s energy requirements and its ability to access, handle and digest food. Accordingly, the profitability of food types may vary between individuals such that conspecifics may differ in their optimal foraging strategy (Svanbäck & Bolnick 2005).
For example, larger individuals have better abilities to ingest and tolerate lower quality food (Bell 1971, Geist 1974, Jarman 1974), and the Jarman-Bell principle predicts that they should exploit a wider foraging niche than smaller individuals. When learned skills are required to efficiently capture and handle different prey types, individuals with contrasted experience vary in the cost and benefit associated with a given diet (Estes et al. 2003, Tinker et al. 2009). In mule deer (*Odocoileus hemionus hemionus*), reproduction constraints alter the foraging strategy of deer, with females feeding with a dependant young preferring feeding grounds of poorer quality but less exposed to predation, whereas males select high-risk, high-energy gain habitats (Main & Coblentz 1996).

Hence, resource partitioning is commonly observed within populations and has been particularly documented between sexes (sexual segregation, Shine 1989), age classes (age structure component, Polis 1984) and morphs (resource polymorphism, Smith & Skulason 1996). More recently, individual specialisation (defined as the inter-individual variation in resource-use that is not accounted by sex, age and morph (Bolnick et al. 2003)) has been shown to be a widespread phenomenon among various taxa (Bolnick et al. 2003, Araújo et al. 2011).

**Influence of the local environment**

While intrinsic factors are considered to be the main drivers of individual variation in resource-use, the diversity, abundance and distribution of prey influence the degree of segregations (Svanbäck & Bolnick 2005, Araújo et al. 2011, Svanbäck et al. 2011). Indeed, the optimal foraging strategy of a consumer depends on how effective it is at detecting, capturing, handling and digesting prey (intrinsic factors), but also on the encounter rates and energetic content of alternative prey (extrinsic factors) (MacArthur
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& Pianka 1966). Hence, where a resource type is highly abundant, encounter rate is high and all individuals are expected to forage upon this particular prey, masking any potential resource segregation (Croxall et al. 1997, Tinker et al. 2008). Conversely, if individuals are restricted in their foraging niche, for example because the environment is fairly uniform in terms of prey and/or habitat type, resources might not be diverse enough to provide the ecological opportunity for conspecifics to diverge (Darimont et al. 2009).

Resource diversity and abundance vary greatly temporally and spatially, at the short-, medium- and long- time and space scales. Consequently, the degree of resource segregation is not a fixed characteristic of a species and is likely to vary through time and between populations. For example, the availability of fruits, a main component of the diet of Egyptian fruit bats (*Rousettus aegyptiacus*), depends highly on the season (Herrera et al. 2008). Accordingly, bats exploit a wider foraging niche and exhibit greater inter-individual variation in spring, when fruits are more abundant and diverse, than in summer or winter (Herrera et al. 2008).

The development of new indices that measure the level of resource partitioning (in particular of individual specialisation: Bolnick et al. 2002, Araújo et al. 2008) has enabled to investigate how individual variability differs among environments and ecological contexts. In particular, biotic factors such as competition, predation and ecological opportunity have been shown to impact the degree of individual variation in diet, most probably by influencing the availability of prey (Svanbäck et al. 2008, Bolnick et al. 2010, Araújo et al. 2011, Tinker et al. 2012). For example, intra-specific competition reduces the encounter rate of the preferable prey, such that predators are expected to broaden their diet to include alternative prey. Accordingly, population niche width increases with the degree of competition (Svanbäck & Persson 2004, Svanbäck & Bolnick 2007). This niche expansion can occur when all individuals
exploit a wider range of prey, which would result in a similar level of individual variation. However, if individuals vary in their prey preferences (either ranking order or willingness to add secondary prey), the degree of individual specialisation will either increase or decrease as competition intensifies (Svanbäck & Bolnick 2005, Lemos-Costa et al. 2015).

**Fitness consequences of resource segregation**

Individual variability in ecological niche has profound implications for population structure and dynamics and how species adapt to the environmental variability (Lomnicki 1978). As individuals exploit different resources, they are not uniformly impacted by perturbations and a higher inter-individual diversity confers a population a better stability and resilience to disturbances (Lomnicki 1978). Furthermore, individual variation in niche provides the raw material for natural selection to occur. Individuals from the same population show differential exposure to different suites of selective pressures (Knudsen et al. 2011) and resource-specific fitness can have important evolutionary implications if individual niche variation is consistent over time and is a heritable factor (Bolnick et al. 2011).

At the individual level, different foraging strategies and/or degree of specialisation might provide contrasting energetic gains and have different fitness payoffs. In the European Eel (*Anguilla anguilla*), head shape determines the diet and foraging habitat of eels, and individuals with narrower or broader head exhibit a better body condition than individuals with intermediate size head (Cucherousset et al. 2011). Male southern elephant seals (*Mirounga leonina*) have a longer life-span when they have an early ontogenetic shift and are consistent in their foraging ground (regardless of the habitat) over the years (Authier et al. 2012). The quality of the winter migratory
habitat is related to the body condition and the timing of arrival in the breeding colony in the American redstart (Setophaga ruticilla), two components strongly correlated to breeding success in this species (Marra et al. 1998). Furthermore, direct diet-specific risk factors may apply because foraging individuals are commonly a vulnerable target for predators and parasites (Darimont et al. 2007, Johnson et al. 2009).

However, contrasting results have been found on the fitness consequences of individual specialisation (e.g. Durell 2000, Watanuki et al. 2003, Norris & Marra 2007, Ceia et al. 2012, Vander Zanden et al. 2014, Robertson et al. 2015). For example, while specialist pigeon guillemots (Cepphus Columba) fledge more chicks than generalist individuals (Golet et al. 2000), a 15 year study on the Brünnich’s guillemot (Uria lomvia) revealed no difference in survival or reproductive success between specialists and generalists (Woo et al. 2008). Results seem to depend on various factors, including the local environment, drivers of specialisations, and factors maintaining individual variability within the population (e.g. environmental variability, social dominance interactions, disruptive selection) (Marra et al. 1998, Woo et al. 2008, Cucherousset et al. 2011, Robertson et al. 2015). Hence, further investigations are necessarily to understand the fitness consequences of individual specialisation and their implications in evolutionary processes.

**Fur seals as model species**

Fur seals exhibit extreme within population variation in morphology, with territorial males being two to six times larger than adult females (Staniland 2005). This high sexual size dimorphism implies that individuals differ greatly in their respective energetic requirements and the range of prey they can potentially access (Boyd 2002, Staniland 2005). In particular, the diving abilities of seals depends on their body...
oxygen stores which is related to their body size (Kooyman 2012). Hence, larger males can efficiently forage within a greater extent of the water column than their female counterparts (Boyd et al. 1998, Page et al. 2005b, Staniland & Robinson 2008). Furthermore, variation in body shape influences seal manoeuvrability (Fish et al. 2003) and, thus, its efficiency at capturing different types of prey. The two sexes differ also greatly in their respective breeding constraints. In this polygynous mating system, males are capital breeders, fasting while maintaining territories throughout the mating season, and do not provide any parental care. In contrast, females suckle their pup for periods from 4 to 36 months (Bonner 1984). They feed at-sea during the breeding period (income breeders), and are restricted in their foraging range as they need to regularly come back to the colony to suckle their offspring.

Accordingly, strong sexual segregation has been observed in various species. The large size and aggressiveness of males, couple with the facts that they spend most of their time at-sea and show an unpredictable response to intravenous or muscular anaesthesia, have implied that only a limited number of studies have investigated the at-sea ecology of male otariids (e.g. Boyd et al. 1998, Campana 1999, Staniland & Robinson 2008, Knox et al. 2014, Sterling et al. 2014). However, in the few studies conducted, differences in foraging niche have been observed between the sexes, both in terms of (i) habitat use (horizontal and/or vertical segregation), with males typically foraging further away from the breeding colonies and diving deeper than females (Boyd et al. 1998, Loughlin et al. 1999, Campagna et al. 2001, Page et al. 2005b, Staniland & Robinson 2008), and (ii) diet, with males feeding upon larger prey of higher trophic level compared to females (Page et al. 2005a, Cherel et al. 2007, Kernaléguen et al. 2012, but see Franco-Trecu et al. 2014). In addition to sexual segregation, individual specialisation has also been recorded in some species (Cherel et al. 2009, Kernaléguen et al. 2012, Franco-Trecu et al. 2014).
Fur seals breed in contrasting habitats, characterised by various levels of prey diversity and abundance. Comparisons at the inter- and intra-species and population levels provide, thus, an interesting opportunity to investigate how the local environment and biotic factors influence the degree of segregation. For instance, while most species are epi-pelagic, the Australian fur seal (*Arctocephalus pusillus doriferus*) is a benthic forager (Arnould & Hindell 2001, Arnould & Kirkwood 2008, Hoskins & Arnould 2014, Hoskins et al. 2015). This foraging mode restricts seals to an unusually narrow range of foraging habitats, mainly the shallow continental shelf region of south-eastern Australia, such that the species has the smallest range of all fur seal species (Wickens & York 1997). Furthermore, while feeding on the seabed, females consume a large diversity of prey, up to 60 species (Gales et al. 1993, Hume et al. 2004, Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009). In contrast, the epi-pelagic female Antarctic fur seals (*Arctocephalus gazella*) are known to target primarily one prey type, the Antarctic krill (*Euphausia superba*) in Antarctic waters (Doidge & Croxall 1985, Casaux et al. 2003), or myctophid fish when foraging in subantarctic waters (Cherel et al. 2007, Lea et al. 2008).

At the species level, populations breed in contrasted environments, hosting different sympatric competitors, and subject to various level of intra-specific competition. In particular, fur seals have been heavily hunted in the 18th and 19th century. Sealing pressure and recovering trajectories vary between locations, such that populations do not experience the same level of competition (Bonner & Laws 1964). For example, subantarctic fur seals (*Arctocephalus tropicalis*) have been less heavily hunted in subtropical than in subantarctic waters where they breed in sympatry with elephant seals which were also targeted by sealers (Bonner & Laws 1964). Hence, while some populations are increasing in size, others have stabilised suggesting they have reached their carrying capacity and are subjected to density-dependence
1. Introduction

processes (Gilpin & Ayala 1973). Furthermore, at the population level, fur seals vary in their breeding constraints throughout the breeding cycle. For example, while females are restricted in their foraging range during the suckling period, they can disperse after weaning and have access to a wider range of foraging grounds and associated prey.

Fur seals represent also a good model to investigate the fitness consequences of specialisation. Indeed, in this highly polygynous mating system, only the largest, most dominant males have access to females such that breeding success can vary dramatically between individuals. Males are expected to be subject to strong selective pressure toward efficient foraging behaviour, hence, any variation in foraging strategy payoff should have strong repercussions in the reproductive success of males.

Research aims and thesis structure

The objectives of this thesis were to: (i) describe and measure resource segregation within population; (ii) investigate the main intrinsic (morphology and breeding constraints) and extrinsic drivers (resource diversity and abiotic factors) shaping segregation; and (iii) address the question of the fitness consequences of individual specialisation.

From a methodological perspective, the present thesis also aims to (iv) raise and test the question of time-scale in individual specialisation studies. Indeed, environments are usually a patchwork of favourable and unfavourable habitats, with patches being available temporarily and appearing at unpredictable times and places. In such inconstant and unpredictable environments, foraging strategies of organisms are likely to vary greatly in time, such that short-term studies are prone to great stochastic errors, misleading our estimation of the degree of specialisation.
Furthermore, the thesis also documents the foraging ecology of fur seals at the individual scale and over the long-term. In particular, the present work provides new insights into poorly documented cryptic life-stages: males and females at early-life, and full-size territorial males.

The thesis is structured with the central chapters reporting on specific studies that have been published or submitted for publication in peer-reviewed journals.

- Chapter 2 provides a documented example of individual specialisation in a generalist species, the Australian fur seal, and critically assess how different methods and time-scales affect our estimation of the degree of specialisation.
- Chapter 3 investigates the ontogeny of sexual segregation in the Antarctic fur seal and determines at which life-stages, associated with which life-history traits, sexual segregation are developing in this highly dimorphic species.
- Chapter 4 addresses the influence of the local environment in the degree of sexual segregation and individual specialisation. The unusual benthic foraging mode of the Australian fur seal restricts seals in their foraging habitat, raising the question of segregation in a restricted environment.
- Chapter 5 examines how three main abiotic factors: inter- and intra-specific competition and ecological opportunity affect the level of individual specialisation in the Antarctic and subantarctic fur seals.
- Chapter 6 investigates the fitness consequences of individual specialisation in males of Antarctic and Australian fur seals, two highly polygynous and dimorphic species where males are expected to be subject to a strong selective pressure towards foraging efficiency.
- Chapter 7, finally, discusses the intrinsic and extrinsic factors shaping segregation and the fitness consequences of specialisation.
CHAPTER 2

From Video Recordings to Whisker Stable Isotopes: 
a Critical Evaluation of Time-Scale in Assessing Individual 
Foraging Specialisation in Australian Fur Seals

A version of this chapter has been published as:

video recordings to whisker stable isotopes: a critical evaluation of timescale in 
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2. Individual Specialisation in Australian Fur Seals

Abstract

Estimating the degree of individual specialisation is likely to be sensitive to the methods used as they record individuals’ resource-use over different time-periods. We combined animal-borne video cameras, GPS/TDR loggers and stable isotope values of plasma, red cells and sub-sampled whiskers to investigate individual foraging specialisation in female Australian fur seals (*Arctocephalus pusillus doriferus*) over various time-scales. Combining these methods enabled to (i) provide quantitative information on individuals’ diet, allowing the identification of prey, (ii) infer the temporal consistency of individual specialisation, and (iii) assess how different methods and time-scales affect our estimation of the degree of specialisation. Short-term inter-individual variation in diet was observed in the video data (mean pairwise overlap=0.60), with the sampled population being composed of both generalist and specialist individuals (nested network). However, the brevity of the temporal window is likely to artificially increase the level of specialisation by not recording the entire diet of seals. Indeed, the correlation in isotopic values was tighter between the red cells and whiskers (mid- to long-term foraging ecology) than between plasma and red cells (short- to mid-term) (R\(^2\)=0.93-0.73 versus 0.55-0.41). \(\delta^{13}C\) and \(\delta^{15}N\) values of whiskers confirmed the temporal consistency of individual specialisation. Variation in isotopic niche was consistent across seasons and years, indicating long-term habitat (WIC/TNW=0.28) and dietary (WIC/TNW=0.39) specialisation. The results also highlight time-averaging issues (under-estimation of the degree of specialisation) when calculating individual specialisation indices over long time-periods, so that no single time-scale may provide a complete and accurate picture, emphasising the benefits of using complementary methods.
2. Individual Specialisation in Australian Fur Seals

Introduction

In most studies and theoretical models, individuals of a population are considered to be ecologically equivalent with inter-individual variability usually being treated as statistical noise (Bolnick et al. 2003, Pires et al. 2011). However, conspecifics may differ in many traits including their sex, age, morphology, physiology, social status or learned abilities. Accordingly, individuals might meet contrasting optimum criteria and adopt different strategies to exploit available resources (Bolnick et al. 2011). Assessments at the individual level, rather than at the population level might, therefore, be necessary for understanding niche use and resource partitioning in a population or ecosystem (Lorrain et al. 2011, Robertson et al. 2014, Tranquilla et al. 2014). For example, many apparent generalist populations exploiting a wide range of resources are composed of heterogeneous specialist individuals that use a small subset of the available population niche (Bolnick et al. 2003, Araújo et al. 2011).

Such individual specialisation has profound implications for population dynamics and how species adapt to the environmental variability (Lomnicki 1978). Individuals are not affected to the same extent by perturbations and a higher diversity within a population confers a greater stability and resilience to disturbances (Lomnicki 1978, Hughes et al. 2008). The level of individual specialisation within a population might also affect species interactions and community structure (Crutsinger et al. 2006, Pruitt & Ferrari 2011) and the ecological functions the population plays in its ecosystem (Bolnick et al. 2011, Cantor et al. 2013). For example, an important role of generalist top order predators is to couple nutrient and energy pathways from discrete food webs (Rooney et al. 2006). However, if the population is composed of specialist individuals feeding on a limited number of prey, it may no-longer serve this food-web connectivity function (Quevedo et al. 2009, Matich et al. 2011).
The time-scale over which we record individuals’ resource-use is an important factor to consider when investigating individual specialisation. For example, in foraging studies, gut contents provide only a recent snapshot of an individual’s diet that might not be representative of its long-term foraging habits, especially if prey are patchily distributed or exhibit temporal variation in abundance (Araújo et al. 2007). Hence, a generalist individual might appear to be specialist if it encountered a patch of a specific prey just before the sampling period. When not recording the entire niche of individuals, short-term studies are likely to over-estimate differences between individuals and artificially increase the apparent degree of individual specialisation of a population (Bearhop et al. 2004a). It is, thus, necessary to study individuals over a sufficient period to account for the intra-individual variation and avoid stochastic sampling effects.

The most direct method to assess the temporal consistency in resource-use is to monitor individuals through time (e.g. Bryan & Larkin 1972, Bridcut & Giller 1995, Tinker et al. 2008). However, such longitudinal studies are labour-intensive as they require repeated observations or captures of the same individuals. Other studies have combined a ‘snapshot method’ to document individual resource-use in detail, with the use of an indirect proxy such as morphological variation (Robinson et al. 1993), parasite fauna (Curtis et al. 1995) or stable isotopes (Fry et al. 1978, Araújo et al. 2007, Rosenblatt et al. 2015) to infer the temporal consistency of individual specialisation. In particular, the isotopic signature of tissues integrate the diet over the period they were synthesised (Tieszen et al. 1983, Dalerum & Angerbjorn 2005). Hence, tissues with various protein turn-over rates provide information on the feeding ecology over different time-scales and provide insights in the temporal consistency of the isotopic niche, a proxy of the foraging niche (Bearhop et al. 2006, Del Rio et al. 2009, Connan et al. 2014).
2. Individual Specialisation in Australian Fur Seals

Numerous dietary studies based on scat and regurgitate content analyses have shown that the Australian fur seal (*Arctocephalus pusillus doriferus*) is a top order predator that forages upon a large variety of prey (45–60 species), characterising it as a generalist species (Hume et al. 2004, Kirkwood et al. 2008). Little is known, however, of variation in foraging niche between individuals and how variable diet is within individuals (but see Arnould et al. 2011). The Australian fur seal represents the largest marine predator biomass in south-eastern Australia (Kirkwood et al. 2010). The degree of individual specialisation, therefore, might be an important factor for this species, how it may respond to environmental variability (Lomnicki 1978), and for understanding its top-down effects on the local marine ecosystem, an area predicted to be greatly affected by climate change (Ridgway 2007).

In the present study, complementary methods were combined and compared to (i) document fine-scale but short-term inter-individual variation in foraging ecology in the Australian fur seal, (ii) infer the temporal consistency of individual specialisation over the long-term, and (iii) critically assess how different methods and time-scales affect our estimation of the degree of individual specialisation. Faced with the difficulties associated with monitoring the foraging behaviour of top order predators with large geographic ranges in the marine environment, animal-borne video cameras offer a novel opportunity to document the diet of cryptic species (Takahashi et al. 2008, Heaslip et al. 2012). Associated with GPS/TDR loggers, they provided a comprehensive picture of individual foraging ecology of Australian fur seals over the short-term. Comparison of the isotopic values of three tissues of contrasting turn-over rates (plasma, red blood cells and sub-sampled whisker) allowed the assessment of the consistency of inter-individual variation in foraging habitat ($\delta^{13}$C values) and diet ($\delta^{15}$N values) across seasons and years.
Similar to other species feeding upon a large variety of prey (Roughgarden 1974, Darimont et al. 2009, Araújo et al. 2011), some individual specialisation is expected to occur in the Australian fur seal. Related otariid species exhibit levels of specialisation ranging from highly specialised to generalist (Franco-Trecu et al. 2014, Kernaléguen et al. 2015a). Considering the broad trophic niche of the population (i.e. high ecological opportunities) and the spatial restrictions in foraging areas of this benthic species (i.e. potential high intra-specific competition), relatively high levels of inter-individual variation are expected in the Australian fur seal compared to other otariid species (Araújo et al. 2011, Kernaléguen et al. 2015a). Furthermore, the degree of specialisation might differ between individuals with some females being more specialised than others (Araújo et al. 2010, Tinker et al. 2012). It was also hypothesised that the measured degree of individual specialisation would vary according to the time-period over which it is calculated, with higher degrees of specialisation found in the short-term.

Material and Methods

Study site and animal handling

The study was conducted on Kanowna Island (39°10’S, 146°18’E), northern Bass Strait, south-eastern Australia, which hosts the third largest Australian fur seal colony with an annual pup production of ca 3,400 (Kirkwood et al. 2010). During the winters of 2008-2012 (May – July), a total of 16 accessible lactating females (i.e. breeding in the highest part of the colony) were captured using a modified hoop-net (Fuhrman Diversified, Flamingo, TX, USA) and anaesthetised using isoflurane delivered via a portable gas vaporizer (Stinger™, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia) (Gales & Mattlin 1998). Morphometric measurements (standard...
length, axillary girth, axis length, right flipper length, ± 0.5 cm) and body mass (± 0.1 kg) were recorded and the longest whisker was cut at its base. A blood sample was collected by venipuncture of an inter-digital vein in a hind-flipper using heparinised syringes, kept cool (4°C) for several hours before separating the red cells from the plasma fraction and then stored frozen at -20°C until analysis.

Each seal was instrumented with a dive behaviour data logger (MK10, Wildlife Computers, Washington, USA), a GPS data logger (FastLoc®, Sirtrack, Havelock North, NZ) and a video data logger (Crittercam® Gen 5.7, National Geographic Society, Washington, USA). Data loggers were glued in series to the dorsal mid-line fur just behind the scapula using quick-setting epoxy (Accumix 268, Huntsman Advanced Materials Pty Ltd, Deer Park, VIC, Australia). To assist in relocating animals for recapture, a small VHF transmitter (Sirtrack, Havelock North, NZ) was also attached, and individual numbered plastic flipper tags (Super TagsH®, Dalton Supplies, Woolgoolga, NSW, Australia) were inserted into both fore-flippers. In total, attached devices weighed < 2% of body mass and represented < 1% of cross sectional surface area. The distance between the camera lens to the tip of the nose as well as the mid-point between the ears and the head width at the ears were measured (± 0.5 cm) to provide a comparative scale for prey observed in the camera field of view. At recapture, devices were retrieved by cutting the hair beneath the glue.

To conserve battery life and sample as much of the foraging trip as possible, animal-borne video cameras were programmed to record on a 1 h on: 3 h off duty cycle. A depth trigger of 40 m was also used (i.e. cameras recorded only after the seal descended below 40 m and stopped once the animal ascended above 40 m), knowing that female Australian fur seals are benthic feeders (Arnould & Hindell 2001, Arnould & Kirkwood 2008, Hoskins & Arnould 2014). Examination of the diving behaviour data of the sampled females confirmed that dives were almost exclusively below 40
m. During night recordings, a near infra-red LED beam was activated. While it was understood that such visual stimuli could potentially affect seals’ foraging behaviour (Heaslip & Hooker 2008), not introducing light would preclude collection of data at night altogether. The low frequency red lights were selected as a compromise, based on the presumption that visual sensitivity of marine animals (fur seals and their prey) should decrease at longer wavelengths as an adaptation for aquatic vision, limiting the bias caused by the camera’s light source (Lythgoe & Partridge 1989, but see e.g. Levenson et al. 2006).

**Spatial and diet analyses**

TDR (Time Depth Recorder) and GPS data loggers were programmed to record depth every second and location information at a minimum interval of 15 minutes when seals were at the surface, respectively. Location data were speed filtered (McConnell et al. 1992) and interpolated at a 10 minutes interval. Dives were classified into benthic or pelagic according to the proportion of the diving time spent at the bottom and the maximum depth of the dive following Hoskins et al. (2015).

Each prey was identified into the lowest taxonomic level possible using identification guides (Kuiter & Kuiter 1996). When possible (for 92% of prey), fish fork length or cephalopod mantle length was measured when in the mouth of the seal to the nearest centimetre using the known seal head measurements as scale. Prey biomass was then estimated using species-specific length-mass allometric equations (Furlani et al., Froese & Pauly 2014). Coefficients of the most common prey species of the corresponding family/order were used for prey that could not be identified to the species level. Average prey length for the species captured by the same individual were used for fish that could not be measured and overall average mantle length was used for cephalopod prey that could not be measured.
The degree of individual specialisation was calculated on the proportion of reconstructed biomass of each prey order consumed by individuals. Similar results were found with numerical abundance but the results for biomasses are reported as they are more representative of the nutritional contribution of each prey category. However, results are likely to be biased towards large prey (e.g. cephalopods, elasmobranchs) because fur seals probably do not consume the entire large prey.

The diet overlap between each individual and the population was measured by the proportional similarity index (PS, Bolnick et al. 2002). If $p_{ij}$ and $q_j$ are the proportion of the $j$th resource category in individual $i$’s and population’s diet, respectively, then,

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

High PS values (tending to 1) indicate the individual consumes resources in the same proportion as the population (generalist individual), and low values of PS (tending to 0) denote the individual forages on prey that were scarce in the population resource use distribution (specialist individual). The degree of individual specialisation of the population IS was then calculated averaging the PS scores across all individuals (Bolnick et al. 2002). As a reference, IS was also calculated on the seven individuals sampled the same year (in 2011, Table 2.1). All indices were calculated using the R package RInSp (Zaccarelli et al. 2013). Significance of IS was assessed using a nonparametric Monte Carlo technique to generate 10,000 replicate datasets under the null hypothesis that all individuals are generalists, from which P-values were calculated (Bolnick et al. 2002).

When individuals vary in their feeding habits, they might be organized into discrete groups (clusters) so that individuals of the same group consume similar resources, and overlap little with individuals belonging to another group (Araújo et al. 2019).
2. Individual Specialisation in Australian Fur Seals

2008, Araújo et al. 2010, Tinker et al. 2012). The “individual niche overlap network” analysis developed by Araújo et al. (2008) was used to test this assumption. The coefficient $C_{ws}$ is a measure of the degree of clustering such as positive values tending to 1 indicate that the population is organized into discrete subgroups (diet clustering), and negative values approaching -1 characterise a population where each individual specialises upon a unique set of resources (over-dispersion of diet). A $C_{ws}$ coefficient close to 0 can be found when individuals are generalists (low IS), so that they all use the same resources and belong to the same group, or when the population is composed of both specialist and generalist individuals and the diet of specialists is nested within the diet of generalists. The $C_{ws}$ coefficient was also calculated using the R package RInSp (Zaccarelli et al. 2013) and its significance was evaluated using resampling methods based on Monte Carlo techniques (using 10,000 replicates).

**Isotopic analyses**

Isotopic analyses were restricted to 10 females sampled in 2010 and 2011 (3 and 7, respectively, Table 2.1), in order to limit potential temporal bias in the isotopic results (i.e. potential temporal variation in the isotopic signature of prey). In the laboratory, whiskers were hand-washed in 100% ethanol and cleaned in distilled water for 5 minutes in an ultrasonic bath. Following Cherel et al. (2009), they were dried, measured and cut into 3 mm-long consecutive sections starting from the proximal (facial) end. Blood plasma and red cells samples were freeze-dried and ground into a fine powder. Since lipids can affect plasma $\delta^{13}C$ values (Cherel et al. 2005) they were removed from plasma using a cyclohexane solvent. The $\delta^{13}C$ and $\delta^{15}N$ values of blood samples and each whisker section were determined by a continuous flow mass spectrometer (Thermo Scientific, Delta V Advantage) coupled to an elemental analyser (Thermo Scientific, Flash EA 1112). Results are presented in the conventional
δ notation relative to Vienna PeeDee Belemnite marine fossil limestone and atmospheric N2 for δ¹³C and δ¹⁵N, respectively. Replicate measurements of internal laboratory standards indicated measurement errors < 0.10‰ for both isotopic ratios.

No blood isotopic turn-over rates have been published in pinnipeds. However, plasma and red blood cells have half-lives of 4 and 28 days in black bear (*Ursus americanus*) (Hilderbrand et al. 1996), a carnivore of comparable size to the Australian fur seal. Hence, in the present study, plasma and red blood cells isotopic values were considered to be a proxy of the foraging ecology of individuals over the last few days and weeks respectively. Otariid whiskers depict a chronology of isotopic values over a different period of time depending on individuals (Kernaléguen et al. 2012). In order to compare females over a similar time-frame, each whisker axis was first converted into a common time-scale. Isotopic signatures along the length of otariid whiskers have previously be shown to represent regular annual cycles in some species (Hirons et al. 2001, Cherel et al. 2009, Kernaléguen et al. 2012, Kernaléguen et al. 2015a, Rea et al. 2015). Hence, periodicity of δ¹³C and δ¹⁵N values was assessed, using the wavelet analysis following Kernaléguen et al. (2012). This analysis allows us to detect: (i) whether the isotopic signature of whiskers consist of a repeated periodic signal; and, more importantly (ii) whether the period of the cyclic pattern is consistent along the length of the whisker (Cazelles et al. 2008). As whiskers were cut and not plucked, their most recently synthesized tissue remained under the skin. This part of the whisker (not analysed) corresponds to a various period of time depending on its length and the specific growth rate of the whisker. As a consequence, the first section of each whisker does not necessarily correspond to the same time. Isotopic values were time-synchronised by doing a phase synchronization based on δ¹³C values for each individual between its carbon time series and the isotopic series of a reference individual randomly chosen, following Kernaléguen et al. (2012).
Temporal consistency of individual isotopic niche was tested by determining and comparing the correlation coefficients between plasma and red blood cell values (mid-term specialisation) and red blood cell and whisker values (long-term specialisation) (Rosenblatt et al. 2015). Isotopic data are biased toward correlation across tissues because the temporal window they integrate partially overlap. However, in both cases, the overlap period was less than 15%. The degree of individual specialisation depicted by whisker isotopic data was then calculated using Roughgarden’s WIC/TNW index for continuous data (Bolnick et al. 2002) (IS and PS indices used for the video data are only for discrete data). Roughgarden (1972) suggested that the population Total Niche Width (TNW, corresponding to the population variance, i.e. overall variance of all isotopic values) can be partitioned into the Within-Individual Component (WIC, intra-individual variance, i.e. average variance between sections calculated at the whisker level) and the Between-Individual Component (BIC, inter-individual variance, i.e. variance between whiskers’ mean isotopic values), where TNW = WIC + BIC. The WIC/TNW ratio is a measurement of the degree of individual specialisation. As for IS and PS indices, high values (approaching 1) indicate that individuals use the full range of the population resources, and low values (approaching 0) characterise specialist individuals. WIC/TNW ratios were calculated on 1.4 years, a time-period covered by all whiskers and that limits time-averaging issues (see Discussion). The R package RInSp (Zaccarelli et al. 2013) was used to calculate individual specialisation indices and significance of WIC/TNW was assessed using a nonparametric Monte Carlo resampling technique (using 10,000 replicate datasets) (Bolnick et al. 2002). The WIC/TNW index assumes individual niches are normal distributions. Distribution of δ¹³C and δ¹⁵N whisker values were tested using a Shapiro test. All individual niches were normal, except for the δ¹⁵N isotopic values of one female.
Similar network analyses as for the video data were performed on whisker $\delta^{13}$C and $\delta^{15}$N values. Network analysis provides a measure of pairwise overlap between each pair of individuals. Pairwise overlap values obtained for the video and whisker $\delta^{15}$N data were compared in order to test the relationship between diet data depicted by the short-term video cameras and the long-term whisker isotopic signatures and to investigate whether individuals that show similar diet in the video data have similar isotopic results.

The relationship between an individual’s morphology and its whisker isotopic values were tested. The morphometric measurements tested were the body mass, standard length, axillary girth, axis length, and the ratio of flipper length to standard length that can influence the manoeuvrability of seals (Fish et al. 2003). As all these factors were highly related, an index of morphological characteristics was calculated using a principal components analysis. The first component accounted for 76% of the distribution of the data and was used as an index of seals’ body shape.

All results are presented as mean ± SD and results were considered significant at the P<0.05 level. All statistics were performed using R 3.0.3. Correlation coefficients were calculated after checking the residuals were normally distributed and the variance were homogenous across the fitted values of the linear models.

Results

Spatial and diet analyses

The majority of seals (11/16) were recaptured when they returned to the colony after a single foraging trip. For the remaining seals, the GPS and TDR loggers recorded spatial information during two (three seals), four (one seal) or five (one seal) foraging trips. However, due to battery life restrictions, video data were only obtained for the
first trip. Hence, only the tracking data for the first trip were used in analyses. These foraging trips lasted an average of $7.2 \pm 5.3$ days, during which seals made an average of $141 \pm 25$ dives per day. With the exception of a single individual, all seals foraged in central Bass Strait (Fig. 2.1). All individuals performed mostly benthic dives ($>75\%$) to the relatively shallow continental shelf (60-80 m).

Figure 2.1 Foraging trip routes of (a) 16 Australian fur seal females over a single foraging trip and (b) female W1881 over two consecutive trips. The continental shelf-edge is indicated by the grey line, representing the 200m bathymetric contour.

The video data loggers recorded on average 9% of all diving time during the foraging trip, corresponding to $183 \pm 67$ minutes of video data per individual, spanning $71 \pm 39$ dives. A total of 1,044 prey captures were recorded, of which 934 were in the camera field of view and could be identified and size estimated (Fig. 2.2). The instrumented individuals consumed a great variety of prey, encompassing 14 orders including three cephalopod, one crustacean, three elasmobranch and seven teleost orders. However, Octopoda, Scorpaeniformes (mainly gurnards and gurnard perches),
Perciformes (bait fish) and Tetraodontiformes (mainly leatherjackets) comprised 94% of the biomass of the observed diet (Table 2.1).

**Figure 2.2** Representative images obtained from video cameras mounted on Australian fur seal females showing a predation on four main preys: (a) an octopus (Octopoda), (b) gunnard (Scorpaeniformes), (c) leatherjacket (Tetraodontiformes), (d) jack mackerels (Perciformes), and two occasional preys: (e) shark (Carcharhiniformes) and (f) stingray (Myliobatiformes).
Table 2.1 Diet of female Australian fur seals as depicted by the animal-borne video cameras.

<table>
<thead>
<tr>
<th>Sampling year</th>
<th>Degree of specialisation</th>
<th>Octopoda</th>
<th>Scorpaeniformes</th>
<th>Perciformes</th>
<th>Tetraodontiformes</th>
<th>Teuthida</th>
<th>Myliobatiformes</th>
<th>Zeiformes</th>
<th>Gadiformes</th>
<th>Sepiida</th>
<th>Decapoda</th>
<th>Ophidiiformes</th>
<th>Squaliformes</th>
<th>Carchariniformes</th>
<th>Beloniformes</th>
<th>Total Biomass (kg)</th>
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<tbody>
<tr>
<td>Population</td>
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<tr>
<td>W1777 2008</td>
<td>0.60</td>
<td>44</td>
<td>28</td>
<td>14</td>
<td>8</td>
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<td>0.5</td>
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<td>0.3</td>
<td>0.1</td>
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<td>W1781 2008</td>
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<td>41</td>
<td>42</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>0.4</td>
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<td>W1817 2009</td>
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<td>68</td>
<td>11</td>
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<td>15</td>
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<td>W1825 2009</td>
<td>0.92</td>
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<td>18</td>
<td>9</td>
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<td>W1849 2010</td>
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<td>91</td>
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<td>2</td>
<td>5</td>
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<tr>
<td>W1855 2011</td>
<td>0.62</td>
<td>69</td>
<td>18</td>
<td>0.1</td>
<td>1</td>
<td>7</td>
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<tr>
<td>W1859 2011</td>
<td>0.75</td>
<td>28</td>
<td>41</td>
<td>4</td>
<td>11</td>
<td>16</td>
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<tr>
<td>W1861 2011</td>
<td>0.72</td>
<td>53</td>
<td>16</td>
<td>25</td>
<td>5</td>
<td>0.9</td>
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<tr>
<td>W1873 2011</td>
<td>0.77</td>
<td>31</td>
<td>21</td>
<td>28</td>
<td>18</td>
<td>2</td>
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<tr>
<td>W1879 2011</td>
<td>0.84</td>
<td>37</td>
<td>45</td>
<td>6</td>
<td>12</td>
<td>0.4</td>
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<tr>
<td>W1881 2011</td>
<td>0.50</td>
<td>39</td>
<td>44</td>
<td>1</td>
<td>13</td>
<td>3</td>
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<tr>
<td>W1905 2012</td>
<td>0.38</td>
<td>94</td>
<td>0.4</td>
<td>0.5</td>
<td>2</td>
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Diet is expressed as the % of reconstructed biomass of each prey order. The degree of specialisation of each individual PS was calculated by measuring the diet overlap between the individual and the population. The degree of specialisation of the whole population IS was obtained by averaging all PS indices (Bolnick et al. 2002). These indices range between 0 (specialist) and 1 (generalist).

Within the observed prey, significant inter-individual variation in resource use occurred. Some individuals were highly specialised, with more than 90% of their reconstructed diet comprising of one prey order (Octopoda or Scorpaeniformes), while others had a more heterogeneous diet encompassing up to eight prey orders. Thus, the degree of specialisation (PS) of each individual differed greatly, ranging from 0.38 to 0.92 (Table 2.1). The average degree of individual specialisation (IS) for the sampled
population was 0.60 (P<0.0001). A similar degree of individual specialisation was observed when calculating IS only on the seven individuals sampled in 2011 (IS = 0.60, P<0.0001). The clustering coefficient $C_{ws}$ of the population was -0.05, and did not significantly differ from zero (P=0.99). There was a continuum in the proportion of the main prey orders between individuals (Fig. 2.3), with specialists and generalists feeding on the same main prey but in different proportions.

**Figure 2.3** Binary network describing the pattern of resource partitioning between individuals based on video data (n=16). An arrow was drawn between two individuals when the degree of pairwise overlap was higher than the average pairwise overlap (edges whose weights were higher than the average network weight). Binary networks allow to visually identify potential discrete subgroups within the population (diet clustering). In the present study, no such clustering was observed; short-term video data exhibited the co-existence of specialist and generalist individuals, the diet of more selective females being ordered, predictable subsets of the diet of generalist females (nestedness).
Isotopic analyses

Plasma $\delta^{13}C$ and $\delta^{15}N$ values ranged from -19.2 to -17.8 ‰ and 15.7 to 16.9 ‰, respectively, while red blood cell values ranged from -19.2 to -18.1 ‰ and 15.5 to 16.5 ‰, respectively (Table 2.2). Mean whisker length was 130 ± 27 mm, corresponding to an average of 43 ± 9 isotopic measurements per individual. Overall $\delta^{13}C$ and $\delta^{15}N$ isotopic values of whiskers varied between -17.6 to -15.5 ‰ and 15.2 to 18.1 ‰, respectively. Isotopic values of plasma were significantly positively correlated to red blood cell isotopic values ($\delta^{13}C$: $R^2=0.55$, $P=0.015$; $\delta^{15}N$: $R^2=0.41$, $P=0.046$, $n=10$) and isotopic values of red blood cells were highly positively correlated to mean whisker isotopic values ($\delta^{13}C$: $R^2=0.93$, $P<0.001$; $\delta^{15}N$: $R^2=0.73$, $P=0.002$, $n=10$). In addition, body morphological characteristics of individuals were negatively correlated to $\delta^{15}N$ but not to $\delta^{13}C$ whisker isotopic values ($R^2=0.51$, $P=0.021$; and $R^2=0.09$, $P=0.39$, respectively, $n=10$), with larger and heavier females displaying lower $\delta^{15}N$ values.

Table 2.2 Temporal integration and isotopic values of plasma, red blood cells and whiskers of 10 Australian fur seal females

<table>
<thead>
<tr>
<th>Temporal integration</th>
<th>Plasma $\delta^{13}C$ (‰)</th>
<th>Red blood cells $\delta^{13}C$ (‰)</th>
<th>Whiskers $\delta^{13}C$ (‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Few days</td>
<td>-18.6 ± 0.5 [-19.2; -17.8]</td>
<td>-18.9 ± 0.3 [-19.2; -18.1]</td>
<td>-16.7 ± 0.3 [-17.6; -15.5]</td>
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<tr>
<td>Few weeks</td>
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<td></td>
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<tr>
<td>Few years</td>
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</table>

<table>
<thead>
<tr>
<th>Temporal integration</th>
<th>Plasma $\delta^{15}N$ (‰)</th>
<th>Red blood cells $\delta^{15}N$ (‰)</th>
<th>Whiskers $\delta^{15}N$ (‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Few days</td>
<td>16.2 ± 0.4 [15.7; 16.9]</td>
<td>15.9 ± 0.3 [15.5; 16.5]</td>
<td>16.6 ± 0.3 [15.2; 18.1]</td>
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<tr>
<td>Few weeks</td>
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<td>Few years</td>
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<table>
<thead>
<tr>
<th>C:N mass ratio</th>
<th>Plasma</th>
<th>Red blood cells</th>
<th>Whiskers</th>
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<tbody>
<tr>
<td>3.5 ± 0.07</td>
<td>3.3 ± 0.03</td>
<td>2.8 ± 0.02</td>
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Values are means ± standard deviation, with ranges in brackets.
Wavelet analyses indicated that all seals exhibited significant periodic oscillations along the length of their whisker in either $\delta^{13}$C or $\delta^{15}$N signals (Fig. 2.4). Eight seals exhibited a cyclic pattern along the entire whisker length, while two seals showed a significant periodicity in only a part of their whisker (Fig. 2.4). Importantly, in all individuals, the period of cycles was constant along the length of the whisker. Periodic oscillations were found in both $\delta^{13}$C and $\delta^{15}$N series for four females. In all cases, the period of cycles was similar in both $\delta^{13}$C and $\delta^{15}$N ratios. Whiskers recorded between 2.9 and 8.0 cycles with an average of $4.2 \pm 1.7$ cycles (Table 2.1). Assuming cycles were annual (Hirons et al. 2001, Cherel et al. 2009, Kernaléguen et al. 2012, Kernaléguen et al. 2015a, Rea et al. 2015), average whisker growth rate was $0.09 \pm 0.03$ mm·d$^{-1}$, similar to the average whisker growth rate of Steller sea lions ($0.10$ to $0.14$ mm.d$^{-1}$, Hirons et al. 2001, Rea et al. 2015), female Antarctic fur seals ($0.05$ to $0.08$ mm.d$^{-1}$, Kernaléguen et al. 2012, Kernaléguen et al. 2015a) and female subantarctic fur seals ($0.09$ mm.d$^{-1}$, Kernaléguen et al. 2012, Kernaléguen et al. 2015a). Each 3 mm-long sampled section had an average temporal integration of $34 \pm 10$ days.

Whisker $\delta^{13}$C and $\delta^{15}$N exhibited a high degree of individual specialisation, with WIC/TNW ratio being $0.28$ and $0.39$, respectively (both P<0.001) (Fig. 2.4). These indices of individual specialisation were calculated over a sub-set of the data, the 1.4 years depicted in all individual. As a reference, WIC/TNW were also calculated for the overall whisker isotopic data : $0.45$ and $0.54$, respectively (both P<0.001). The clustering coefficient $C_{ws}$ was $-0.008$ and $-0.006$ for $\delta^{13}$C and $\delta^{15}$N, respectively. No relation was found between the pairwise overlap values calculated in network analyses using video and whisker $\delta^{15}$N data ($R^2<0.001$, P=0.99, n=45).
2. Individual Specialisation in Australian Fur Seals

Figure 2.4 Whisker $\delta^{13}$C (a, c, e) and $\delta^{15}$N (b, d, f) isotopic signature of female Australian fur seals. Figures show the isotopic signature of (a and b) all females over four years (n=10); (c and d) two or three representative females over four years (including female W1881 which exhibited atypical $\delta^{13}$C high values); and (e and f) all females over 1.4 years, a time-period depicted by all whiskers over which individual specialisation indices (WIC/TNW) were calculated (n=10).

Discussion

The time-scale over which individuals’ resource-use is recorded is an important factor to consider when investigating individual specialisation. The video approach (short-term method) provided valuable information regarding variable fine scale foraging behaviour of individuals which was not apparent using assessment techniques accounting for longer time-scales. Similarly, GPS and dive behaviour loggers
2. Individual Specialisation in Australian Fur Seals

indicated individual foraging sites but could not account for temporal variability in foraging behaviour. Hence, combining video camera and GPS/TDR loggers with the isotopic analysis of tissues of contrasting turn-over rates provided complementary quantitative, qualitative and temporal information of individual foraging specialisation in the Australian fur seal.

Females foraged entirely within the shallow continental shelf of Bass Strait and displayed mostly benthic U-shaped dives, as previously reported for this species (Arnould & Hindell 2001, Arnould & Kirkwood 2008, Hoskins & Arnould 2014). With the exception of a single female which foraged near the eastern boundary of the continental shelf (W1881, Fig. 2.1), all individuals foraged within the Bass Strait Basin. While the foraging location of female W1881 contrasts with the other sampled seals, similar foraging behaviour has been recorded in a small proportion of females breeding in the same colony (Hoskins et al. 2015). The Bass Strait Basin has been previously described as a largely featureless and uniform habitat (Passlow et al. 2004) characterised by low marine primary productivity (Gibbs 1992). However, it may be possible that Australian fur seals target specific small-scale habitat features (Kirkwood & Arnould 2011) and that these may vary between individuals. This was evident in some of the video captured where foraging was observed in complex reef structure with dense sponge dominated assemblages. Analysis of multiple foraging trips of the same individuals is needed to determine whether this species displays inter-individual variation in fine-scale habitat use (Kirkwood & Arnould 2011).

Individuals instrumented with video data loggers consumed a large variety of prey, including benthic and bentho-pelagic teleost fish, elasmobranches, cephalopods and crustaceans which is consistent with previous diet studies based on scat and regurgitate contents (Gales et al. 1993, Hume et al. 2004, Littnan et al. 2007, Kirkwood et al. 2008, Deagle et al. 2009). Substantial variation in diet was found between
individuals (IS = 0.60). It is possible that this is just an artefact of variation in prey distribution and abundance between the sampling years (Hume et al. 2004, Kirkwood et al. 2008, Knox et al. 2014). While it was not possible to test the year effect due to the small sample size, a similar degree of individual specialisation was found between females instrumented within the same year (2011, n = 7, IS = 0.60) as within the whole sample. Specifically, these females differed greatly in their proportion of Perciformes and Tetraodontiformes, which include schooling fish species that are known to vary in abundance and distribution between years (Harris et al. 1991, Young et al. 1993). Therefore, temporal variation in prey abundance seems unlikely to be the main factor explaining the observed inter-individual differences in diet of the females instrumented with video data loggers.

The degree of individual specialisation found in the Australian fur seal was relatively high when compared to the level of specialisation reported in other otariid species. Published indices were all calculated over long time-periods using whisker isotopic data. In the Australian fur seal, the specialisation indices equals 0.28 and 0.39 when using this methodology, compared to 0.59 in the South American sea lion (Otaria flavescens) (Franco-Trecu et al. 2014), 0.81 to 0.96 in the South American fur seal (Arctocephalus australis) (depending on the method used to calculate the specialisation index, Franco-Trecu et al. 2014), 0.49 to 0.93 in the Antarctic fur seals (A. gazella) (depending on the breeding colony and period of the year, Kernaléguen et al. 2015a), and 0.37 to 0.85 in the subantarctic fur seal (A. tropicalis) (Kernaléguen et al. 2015a). Dietary specialisation is more likely to occur when the population feed upon a large diversity of prey as it provides the ecological opportunity for different strategies to occur (Roughgarden 1974, Araújo et al. 2011). Accordingly, dietary individual specialisation has been reported to be stronger in individuals that are not spatially constrained by the need to come back to the colony to feed their offspring.
and, thus, have potentially access to a greater range of resources, e.g. non-breeding females (Kernaléguen et al. 2015a), males (Cherel et al. 2009, Kernaléguen et al. 2012) or phocids which are capital breeders (Tollit et al. 1998, Bradshaw et al. 2004). Diet variation between individuals can be attributed to variation in foraging location (Tollit et al. 1998, Meynier et al. 2014). When feeding in different areas, individuals have access to different prey and vary in their diet. In this study, we report dietary individual specialisation in breeding females feeding in a spatially limited and similar habitat.

Individuals varied in their diet and also in their degree of specialisation. Network analysis confirmed the co-existence of specialist and generalist individuals within the small sampled group. Furthermore, the results indicate that the short-term diet of the more selective seals were ordered, predictable subsets of the diet of the generalist females. Such nested networks have been recently described in various taxa, suggesting nestedness is the prevalent pattern in individual-resource networks (Araújo et al. 2010, Pires et al. 2011, Tinker et al. 2012, Cantor et al. 2013). A possible mechanistic explanation of nestedness is proposed by Optimum Diet Theory models where individuals share the same preferred prey and ranking order but vary in their willingness to include the less-preferred prey (Shared preference model, Svanbäck & Bolnick 2005). Such variation in dietary selectivity leads to individuals with broad and narrow trophic niche, the diet of the most selective individuals being composed only by the preferred prey, which represents a subset of the diet of more opportunist individuals.

However, the data from the animal-borne video cameras reflects the diet of individuals over a limited time-period. Even if a high number of prey captures were recorded per seal, the video data might not be representative of the entire trophic niche of individuals, which could lead to an over-estimation of the degree of individual specialisation (Bearhop et al. 2004a, Araújo et al. 2007). No relationship was found
between the short-term video data and the long-term whisker δ\(^{15}\)N values of the same females. Individuals that exhibited similar diet in the videos did not have similar whisker nitrogen values. The lack of correlation could potentially highlight a mismatch between the short- and long-term diets. However, it is also possible that prey of distinct prey categories have similar isotopic values and/or different prey of the same category have distinct δ\(^{15}\)N values, making the comparison of the two methods difficult.

Previous studies in far eastern Bass Strait found the δ\(^{15}\)N signatures of fur seal prey were spread over a small range of values (between 11.5-13.9‰, with the main prey ranging between 11.5-12.8‰, Davenport & Bax 2002). Assuming similar variation between the isotopic signature of prey in the adjacent Bass Strait Basin, the range of isotopic values found in the Australian fur seal is consistent with what would be expected if the inter-individual variation observed in the video cameras were consistent in time.

Comparing the isotopic values of tissues that integrate contrasting time-periods is an alternative to investigate which time-scale is representative of an individual’s niche width (Bearhop et al. 2004a, Del Rio et al. 2009). Plasma, red blood cells and whiskers of fur seals integrate diet over the last few days, weeks and years, respectively (Hilderbrand et al. 1996). Isotopic values of the three tissues were correlated indicating a consistency in individual foraging niche over time. However, the correlation was stronger between whisker and red blood cells data than between red blood cells and plasma data (R\(^2\)=0.93 and 0.73 versus 0.55 and 0.41, respectively). These results suggest that plasma values, and by extension video data which represents a shorter temporal window than plasma, might not be representative of the entire trophic niche of individuals. It, thus, appears crucial to test whether the individual specialisation depicted by the video data were consistent over time. In that context,
2. Individual Specialisation in Australian Fur Seals

whiskers of the same individuals recorded at a fine scale their isotopic niche (a proxy of their trophic niche), over several years.

With the exception of a single seal (W1881), all individuals displayed close whisker average $\delta^{13}C$ values. Interestingly, female W1881 is the only individual that foraged away from the central Bass Strait Basin (towards the east boundary of the continental shelf). Furthermore, GPS and dive behaviour data revealed that this individual foraged in the same area during the subsequent foraging trip (Fig. 2.1.b). It is likely, therefore, that the consistently higher $\delta^{13}C$ values in the whisker of this individual reflects her repeatedly foraging in that general area over several years. Furthermore, even with the isotopic values of the nine remaining females being spread over a small range, they still showed long-term inter-individual variation in their $\delta^{13}C$ isotopic niche (overall WIC/TNW = 0.28). Female Australian fur seals are known to forage in individually preferred “hotspots” during consecutive foraging trips (Kirkwood & Arnould 2011). Hence, whisker $\delta^{13}C$ values may confirm the occurrence of foraging site fidelity, at least among some females (the more specialised individuals depicted in network analysis), and extend it over longer time-scale, spatial inter-individual variation being consistent across seasons and years.

Female Australian fur seals also exhibited a high degree of inter-individual variation in $\delta^{15}N$ isotopic niche (WIC/TNW = 0.39), confirming the existence of long-term individual foraging specialisation. A larger sample size would be required to run a comprehensive individual-resource network analysis over the long term. However, the few individuals analysed appeared to be also organised into a nested network (presence of both specialists and generalists in the sampled population, with the diet of specialists being ordered subsets of the diet of generalist individuals). Despite a large diversity of prey in the Australian fur seal diet (present study, Hume et al. 2004,
Kirkwood et al. 2008), whisker $\delta^{15}N$ data were spread over a small range of values, reflecting small isotopic variation between prey types (Davenport & Bax 2002). Such a narrow isotopic range in prey is a limitation of the stable isotope method in the Bass Strait region since even a small variation, which may be difficult to detect due to instrument precision, may have biological significance. Multiple isotopic measurements on the same individuals provided by whiskers used in this study have come some way in addressing this methodological limitation, allowing to distinguish actual inter-individual variation from stochastic measurement errors.

The degree of individual specialisation was higher in the whisker $\delta^{15}N$ data than in the video data. This is a surprising result as short-term studies have been shown to be more likely to artificially increase the level of specialisation by not recording the entire trophic niche of individuals (Bearhop et al. 2004a). Non-exclusive biological and methodological reasons might explain this pattern. Firstly, females might be more specialised in summer due to specific energy requirements associated with reproduction or seasonal variation in prey assemblage in Bass Strait (Hume et al. 2004). Secondly, females might specialise upon specific prey that were pooled into the same category (prey of same order) in the video data analysis but have distinct $\delta^{15}N$ values. Finally, it is important to note that the stable isotope method can potentially increase the apparent degree of specialisation compared to other methods. Indeed, individuals that feed on the same prey items but in different proportions may exhibit different $\delta^{15}N$ values. If they consistently eat the same proportion of these prey over time, their isotopic niche will show no overlap, while their actual diet is overlapping to a certain degree (Matthews & Mazumder 2004).

An underlying question in individual specialisation is why individuals vary in their foraging strategy. According to the Optimal Foraging Theory they should all feed on the most valuable resources that maximize the energy intake per unit handling time.
Individual Specialisation in Australian Fur Seals (MacArthur & Pianka 1966). However, intrinsic phenotypic variability between individuals may lead to variation in the ability to detect, capture, handle and/or digest different prey (Svanbäck & Bolnick 2005). For example, in diving mammals, body size is directly related to an individual’s oxygen stores which determine its aerobic dive limit (Kleiber 1961). The shape of the body also influences the manoeuvrability of seals and their swimming abilities (Fish et al. 2003). In the present study, larger, heavier females had lower whisker $\delta^{15}$N values indicating they foraged on prey of lower trophic levels (e.g. redbaits, leatherjackets), as previously reported in this species (Arnould et al. 2011). Larger individuals might have better abilities to hunt cryptic prey on the sea-floor or chase high energetic prey of lower trophic level that require a longer chasing time. Alternatively, other prey might be less accessible to them due to their lower manoeuvrability compared to smaller conspecifics.

While it is crucial to monitor individuals over a sufficient period of time to account for the intra-individual variability of diet, time averaging over long periods of time might raise other issues (Novak and Tinker 2015). Indeed, current indices of individual specialisation do not integrate the temporal component in their calculation. Time averaging or aggregating consists of pooling all data together for repeated measurements on the same individuals, or in considering the isotopic signature of a tissue of long temporal integration for stable isotopes analyses. This step might underestimate the degree of specialisation if the diet of individuals and/or the isotopic values of the food source vary over time (e.g. diel change in foraging behaviour, seasonal variation in prey availability). For example, the two individuals represented in Fig. 2.4.d differ in their isotopic signature at each time while their overall isotopic niche (on which the index of individual specialisation is calculated) exhibit a great overlap. Accordingly, if the indices of individual specialisation were calculated over the whole period of time depicted by whiskers (between 2.9 and 8.0 years, depending on
individuals), they would under-estimate the degree of inter-individual variation in $\delta^{13}C$ and $\delta^{15}N$ isotopic niche ($\text{WIC/TNW} = 0.45$ and $0.54$ when calculated on the whole whiskers as opposed to $0.28$ and $0.39$ when calculated over $1.4$ years). This result illustrates the importance of choosing an appropriate time-scale to study individual specialisation within a population. A sufficient period of time is necessary to avoid stochastic sampling effects and account for the intra-individual variability. However, the longest period available might not be the most appropriate due to time-averaging issues (Novak and Tinker 2015). As no single time-scale may provide a complete and accurate picture, the use of complementary methods remain the most powerful way to investigate individual specialisation.

In summary, the present study revealed long-term individual foraging specialisation in breeding female Australian fur seals. The sampled seals were composed of both generalist and specialist individuals, with specialists consuming diets that were a subset of the diet of generalists (nested network). Such diet variation between individuals may have important implications in individual life-history traits and population demography as individuals are not uniformly affected by environmental variability and experience different species interactions. The results of the present study also emphasise the importance of studying individuals over an appropriate time-scale. While snapshot methods such as animal-borne video cameras and gut contents provide essential diet information, allowing the identification of prey, they might not be representative of an individual’s long-term diet and, thus, lead to incorrect measures of individual specialisation. At the opposite end, studies over longer time-scales may face time-averaging issues resulting in under-estimating the level of inter-individual variation in trophic niche. Combining GPS/TDR and video camera loggers with the isotopic signature of tissues of contrasting turn-over rates provided complementary information, allowing to document fine-scale inter-
individual variation in foraging location and prey items but also to infer the temporal consistency of individual specialisation.
CHAPTER 3

Early-Life Sexual Segregation: Ontogeny of Niche Differentiation in the Antarctic Fur Seals

A version of this chapter has been submitted as:

Abstract

Investigating the ontogeny of niche differentiation enables to determine at which life-stages sexual segregation arises, providing insights into the main factors driving resource partitioning. We investigated the ontogeny of foraging ecology in Antarctic fur seals (*Arctocephalus gazella*), a highly dimorphic species with contrasting breeding strategies between sexes. The sequential $\delta^{13}C$ and $\delta^{15}N$ values of whiskers provided a longitudinal proxy of the foraging niche throughout the whole life of seals, from weaning, when size dimorphism is minimal (<15%), to the age of 5. Females exhibited an early-life ontogenetic shift, from a total segregation during their first year at-sea, to a similar isotopic niche as breeding females as early as age 2. In contrast, males showed a progressive change in isotopic niche throughout their development such that 5-year-old males did not share yet the same niche as territorial bulls. Interestingly, males and females segregated straight after weaning with males feeding in southern habitats than females. Spatial segregation was of similar amplitude as observed in breeding adults and was maintained throughout development. Such early-life niche differentiation is an unusual pattern and indicates size dimorphism and breeding constraints do not directly drive sexual segregation contrary to what has previously been assumed in otariid seals.
Introduction

In many species, the ecology of males and females differ greatly, the two sexes occupying distinct niches and playing different roles and functions in their ecosystem to the extent that they may be regarded as separate species (Clutton-Brock & Guinness 1982, Ruckstuhl & Neuhaus 2005). While sexual segregation is likely to be caused by a combination of factors, it is important to disentangle the effect of each parameter to understand their respective role. However, differentiating the influence of various factors is often difficult in empirical studies. In that context, studying the ontogeny of sexual segregation provides a good opportunity to understand underlying mechanisms explaining sex-specific variability (Stewart 1997, Breed et al. 2011). Indeed, most organisms exhibit ontogenetic shifts in their resource-use associated with changes in life-history requirements (e.g. growth, reproduction, social interactions) (Polis 1984, Carlisle et al. 2015). Hence, comparing the ecological niche of males and females as they age enables to determine when segregation occurs in the species development and provides insights into the major factors driving sexual niche differentiation. For instance, in dimorphic species, does niche divergence mirror size divergence? Does sexual segregation arise only when individuals reach sexual maturity?

Furthermore, when the two sexes are characterised by contrasted life-history traits, comparing their respective ontogenetic trajectories enables to investigate the factors influencing an individual to change its resource-use as it ages. However, only few studies have investigated the development of sexual segregation (Tucker et al. 2007, Jaeger et al. 2014), with juveniles of both sexes being pooled in a single group in most studies investigating the effect of age and sex on niche partitioning. Furthermore, when comparing the ecological niche of males and females of different age groups, cross-population studies do not account for the inter- and intra-individual
variability which is increasingly recognised as accounting for a major component of population variability (but see Stewart 1997, Martin et al. 2011 for examples of longitudinal studies).

Adult Antarctic fur seal (*Arctocephalus gazella*) exhibits strong niche differentiation between the sexes (Staniland & Robinson 2008, Kernaléguen et al. 2012). Males and females segregate spatially, with males typically foraging deeper and further away from the breeding colonies than females (Cherel et al. 2007, Staniland & Robinson 2008, Kernaléguen et al. 2012). Furthermore, when feeding in the same water masses, the two genders differ in their diet, males feeding at a higher trophic level than their female counterparts (Cherel et al. 2007, Kernaléguen et al. 2012). As for many other otariid species, sexual size dimorphism and variation in breeding constraints have been proposed as the main drivers explaining niche variation. Indeed, the Antarctic fur seal is a highly dimorphic species, with territorial bulls being up to four times the mass of the largest females (Boyd & Duck 1991) and males and females differ greatly in their reproductive strategy. While the two sexes reach sexual maturity by the age of 3-5, males do not start to reproduce before they are 6-10, when they are large enough to hold a territory (Payne 1979). They do not provide any parental care and can disperse after the mating season, while breeding females suckle their single pup on land for four months. As females need to regularly come back to the breeding colony, their at-sea foraging grounds are spatially restricted during the pup-rearing period.

Whiskers of otariid seals (fur seals and sea lions) are a keratinous (i.e. metabolically inert) tissue that grows continuously at a constant rate (Hirons et al. 2001, Kernaléguen et al. 2012, Rea et al. 2015). It has been shown on subantarctic (n=2, Kernaléguen et al. 2012) and South American (n=3, Vales et al. 2015) fur seals that serially sampled whiskers could potentially record the isotopic niche over the
3. Ontogeny of Sexual Segregation

entire life of seals at a fine scale (δ¹³C and δ¹⁵N values as proxies of the foraging
habitat and trophic level, respectively). In the present study, the isotopic signature of
male and female Antarctic fur seal whiskers were analysed to document the foraging
ecology of seals during their early-life, and compare their ontogenetic trajectories from
weaning, when size dimorphism is minimal (<15%, Lunn et al. 1993), to age 5, when
individuals have reached sexual maturity. We expected that:

(i) in relation to their younger age at breeding, young females would reach the
isotopic niche of breeding females at a younger age than young males would
reach the isotopic niche of territorial bulls;

(ii) the isotopic niche of males and females would progressively diverge throughout
ontogeny, from identical niches in the first months at-sea to the well-defined and
distinct niches of breeding adults, in parallel with the progressive increase in
sexual size dimorphism.

Methods

Fieldwork and isotopic analysis

The study was conducted during the 2013 mating season (November – December), at
the Pointe Suzanne breeding colony (49°26’S, 70°26’E), Kerguelen Archipelago,
which is located north of the Polar Front in the southern Indian Ocean. Eight young
fur seals of each sex were captured using a hoop net and anaesthetised using isoflurane
delivered via a portable gas vaporizer. The longest whisker was collected in each
individual by cutting it as close to the skin as possible. Young males were not breeders,
while all but one female were provisioning a pup. At capture, seals were of unknown
age except for one 5-year-old male tagged as a pup. A whisker from five additional
breeding females and five adult males holding a territory were sampled in order to
describe sexual segregation in full-size breeding adults; and compare the isotopic niche of younger seals throughout their development with the niche of adults (during the same year, i.e. same environmental conditions). While seals were adults at 5-year-old (i.e. sexually mature), younger and older seals are referred as “young” and “adults”, respectively, hereafter in order to distinguish the two groups. Adult females were captured and anaesthetised as previously described. Territorial bulls were manually restrained using a hoop net before being sedated by intramuscular injection of a tiletamine-zolazepam mixture (Zoletil, Virbac, France, 0.75 mg/kg estimated weight).

In the laboratory, whiskers were hand-washed in 100% ethanol and cleaned in distilled water for 5 minutes in an ultrasonic bath. They were cut into 3 mm-long consecutive sections starting from the proximal (facial) end, and the $\delta^{13}C$ and $\delta^{15}N$ values of each whisker section were measured. Results are presented in the conventional $\delta$ notation relative to Vienna PeeDee Belemnite marine fossil limestone and atmospheric $N_2$ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors < 0.10‰ for both $\delta^{13}C$ and $\delta^{15}N$.

**Age determination**

Studies on subantarctic and South American fur seals have previously shown that three stages could potentially be identified in the whiskers of young seals: the lactation, weaning and post-weaning periods (Kernaléguen et al. 2012, Vales et al. 2015). During the lactation period, females mobilise their own tissues to synthesise milk, such that their pup appears to feed at a higher trophic level than their mother and exhibit high $\delta^{15}N$ values (Cherel et al. 2015). Weaning is then characterised by an abrupt drop in $\delta^{15}N$ values, which is followed by the post-weaning period when the pup forages by
itself and its $\delta^{15}N$ signature reflects its diet (Hobson & Sease 1998, Martin et al. 2011). Hence, in the present study, high $\delta^{15}N$ values in the tip (i.e. oldest part) of the whisker, followed by an abrupt drop were considered to correspond to the lactation and weaning periods, respectively, and an indication that the whisker recorded the whole life of the individual.

In some species of otariids, whiskers exhibit a consistent periodicity of $\delta^{13}C$ and/or $\delta^{15}N$ values along their length, corresponding to the annual cycle of seals (Hirons et al. 2001, Cherel et al. 2009, Kernaléguen et al. 2015c, Rea et al. 2015). The periodicity of $\delta^{13}C$ and $\delta^{15}N$ values of young and adult seals was assessed, using the wavelet analysis following Kernaléguen et al. (2012). This analysis allowed us to detect: (i) if the isotopic signature of whiskers consist of a repeated periodic signal; and (ii) if the period of the cyclic pattern is consistent along the length of the whisker (Cazelles et al. 2007, Cazelles et al. 2008). The assumptions of a constant growth rate and that isotopic cycles (of consistent period) correspond to annual breeding cycles were cross-validated by comparing the age determined by the wavelet analysis (i.e. number of cycles of consistent period) and the actual age of the 5-year-old tagged male.

Comparison of isotopic niches

The temporal variation of the isotopic niche was investigated (i) for a given sex, i.e. evolution of an individual’s niche as it ages (males and females separately), and (ii) between the sexes, i.e. comparison of males and females of the same age, during the same years (i.e. same environmental conditions). The isotopic niche of each individual was determined for each class-age: from the end of weaning until the seal is one (age 0, when seals are called young of the year (YOY)), from age one to two (age 1), and
so on until age 4. The isotopic values of full-size territorial bulls and breeding females were also analysed, as a control. Only the isotopic values corresponding to the last, most recent year were considered as the breeding status of the sampled adult seals was unknown during the previous years.

Niche segregation was estimated as the percentage of niche overlap and variation in niche size between two age-classes / sexes. These two parameters were calculated on the 2 dimensions of the isotopic niche (δ\(^{13}\)C and δ\(^{15}\)N combined) using the Bayesian ellipse-based metrics SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011), using the SIAR package in R (Jackson et al. 2011). The standard ellipse area corrected for unbalanced sample sizes (SEAc) provides an estimation of the core isotopic niche of a group (equivalent of standard deviation for bivariate data). Variation in SEAc size was statistically estimated using \(10^4\) posteriori draws. SEAc were estimated at the population and individual levels (Methods S1). At the population level, all male or female data were pooled together. However, whisker isotopic signature provides multiple values per individual that are not independent. Hence, results at the population level should only be interpreted in combination with results from the mixed effect models.

Segregation can occur either along the δ\(^{13}\)C axis, the δ\(^{15}\)N axis, or both axes together. Hence, comparison of δ\(^{13}\)C and δ\(^{15}\)N values were also performed separately. Mixed effect models were used in order to account for the repeated measurements per individual and the time-correlation of the data. The effects of age / sex (fixed effect) and individual (random effect) on δ\(^{13}\)C and δ\(^{15}\)N values were tested for each age-class using \(t\)-tests, after checking the residuals were normally distributed and the variance were homogenous across the fitted values. All results are presented as mean ± SD, and
results were considered significant at the P<0.05 level. All statistics were performed using R 3.0.3.

Results

Age determination

Seven young male and five young female whiskers exhibited high $\delta^{15}N$ values at the tip, followed by an abrupt drop characteristic of the lactation and weaning periods, respectively (Fig. 3.1). Wavelet analyses indicated that all seals (young and adult) exhibited significant periodic oscillations along the length of their whisker in either $\delta^{13}C$ or $\delta^{15}N$ values (along the entire length or only a part of the whisker). Importantly, the period of cycles was constant along the length of every whisker, supporting the assumption of a constant whisker growth rate from weaning throughout the entire development of seals (Table S3.1). Assuming the isotopic cycles correspond to the annual cycle of seals (Hirons et al. 2001, Kernaléguen et al. 2012, Rea et al. 2015), the wavelet analysis estimation of the age of tagged 5-year-old male was 4.9 (Fig. S3.1), thus confirming the utilisation of the annual isotopic cycles to estimate seal age and whisker growth rate. All young seals were either 5- or 6-years-old. Whiskers from breeding males and females recorded on average $6.6 \pm 0.8$ and $7.3 \pm 2.1$ y, respectively.
Ontogeny of female and male isotopic niche

The isotopic niche of females showed a step-change as seals aged (Figs. 3.2 and S3.2). Females showed a complete segregation at age 0, with no overlap in their isotopic niche with all other age-classes, including breeding adults (Table S3.3). Following that first year at-sea, individuals exhibited similarities in their respective isotopic niche throughout their development. Ontogenetic variation in female isotopic niche occurred exclusively along the $\delta^{13}$C axis. Females had significantly lower $\delta^{13}$C values at age 0 than the following years (Tables 3.1 and S3.4), while individuals showed similar $\delta^{15}$N data at all age-classes (Fig. 3.2, Table S3.4).

Unlike females, males exhibited a progressive change in isotopic niche through time (Figs. 3.2 and S3.2). The overlap was minimal between territorial bulls and young
males at age 0 and 1 (0 and 2% overlap, respectively), and increased after age 2 (41, 75 and 74%, Table S3.5). Variation in male isotopic niche occurred both along the δ¹³C and δ¹⁵N axes (Tables 3.1 and S3.6). In particular, δ¹⁵N increased with age until age 3. Territorial males encompassed a greater range of δ¹³C and δ¹⁵N values, which were on average higher than isotopic values of young seals (Table S3.6).

Table 3.1 Sexual variation in whisker δ¹³C and δ¹⁵N values at each age-class. t-tests were performed using mixed effect models to account for the repeated measurements for each individual (random effect) and the time-correlation of the data (auto-correlation coefficient).

<table>
<thead>
<tr>
<th>Class-age</th>
<th>Male (‰)</th>
<th>Female (‰)</th>
<th>Statistics (P value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>δ¹³C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 0</td>
<td>-22.2 ± 1.3</td>
<td>-21.0 ± 0.8</td>
<td>t₁₀,₄₄=-2.47 (0.03)</td>
</tr>
<tr>
<td>Age 1</td>
<td>-21.3 ± 1.5</td>
<td>-19.8 ± 0.9</td>
<td>t₁₀,₁₀₉=-2.80 (0.02)</td>
</tr>
<tr>
<td>Age 2</td>
<td>-21.2 ± 1.3</td>
<td>-19.6 ± 0.9</td>
<td>t₁₀,₁₀₈=-3.21 (0.01)</td>
</tr>
<tr>
<td>Age 3</td>
<td>-20.9 ± 1.0</td>
<td>-19.2 ± 0.7</td>
<td>t₁₀,₁₀₉=-4.60 (0.001)</td>
</tr>
<tr>
<td>Age 4</td>
<td>-21.7 ± 0.8</td>
<td>-18.8 ± 0.4</td>
<td>t₁₀,₉₇=-9.40 (&lt;0.001)</td>
</tr>
<tr>
<td>Adult</td>
<td>-21.2 ± 1.5</td>
<td>-18.9 ± 0.4</td>
<td>t₈,₉₆=-3.89 (0.005)</td>
</tr>
<tr>
<td>δ¹⁵N</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 0</td>
<td>9.0 ± 0.9</td>
<td>10.2 ± 0.4</td>
<td>t₁₀,₄₄=-3.43 (0.006)</td>
</tr>
<tr>
<td>Age 1</td>
<td>9.6 ± 0.8</td>
<td>10.3 ± 0.4</td>
<td>t₁₀,₁₀₉=-2.23 (0.05)</td>
</tr>
<tr>
<td>Age 2</td>
<td>10.1 ± 0.7</td>
<td>10.2 ± 0.4</td>
<td>t₁₀,₁₀₈=-0.17 (0.87)</td>
</tr>
<tr>
<td>Age 3</td>
<td>10.6 ± 0.6</td>
<td>10.4 ± 0.4</td>
<td>t₁₀,₁₀⁷=1.00 (0.34)</td>
</tr>
<tr>
<td>Age 4</td>
<td>10.2 ± 0.7</td>
<td>10.5 ± 0.3</td>
<td>t₁₀,₉₇=-1.28 (0.23)</td>
</tr>
<tr>
<td>Adult</td>
<td>11.0 ± 1.1</td>
<td>10.6 ± 0.4</td>
<td>t₈,₉₆=1.10 (0.30)</td>
</tr>
</tbody>
</table>
Figure 3.2 Ontogenetic changes in the isotopic niche of young female (orange) and male (light blue) Antarctic fur seals during the first 5 years of life. The isotopic niche of adult females (dark red) and males (dark blue) are displayed for a better comparison. Solid lines correspond to the SEAc of each group. Convex hull areas are represented in dotted lines, as a reference.
Ontogeny of sexual isotopic niche segregation

During lactation, males and females exhibited similar δ^{13}C and δ^{15}N values (δ^{13}C: -18.9 ± 0.4‰ and -18.5 ± 0.6‰, respectively, t_{6,4}=-1.14, P=0.29, δ^{15}N: 12.7 ± 0.4‰ and 12.8 ± 0.3‰, respectively, t_{6,4}=-0.91, P=0.39). At weaning, all seals of both sexes exhibited an abrupt drop in their δ^{13}C and δ^{15}N values (Fig. 3.1). However, the drop was more pronounced in males, such that males had lower values than females during their first year (δ^{13}C: -22.2 ± 1.3‰ and -21.0 ± 0.8‰, δ^{15}N: 9.0 ± 0.9‰ and 10.2 ± 0.4‰, respectively).

Males and females exhibited a complete niche differentiation at all life-stages, except for age 1 where the overlap was 18 and 29% for males and females, respectively (Fig. 3.3, Table 3.2). While the two sexes varied in both δ^{13}C and δ^{15}N values at age 0, sexual segregation occurred exclusively along the δ^{13}C axis later in seals’ development, with males exhibiting consistently lower δ^{13}C values than females (Table 3.1). Young males occupied a larger isotopic space than females at early stages (ages 0 and 1), and at age 4 (Table 3.2). However, individual niches were similar in size (Table S3.2), denoting either (i) smaller sample sizes at the individual level (lack of statistical power) and/or (ii) greater inter-individual variation in isotopic niche between males (Fig. S3.3).

Full-size breeding males and females exhibited a complete segregation in their respective isotopic niche (Fig. 3.3). Variation occurred along two axes: (i) adult males had depleted ^{13}C values compared to adult females, but no difference in average δ^{15}N values (Table 3.1); and (ii) adult males showed a much wider isotopic niche than breeding females, both at the population and individual levels (4.5 and 6.9 times larger, respectively, Figs. 3.3 and S3.3).
3. Ontogeny of Sexual Segregation

**Figure 3.3 Sexual segregation in isotopic niche at each class-age.** Young males and females are represented in light blue and orange, respectively, and full-size territorial males and breeding females are represented in dark blue and dark red, respectively. Solid lines correspond to the SEAc of each group. Convex hull areas are represented in dotted lines, as a reference.
Table 3.2 Sexual variation in two-dimension isotopic niche, at each age-class. Sexual segregation was estimated as the percentage of overlap between males’ and females’ SEAc and variation in SEAc size. Variation in SEAc size was statistically estimated using $10^4$ posteriori draws.

<table>
<thead>
<tr>
<th>Class-age</th>
<th>SEAc Overlap (%)</th>
<th>SEAc size (%$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Age 0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 1</td>
<td>18</td>
<td>29</td>
</tr>
<tr>
<td>Age 2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Age 4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adults</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Discussion

The whisker stable isotope patterns observed in the present study depict for the first time the early-life of individual pinnipeds, documenting the ontogenetic patterns of habitat and resource-use and revealing new insights into cryptic stages of a seal’s life. The sexual niche differentiation of Antarctic fur seals is a rather abrupt process occurring early after weaning being, thus, mostly decoupled from sexual size dimorphism. Foraging ecology appears strongly linked to sex-specific life-history traits. In the earlier maturing and breeding sex (females), young individuals shared the isotopic (ecological) niche of adults at 1-2 years old, while the later maturing and breeding sex (males) shifts more progressively their isotopic niche to that of adults. In males, there was a temporal decoupling between the isotopic niche at sexual maturity and reproduction with the mature (5-years-old) individuals occupying only a part of the isotopic niche of the territorial bulls. As adult males and females are characterised by dramatic differences in life-history traits, comparing the ontogenetic trajectories of individuals sampled the same year (i.e. experiencing the same environmental
conditions) enabled factors influencing seals to change their foraging ecology as they age, as well as the driving forces shaping sexual segregation to be investigated.

**Ontogeny of female isotopic niche**

Female Antarctic fur seals exhibited a rapid change in their isotopic niche as they aged, from a complete segregation with adults during their first year at-sea, to a similar isotopic niche as soon as they reached the age of 2. This early-life ontogenic shift occurred exclusively along the $\delta^{13}C$ axis. Weaning was characterised in every sampled females by an abrupt drop in carbon values, such that there was no overlap between YOY and adults’ $\delta^{13}C$ values. In the Southern Ocean, lower latitude plankton food bases are enriched in $^{13}C$ relative to higher latitude waters (François et al. 1993), a latitudinal gradient also reflected in top order predators (Cherel & Hobson 2007, Jaeger et al. 2010). Results indicate females travelled south of the breeding colony at weaning, and foraged exclusively in Antarctic waters south of the Polar Front. Such spatial segregation could potentially denote an early-life exploration phase in females, or reflect YOY exploiting more productive foraging grounds further away from the breeding colony as they are not spatially constrained, unlike breeding females. Alternatively, niche differentiation could be the result of social exclusion, YOY exploiting sub-optimal foraging areas as they are excluded from higher quality grounds by older dominant individuals (Ebenman 1987, Sol et al. 2000).

Surprisingly, the sampled females exhibited no variation in $\delta^{15}N$ values as they aged. YOY females fed at the same trophic level as adult breeding females, suggesting that females primarily forage on myctophid fish throughout their life (Cherel et al. 1997, Cherel et al. 2007, Kernaléguen et al. 2015a). In many species, individuals show an ontogenetic variation in their diet, be it a sudden shift or a progressive change. Temporal change in feeding behaviour is often observed when specific foraging skills
are required to capture prey (Estes et al. 2003), prey size is directly linked to predator’s size (Shine et al. 1998), and/or individuals differ in their food requirements depending on their breeding status (Carlisle et al. 2015) or growth rate (Stewart 1997). However, in the present study, small and naïve females fed at the same trophic level, and most probably upon the same prey, just after the weaning period compared to when they became older, larger breeding females.

**Ontogeny of male isotopic niche**

Unlike females which displayed a rather abrupt early-life ontogenetic shift, males exhibited a more progressive change in their isotopic niche with age. YOY males exhibited very low $\delta^{13}$C and $\delta^{15}$N values straight after weaning, corresponding to the lowest extent of the isotopic niche of territorial bulls. This indicates the sampled males travelled south after weaning, up to the southern foraging grounds of breeding bulls in Antarctic waters where they fed at least partly on low-trophic level prey, likely Antarctic krill (*Euphausia superba*), as indicated by their relatively low $\delta^{15}$N values (Cherel et al. 2009, Kernaléguen et al. 2012). Following their first year at-sea, young males foraged in northern areas where krill is not as abundant and fed at the same trophic level as females. Young males’ $\delta^{15}$N values increased progressively with age, and 5-year-old males exhibited lower isotopic values than breeding males when foraging within similar water masses, indicating that males feed on higher trophic level as they get older, larger and more experienced.

Furthermore, while females occupied a similar isotopic niche as adults as soon as the age of 2, 5-year-old males did not share yet the same foraging niche as full-size territorial bulls. Adults exhibited (i) higher $\delta^{15}$N values when feeding in the same water masses, and (ii) an extreme range of $\delta^{13}$C and $\delta^{15}$N values, encompassing young males’
3. Ontogeny of Sexual Segregation

isotopic niche. Indeed, territorial bulls exhibited synchronous peaks in $\delta^{13}C$ and $\delta^{15}N$ values. These atypical high isotopic values were not present in young males and were observed exclusively during the most recent years in breeding adults’ whiskers (Fig. S3.1), suggesting peaks are associated with reproduction. While physiological variation or the latitudinal gradient are unlikely to explain these values, isotopic results are more likely to depict a benthic foraging behaviour on the continental shelf around the breeding colony, with benthic consumers consistently showing high $\delta^{13}C$ and $\delta^{15}N$ values (France 1995, Cherel & Hobson 2007). Accordingly, two tracking studies on full-size male Antarctic fur seals have shown they displayed benthic dives on the continental shelf during the mating season (Green 1997, Staniland & Robinson 2008). Benthic foraging behaviour appears late in males’ development, most probably when they start holding territories. Breeding status of males, and not females, thus drives foraging strategies, as recently demonstrated in another species of the Southern Ocean, the wandering albatross (Jaeger et al. 2014).

Males and females showed contrasted ontogenetic trajectories which mirror their respective growth and reproductive status development. Indeed, females achieve 90% of their growth by the age of 4 (Payne 1979), and the majority of them first give birth at 3 or 4 (Lunn et al. 1994). Hence, the first females to reproduce are gestating at 2, and meet most of the nutritional and energetic requirements of full-size breeding adults with which they share the same isotopic niche. In contrast, males grow constantly until the age of 7 (Payne 1979), when the dominant individuals start to hold territories and reproduce. As they dramatically but progressively increase in body size, they vary in their energetic requirements and ability to catch larger prey. Furthermore, body size is directly related to an individual’s oxygen stores which determine its aerobic dive limit (Kleiber 1961) and, thus, the extent of the water column that can be
efficiently exploited. In particular, males need to have a sufficient body size in order to have the physiological requirements to reach the seabed over the Kerguelen shelf.

**Ontogeny of sexual segregation**

Comparison of the isotopic niche of full-size males and females confirmed the presence of strong sexual segregation in dimorphic breeding adults of Antarctic fur seals at Kerguelen, as previously described elsewhere (Cherel et al. 2007, Staniland & Robinson 2008, Kernaléguen et al. 2012). In particular, males exhibited lower $\delta^{13}C$ values indicating they foraged in Antarctic waters most of the breeding cycle while females remained closer to the breeding colony. Sexual size dimorphism and contrasting breeding strategies have often been proposed as the main factors explaining sexual segregation in Antarctic fur seals (Cherel et al. 2007, Staniland & Robinson 2008, Kernaléguen et al. 2012), and other otariids (Page et al. 2005b, Franco-Trecu et al. 2014, Kernaléguen et al. 2015b). This suggests males and females should exhibit a similar foraging niche during their early development, and diverge in their feeding behaviour and diet as size dimorphism increases and/or seals start to reproduce (Stewart 1997, Chaigne et al. 2013).

Interestingly however, males and females showed a complete segregation in their isotopic niche straight after weaning, when size dimorphism is minimal (between 0 and 15%, Lunn et al. 1993) and seals do not face any breeding constraints. Variation in $\delta^{13}C$ values was of similar amplitude as observed in breeding adults and niche differentiation was maintained throughout seals’ development until they reached sexual maturity. Variation in foraging grounds between weaned males and females has previously been reported in Antarctic fur seals breeding at Bird Island (Warren et al. 2006). However, while males travelled on average further west and further away from
the breeding beaches than females, both sexes exhibited a great overlap in their respective foraging location. Furthermore, males and females, which were tracked in different years, remained in the vicinity of the breeding island: on average <150 km the first month, <360 km the first three months, and foraged both over and beyond the continental shelf during that period (Warren et al. 2006). In contrast, in the present study, the abrupt drop in $\delta^{13}$C values observed at weaning (drop of 3.7 and 2.8‰ in males and females, respectively) suggests that all sampled individuals left the Kerguelen shelf at weaning, foraged south of the Polar Front, in the Antarctic Zone, and that males travelled longer distances and foraged further south than females.

Such an early development of sexual niche differentiation is a surprising and unusual pattern. Studies across various taxa have shown that, in most cases, when sexual segregation occurs between adults, male and female juveniles share the same ecological niche (e.g. Haraldstad & Jonsson 1983, Bon et al. 2001, Bailleul et al. 2010, Jaeger et al. 2014). When the timing of niche differentiation could be identified, some studies highlighted factors likely to explain sexual segregation in adults, such as body size (Shine et al. 1998, Vincent et al. 2004), growth rate (Stewart 1997), or social interactions (behavioural dominance hypothesis, Marra 2000, Catry et al. 2004). Why then do male and female Antarctic fur seals segregate as soon as they wean? During lactation, mothers of males and females exploited a similar isotopic niche and weaned pups foraged independently from their mother or elders (McCafferty et al. 1998), thus excluding all vertical transmission hypotheses.

It is possible that small size difference at weaning and/or variation in behaviour between males and females could enable male YOY to exclude female YOY from their foraging grounds. Alternatively, niche segregation in weaned pups could be the result of differential nutritional needs between the two sexes. Indeed, Antarctic fur seal
pups are known to already diverge in the way they utilise the energy delivered by their mother during lactation (Arnould et al. 1996). While there is no difference in maternal investment depending on the sex of the offspring (in terms of milk composition or amount of delivered milk), male and female pups differ in their body composition at weaning. Females accumulate greater body lipid reserves than males which direct more energy into lean tissue growth (Arnould et al. 1996). Hence, it is likely that after lactation, males would continue to favour growth and target protein rich prey, while females would favour survival during this high mortality post-weaning phase and target more lipid rich prey. Accordingly, the main myctophid fish species eaten by breeding females in Kerguelen have high protein but also lipid content (Gymnoscopelus nicholsi: 18% of wet mass, G. fraseri: 12%, Electrona subaspera: 9%, Lea et al. 2002), which contrasts with the low lipid content of Antarctic krill (2 to 6% of wet mass, Clarke 1980).

Furthermore, males and females might vary in their respective post-weaning dispersal behaviour. Indeed, males might benefit from exploring a greater diversity of foraging grounds while a more profitable strategy for females would be to gain rapidly knowledge on the local area by staying closer to the breeding colony. Accordingly, the sampled males exploited an isotopic niche five times larger than females and exhibited more inter-individual variation. Hence, it is likely that males and females differ in their dietary and dispersal benefits in preparation to future requirements. Selective pressures might favour females that gain rapidly local knowledge of foraging habitats closer to the breeding colony and allocate more resource in survival than growth. In contrast, a more beneficial strategy for males might be a broader and exploratory dispersal and a diet that favour a rapid growth, as soon as weaning, resulting in an early-stage sexual segregation. While it is often difficult to distinguish between innate and learned behaviour (Riotte-Lambert & Weimerskirch 2013), the abruptness and consistency of
δ¹³C and δ¹⁵N drops at weaning, in every sampled individuals, suggest that early-life foraging is an innate behaviour and that sexual segregation is caused by differential innate resource preferences by the two sexes. While the ultimate drivers of this segregation still need to be investigated, the present study reveals that size dimorphism and breeding constraints are, surprisingly, not the main factors shaping sexual niche differentiation in the Antarctic fur seals.
Supplementary Material

Methods S1. Measurement of sexual niche differentiation at the individual level.

Comparisons at the individual level provide an estimation of the average segregation between age-classes (for each individual) or between a male and a female. The SEAc of each individual seal was estimated. For comparison between age-classes, the same individuals were compared over the years, so that the overlap was defined as the average overlap between the SEAc of an individual at different ages. For comparison between young and adult seals or between the sexes, the overlap was defined as the average overlap between the SEAc of an individual of each group. The index was calculated on $10^4$ pairs randomly chosen. Finally, the SEAc size of a group was measured as the average SEAc size of each individual. Variation in SEAc size between the two groups was calculated by comparing the SEAc size of $10^4$ pairs (one individual of each group) randomly chosen.
3. Ontogeny of Sexual Segregation

Figure S3.1 Whisker $\delta^{13}$C (filled circles) and $\delta^{15}$N (open circles) values of one representative young and full-size breeding male and female (C and D). All young individuals presented high $\delta^{15}$N values in the tip (i.e. oldest part displayed on the left) of the whisker, followed by an abrupt drop of both $\delta^{13}$C and $\delta^{15}$N values, corresponding to the lactation and weaning periods, respectively. The young male in (A) was a tagged 5-year-old seal.
Figure S3.2 Ontogenetic changes in the isotopic niche of female (orange) and male (light blue) Antarctic fur seals during the first 5 years of life. The isotopic niche of adult females (dark red) and males (dark blue) are displayed for a better comparison. The SEAc of each individual is displayed using a solid line, while the dotted lines indicate the corresponding convex hull areas of the whole group, as a reference.
Figure S3.3 Sexual segregation in isotopic niche at each class-age. Young males and females are represented in light blue and orange, respectively, and full-size territorial males and breeding females are represented in dark blue and dark red, respectively. The SEAc of each individual is displayed using a solid line, while the dotted lines indicate the corresponding convex hull areas of the whole group, as a reference.
### Table S3.1 Whisker length and estimated growth rate. Results are mean ± SD.

<table>
<thead>
<tr>
<th></th>
<th>Length (mm)</th>
<th>Growth rate (mm·d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young males</td>
<td>170 ± 38</td>
<td>0.09 ± 0.03</td>
</tr>
<tr>
<td>Young females</td>
<td>134 ± 15</td>
<td>0.07 ± 0.01</td>
</tr>
<tr>
<td>Adult males</td>
<td>261 ± 68</td>
<td>0.11 ± 0.03</td>
</tr>
<tr>
<td>Adult females</td>
<td>166 ± 21</td>
<td>0.06 ± 0.01</td>
</tr>
</tbody>
</table>
Table S3.2 Sexual variation in two-dimension isotopic niche, at each age-class, at the individual level. Sexual segregation was estimated as the percentage of overlap between males’ and females’ SEAc and variation in SEAc size. Analyses were performed at the individual level which corresponds to the average segregation between one individual of each sex.

<table>
<thead>
<tr>
<th>Class-age</th>
<th>SEAc Overlap (%)</th>
<th>SEAc size (‰²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Age 0</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Age 1</td>
<td>13</td>
<td>15</td>
</tr>
<tr>
<td>Age 2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Age 3</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Age 4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adults</td>
<td>2</td>
<td>13</td>
</tr>
</tbody>
</table>
3. Ontogeny of Sexual Segregation

Table S3.3 Ontogenetic changes in females’ isotopic niche during the first 5 years of life. Niche variation was estimated by the niche overlap (down left values) and variation in niche size (SEAc size in brackets (‰²), with top right values presenting the P value corresponding of the comparison of SEAc sizes) using the Bayesian ellipse-based metrics SIBER. Overlap values are given as the percentage of overlap over the total niche area of a given class-age. The first value is the overlap of the youngest age-class over the oldest, and the second value corresponds to the overlap of the oldest age-class over the youngest. Analyses were performed at the population and individual levels (see Methods).

<table>
<thead>
<tr>
<th>Population level</th>
<th>Age 0 (0.5)</th>
<th>Age 1 (1.4)</th>
<th>Age 2 (1.2)</th>
<th>Age 3 (1.7)</th>
<th>Age 4 (0.5)</th>
<th>Adult (1.3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age 0 (0.5)</td>
<td>0.04</td>
<td>0.15</td>
<td>0.01</td>
<td>0.13</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>Age 1 (1.4)</td>
<td>0 / 0</td>
<td>0.18</td>
<td>0.20</td>
<td>&lt;0.001</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td>Age 2 (1.2)</td>
<td>0 / 0</td>
<td>55 / 67</td>
<td>0.04</td>
<td>0.01</td>
<td>0.36</td>
<td></td>
</tr>
<tr>
<td>Age 3 (1.7)</td>
<td>0 / 0</td>
<td>71 / 57</td>
<td>87 / 57</td>
<td>&lt;0.001</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>Age 4 (0.5)</td>
<td>0 / 0</td>
<td>21 / 57</td>
<td>27 / 61</td>
<td>29 / 98</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Adult (1.3)</td>
<td>0 / 0</td>
<td>46 / 51</td>
<td>58 / 53</td>
<td>65 / 90</td>
<td>92 / 37</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Individual level</th>
<th>Age 0 (0.1)</th>
<th>Age 1 (1.0)</th>
<th>Age 2 (0.7)</th>
<th>Age 3 (1.1)</th>
<th>Age 4 (0.5)</th>
<th>Adult (0.8)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age 0 (0.1)</td>
<td>0.50</td>
<td>0.40</td>
<td>0.49</td>
<td>0.32</td>
<td>0.38</td>
<td></td>
</tr>
<tr>
<td>Age 1 (1.0)</td>
<td>0 / 0</td>
<td>0.38</td>
<td>0.49</td>
<td>0.29</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>Age 2 (0.7)</td>
<td>0 / 0</td>
<td>30 / 41</td>
<td>0.39</td>
<td>0.40</td>
<td>0.48</td>
<td></td>
</tr>
<tr>
<td>Age 3 (1.1)</td>
<td>0 / 0</td>
<td>25 / 23</td>
<td>59 / 39</td>
<td>0.29</td>
<td>0.36</td>
<td></td>
</tr>
<tr>
<td>Age 4 (0.5)</td>
<td>0 / 0</td>
<td>12 / 27</td>
<td>25 / 41</td>
<td>19 / 47</td>
<td>0.45</td>
<td></td>
</tr>
<tr>
<td>Adult (0.8)</td>
<td>0 / 0</td>
<td>15 / 20</td>
<td>18 / 17</td>
<td>17 / 25</td>
<td>22 / 13</td>
<td></td>
</tr>
</tbody>
</table>
Table S3.4 Age-dependent changes in whisker $\delta^{13}C$ and $\delta^{15}N$ values of females. T-tests were performed using mixed effect models to account for the repeated measurements for each individual (random effect) and the time-correlation of the data (auto-correlation coefficient).

<table>
<thead>
<tr>
<th>$\delta^{13}C$ (‰)</th>
<th>Age 0</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
<th>Age 4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(-20.9 ± 0.3)</td>
<td>(-19.4 ± 0.5)</td>
<td>(-19.1 ± 0.4)</td>
<td>(-18.9 ± 0.4)</td>
<td>(-18.6 ± 0.4)</td>
</tr>
<tr>
<td>Age 0 (-20.9 ± 0.3)</td>
<td>$t_{222,222}=7.69$</td>
<td>$t_{222,222}=9.80$</td>
<td>$t_{222,222}=10.29$</td>
<td>$t_{222,222}=14.15$</td>
<td>$t_{222,222}=19.58$</td>
</tr>
<tr>
<td>Age 1 (-19.4 ± 0.5)</td>
<td>$t_{222,222}=7.69$ (0.001)</td>
<td>$t_{222,222}=9.80$ (0.001)</td>
<td>$t_{222,222}=10.29$ (0.001)</td>
<td>$t_{222,222}=14.15$ (0.001)</td>
<td>$t_{222,222}=19.58$ (0.001)</td>
</tr>
<tr>
<td>Age 2 (-19.1 ± 0.4)</td>
<td>$t_{222,222}=7.69$ (0.001)</td>
<td>$t_{222,222}=9.80$ (0.001)</td>
<td>$t_{222,222}=10.29$ (0.001)</td>
<td>$t_{222,222}=14.15$ (0.001)</td>
<td>$t_{222,222}=19.58$ (0.001)</td>
</tr>
<tr>
<td>Age 3 (-18.9 ± 0.4)</td>
<td>$t_{222,222}=7.69$ (0.001)</td>
<td>$t_{222,222}=9.80$ (0.001)</td>
<td>$t_{222,222}=10.29$ (0.001)</td>
<td>$t_{222,222}=14.15$ (0.001)</td>
<td>$t_{222,222}=19.58$ (0.001)</td>
</tr>
<tr>
<td>Age 4 (-18.6 ± 0.4)</td>
<td>$t_{222,222}=7.69$ (0.001)</td>
<td>$t_{222,222}=9.80$ (0.001)</td>
<td>$t_{222,222}=10.29$ (0.001)</td>
<td>$t_{222,222}=14.15$ (0.001)</td>
<td>$t_{222,222}=19.58$ (0.001)</td>
</tr>
<tr>
<td>Adult (-18.8 ± 0.5)</td>
<td>$t_{222,222}=7.69$ (0.001)</td>
<td>$t_{222,222}=9.80$ (0.001)</td>
<td>$t_{222,222}=10.29$ (0.001)</td>
<td>$t_{222,222}=14.15$ (0.001)</td>
<td>$t_{222,222}=19.58$ (0.001)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$\delta^{15}N$ (‰)</th>
<th>Age 0</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
<th>Age 4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(10.3 ± 0.4)</td>
<td>(10.5 ± 0.3)</td>
<td>(10.3 ± 0.3)</td>
<td>(10.6 ± 0.3)</td>
<td>(10.6 ± 0.3)</td>
</tr>
<tr>
<td>Age 0 (10.3 ± 0.4)</td>
<td>$t_{222,222}=1.42$ (0.16)</td>
<td>$t_{222,222}=0.29$ (0.77)</td>
<td>$t_{222,222}=1.91$ (0.06)</td>
<td>$t_{222,222}=2.51$ (0.01)</td>
<td>$t_{222,222}=1.39$ (0.20)</td>
</tr>
<tr>
<td>Age 1 (10.5 ± 0.3)</td>
<td>$t_{222,222}=1.42$ (0.16)</td>
<td>$t_{222,222}=0.29$ (0.77)</td>
<td>$t_{222,222}=1.91$ (0.06)</td>
<td>$t_{222,222}=2.51$ (0.01)</td>
<td>$t_{222,222}=1.39$ (0.20)</td>
</tr>
<tr>
<td>Age 2 (10.3 ± 0.3)</td>
<td>$t_{222,222}=1.42$ (0.16)</td>
<td>$t_{222,222}=0.29$ (0.77)</td>
<td>$t_{222,222}=1.91$ (0.06)</td>
<td>$t_{222,222}=2.51$ (0.01)</td>
<td>$t_{222,222}=1.39$ (0.20)</td>
</tr>
<tr>
<td>Age 3 (10.6 ± 0.3)</td>
<td>$t_{222,222}=1.42$ (0.16)</td>
<td>$t_{222,222}=0.29$ (0.77)</td>
<td>$t_{222,222}=1.91$ (0.06)</td>
<td>$t_{222,222}=2.51$ (0.01)</td>
<td>$t_{222,222}=1.39$ (0.20)</td>
</tr>
<tr>
<td>Age 4 (10.6 ± 0.3)</td>
<td>$t_{222,222}=1.42$ (0.16)</td>
<td>$t_{222,222}=0.29$ (0.77)</td>
<td>$t_{222,222}=1.91$ (0.06)</td>
<td>$t_{222,222}=2.51$ (0.01)</td>
<td>$t_{222,222}=1.39$ (0.20)</td>
</tr>
<tr>
<td>Adult (10.7 ± 0.6)</td>
<td>$t_{222,222}=1.42$ (0.16)</td>
<td>$t_{222,222}=0.29$ (0.77)</td>
<td>$t_{222,222}=1.91$ (0.06)</td>
<td>$t_{222,222}=2.51$ (0.01)</td>
<td>$t_{222,222}=1.39$ (0.20)</td>
</tr>
</tbody>
</table>
### Table S3.5 Ontogenetic changes in males’ isotopic niche during the first 5 years of life.

Niche variation was estimated by the niche overlap (down left values) and variation in niche size (SEAc size in brackets (‰²), with top right values presenting the P value corresponding of the comparison of SEAc sizes) using the Bayesian ellipse-based metrics SIBER. Overlap values are given as the percentage of overlap over the total niche area of a given class-age. The first value is the overlap of the youngest age-class over the oldest, and the second value corresponds to the overlap of the oldest age-class over the youngest. Analyses were performed at the population and individual levels (see Methods).

<table>
<thead>
<tr>
<th>Age level</th>
<th>Age 0 (2.8)</th>
<th>Age 1 (2.2)</th>
<th>Age 2 (1.2)</th>
<th>Age 3 (1.5)</th>
<th>Age 4 (2.2)</th>
<th>Adult (5.8)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population level</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age 0 (2.8)</td>
<td>0.16</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.14</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Age 1 (2.2)</td>
<td>32 / 40</td>
<td>&lt;0.001</td>
<td>0.01</td>
<td>0.45</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Age 2 (1.2)</td>
<td>3 / 7</td>
<td>30 / 54</td>
<td>0.14</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Age 3 (1.5)</td>
<td>0 / 0</td>
<td>14 / 20</td>
<td>69 / 56</td>
<td>0.01</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Age 4 (2.2)</td>
<td>17 / 21</td>
<td>14 / 14</td>
<td>35 / 19</td>
<td>49 / 34</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Adult (5.8)</td>
<td>0 / 0</td>
<td>2 / 1</td>
<td>41 / 9</td>
<td>75 / 19</td>
<td>74 / 28</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Individual level</th>
<th>Age 0 (0.8)</th>
<th>Age 1 (1.1)</th>
<th>Age 2 (0.8)</th>
<th>Age 3 (1.1)</th>
<th>Age 4 (1.3)</th>
<th>Adult (5.5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age 0 (0.8)</td>
<td>0.46</td>
<td>0.35</td>
<td>0.33</td>
<td>0.48</td>
<td>0.14</td>
<td></td>
</tr>
<tr>
<td>Age 1 (1.1)</td>
<td>7 / 5</td>
<td>0.35</td>
<td>0.42</td>
<td>0.46</td>
<td>0.08</td>
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<tr>
<td>Age 2 (0.8)</td>
<td>9 / 10</td>
<td>13 / 19</td>
<td>0.48</td>
<td>0.33</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>Age 3 (1.1)</td>
<td>15 / 11</td>
<td>5 / 5</td>
<td>51 / 38</td>
<td>0.33</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>Age 4 (1.3)</td>
<td>6 / 4</td>
<td>3 / 2</td>
<td>20 / 12</td>
<td>29 / 24</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td>Adult (5.5)</td>
<td>11 / 2</td>
<td>12 / 2</td>
<td>37 / 10</td>
<td>54 / 10</td>
<td>53 / 12</td>
<td></td>
</tr>
</tbody>
</table>
Table S3.6 Age-dependent changes in whisker $\delta^{13}C$ and $\delta^{15}N$ values of males. T-tests were performed using mixed effect models to account for the repeated measurements for each individual (random effect) and the time-correlation of the data (auto-correlation coefficient).

<table>
<thead>
<tr>
<th>Age 0 (-22.2 ± 0.7)</th>
<th>Age 1 (-21.0 ± 0.7)</th>
<th>Age 2 (-20.9 ± 0.6)</th>
<th>Age 3 (-20.9 ± 0.6)</th>
<th>Age 4 (-21.8 ± 0.6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta^{13}C (‰)$</td>
<td>$\delta^{15}N (‰)$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Age 0 (9.0 ± 0.4)</strong></td>
<td><strong>Age 1 (9.8 ± 0.4)</strong></td>
<td><strong>Age 2 (10.3 ± 0.4)</strong></td>
<td><strong>Age 3 (10.6 ± 0.4)</strong></td>
<td><strong>Age 4 (10.1 ± 0.4)</strong></td>
</tr>
<tr>
<td>Age 0 (9.0 ± 0.4)</td>
<td>Age 1 (9.8 ± 0.4)</td>
<td>Age 2 (10.3 ± 0.4)</td>
<td>Age 3 (10.6 ± 0.4)</td>
<td>Age 4 (10.1 ± 0.4)</td>
</tr>
<tr>
<td>$\delta^{13}C (‰)$</td>
<td>$\delta^{15}N (‰)$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Age 0 (9.0 ± 0.4)</strong></td>
<td><strong>Age 1 (9.8 ± 0.4)</strong></td>
<td><strong>Age 2 (10.3 ± 0.4)</strong></td>
<td><strong>Age 3 (10.6 ± 0.4)</strong></td>
<td><strong>Age 4 (10.1 ± 0.4)</strong></td>
</tr>
<tr>
<td>Age 0 (9.0 ± 0.4)</td>
<td>Age 1 (9.8 ± 0.4)</td>
<td>Age 2 (10.3 ± 0.4)</td>
<td>Age 3 (10.6 ± 0.4)</td>
<td>Age 4 (10.1 ± 0.4)</td>
</tr>
<tr>
<td>$\delta^{13}C (‰)$</td>
<td>$\delta^{15}N (‰)$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Age 0 (9.0 ± 0.4)</strong></td>
<td><strong>Age 1 (9.8 ± 0.4)</strong></td>
<td><strong>Age 2 (10.3 ± 0.4)</strong></td>
<td><strong>Age 3 (10.6 ± 0.4)</strong></td>
<td><strong>Age 4 (10.1 ± 0.4)</strong></td>
</tr>
<tr>
<td>Age 0 (9.0 ± 0.4)</td>
<td>Age 1 (9.8 ± 0.4)</td>
<td>Age 2 (10.3 ± 0.4)</td>
<td>Age 3 (10.6 ± 0.4)</td>
<td>Age 4 (10.1 ± 0.4)</td>
</tr>
<tr>
<td>$\delta^{13}C (‰)$</td>
<td>$\delta^{15}N (‰)$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Age 0 (9.0 ± 0.4)</strong></td>
<td><strong>Age 1 (9.8 ± 0.4)</strong></td>
<td><strong>Age 2 (10.3 ± 0.4)</strong></td>
<td><strong>Age 3 (10.6 ± 0.4)</strong></td>
<td><strong>Age 4 (10.1 ± 0.4)</strong></td>
</tr>
<tr>
<td>Age 0 (9.0 ± 0.4)</td>
<td>Age 1 (9.8 ± 0.4)</td>
<td>Age 2 (10.3 ± 0.4)</td>
<td>Age 3 (10.6 ± 0.4)</td>
<td>Age 4 (10.1 ± 0.4)</td>
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CHAPTER 4

Sexual Niche Segregation and Gender-Specific Individual Specialisation in a Highly Dimorphic Marine Mammal

A version of this chapter has been published as:

Abstract

While sexual segregation is expected in highly dimorphic species, the local environment is a major factor driving the degree of resource partitioning within a population. Sexual and individual niche segregation was investigated in the Australian fur seal (*Arctocephalus pusillus doriferus*), which is a benthic foraging species restricted to the shallow continental shelf region of south-eastern Australia. Tracking data and the isotopic values of plasma, red blood cells and whiskers were combined to document spatial and dietary niche segregation throughout the year. Tracking data indicated that, in winter, males and females overlapped in their foraging habitat. All individuals stayed within central Bass Strait, relatively close (< 220 km) to the breeding colony. Accordingly, both genders exhibited similar plasma and red cell δ¹³C values. However, males exhibited greater δ¹³C intra-individual variation along the length of their whisker than females. This suggests that males exploited a greater diversity of foraging habitats throughout the year than their female counterparts which are restricted in their foraging grounds by the need to regularly return to the breeding colony to suckle their pup. The degree of dietary sexual segregation was also surprisingly low, both sexes exhibiting a great overlap in their δ¹⁵N values. Yet, males displayed higher δ¹⁵N values than females, suggesting they fed upon a higher proportion of higher trophic level prey. Given that males and females exploit different resources (mainly foraging habitats), the degree of individual specialisation might differ between the sexes. Higher degrees of individual specialisation would be expected in males which exploit a greater range of resources. However, comparable levels of inter-individual variation in δ¹⁵N whisker values were found in the sampled males and females, and, surprisingly, all males exhibited similar seasonal and inter-annual variation in their δ¹³C whisker values, suggesting they all followed the same general dispersion pattern throughout the year.
Introduction

The extent to which different individuals of a same population vary in their resource use is an important feature in foraging ecology. Resource partitioning at the population level has been observed in a wide range of taxa, particularly in the context of sexual segregation (Shine 1989, Ruckstuhl & Neuhaus 2005). Given that males and females often vary in their morphology, physiology and/or life history constraints, they might not have the same dietary requirements, activity budget and/or meet the same selection criteria in their respective foraging strategy. For example, sexual segregation in trophic niche is often associated with sexual dimorphism (Mysterud 2000, Kamilar & Pokempner 2008). Larger individuals (often males) have higher energetic needs, can potentially have access to a larger range of prey, or exclude conspecifics from favourable patches through dominance interactions (Clutton-Brock & Guinness 1982, Marra 2000, Bearhop et al. 2006).

Conspecifics of the same sex might also differ in their foraging behaviour (Bolnick et al. 2003, Araújo et al. 2011). While individual specialisation is, in most cases, investigated at the population level, the degree of specialisation may vary within males and females (Kernaléguen et al. 2012, Elliott Smith et al. 2015). Indeed, when foraging in different habitats, upon different prey, or during different time-periods, the two sexes may have access to a contrasting range of resources and experience distinct levels of competition and predation that will influence the degree of specialisation among individuals (Svanbäck & Bolnick 2005, Araújo et al. 2011, Kernaléguen et al. 2015a). For example, in sea otters (*Enhydra lutris nereis*) females are restricted in their foraging grounds by the necessity to come back regularly to the breeding location to feed their offspring (Elliott Smith et al. 2015). In areas of high population density, they experience a higher degree of intra-specific competition than males and exhibit higher
individual variation in diet. However, only a limited number of studies has investigated gender-specific degree of individual specialisation within a population (Kernaléguen et al. 2012, Elliott Smith et al. 2015).

Otariids (fur seals and sea lions) show extreme sexual dimorphism with males weighing two to four times the mass of females (Staniland 2005). Furthermore, their reproductive strategy induces very different constraints on male and female foraging behaviour. Specifically, while males do not provide any parental care and can disperse after the mating period, females suckle their young for the duration of the lactation (4 to 36 mo) (Bonner 1984). Hence, adult female otariids need to regularly return to their breeding colony to provision dependent offspring and are spatially constrained in foraging trip distance and duration by the fasting ability of their young. Accordingly, differences in foraging behaviour have been observed between the sexes in several species of otariids, both in terms of (i) habitat use (horizontal and/or vertical segregation), with males typically foraging further away from the breeding colonies and diving deeper than females (Boyd et al. 1998, Loughlin et al. 1999, Campagna et al. 2001, Page et al. 2005b, Staniland & Robinson 2008), and (ii) diet, with males feeding upon larger prey of higher trophic level compared to females (Page et al. 2005a, Cherel et al. 2007, Kernaléguen et al. 2012, but see Franco-Trecu et al. 2014). As male otariids have potentially access to a wider range of resources than females, they should exhibit a wider trophic niche associated with a higher level of individual variation (Araújo et al. 2011, Kernaléguen et al. 2015a). However, comparison of the degree of individual specialisation between sexes have previously only been documented in two sympatric fur seal species, of which the study revealed contrasting results (Kernaléguen et al. 2012).

The Australian fur seal (Arctocephalus pusillus doriferus) is the largest fur seal species, with males and females weighing on average 279 kg and 76 kg, respectively
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(Warneke & Shaughnessy 1985). Given the contrasting energetic requirements and constraints of the two sexes, sexual diet segregation would be expected in this species (Mysterud 2000). However, the local environment is also a major factor driving the degree of resource partitioning within a population (Darimont et al. 2009). In particular, resources need to be diverse enough to provide the ecological opportunity for conspecifics to diverge in their foraging niche. While the foraging behaviour of male Australian fur seals is poorly known, both males and females appear to be benthic foragers, restricted in their foraging habitat to the shallow continental shelf region of south-eastern Australia (Hindell & Pemberton 1997, Kirkwood et al. 2006, Arnould & Kirkwood 2008). Therefore, this species represents an interesting model to investigate to what extent a highly dimorphic species, characterised with contrasting sexual breeding constraints, segregates at the sexual and individual levels, in a restricted environment. The degree of niche partitioning may vary in time, as constraints related to the annual cycle take effect (e.g. reproductive investment, migration) or the distribution and abundance of prey fluctuate (Phillips et al. 2004, Breed et al. 2006).

Hence, the aim the study were to investigate spatial and dietary sexual niche segregation in the Australian fur seal over different time-scales, and gender-specific individual specialisation over the long-term.

Material and Methods

Animal handling and data collection

The study was conducted in June-July 2013, while males do not have any mating or breeding constraint and adult females suckle their single pup and, thus, need to regularly come back to the breeding colony (on average every 6.8 ± 0.6 d, Arnould & Hindell 2001)). The Australian fur seal mating and pupping period occurs in
November – December, and lactation lasts 10–11 months although some females may nurse a pup for a second or even third year (Shaughnessy & Warneke 1984). Fieldwork was carried out on Kanowna Island (39º10’S, 146º18’E), northern Bass Strait, southeastern Australia. Bass Strait is a broad area of continental shelf between Tasmania and the Australian mainland, characterised by a shallow and even bathymetry (average 86 m) (Gibbs 1992). The six largest and most accessible males present in the colony were chemically restrained using tiletamine-zolazepam (Zoletil, Virbac, France; 1.5 mg/kg estimated weight), that was remotely administered using 1.5 cc darts (Pneu dart) and a CO2 powered tranquiliser gun (Dan Inject JM Standard) (Baylis et al. 2015). Anaesthesia was maintained using isoflurane delivered via a portable gas vaporizer (Stinger, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia). Six adult females suckling a pup were also captured using a modified hoop-net (Fuhrman Diversified, Flamingo, TX, USA), manually restrained and anaesthetised using isoflurane as described above.

Each seal was instrumented with a GPS data logger programmed to collect location data every 10 min (males: MK 10AF, Wildlife Computers, Redmond, WA, USA; females: FastLoc, Sirtrack, Havelock North, NZ) in order to assess the degree of overlap in foraging areas between sexes, and a small VHF transmitter (Sirtrack) to assist with recapture. Instruments were glued in series to the dorsal mid-line fur just behind the scapula using quick-setting two part epoxy (Accumix 268, Huntsmen, Texas, USA), and devices were retrieved by cutting the hair beneath the glue at recapture. At the first capture, standard length and axillary girth were measured (± 0.5 cm) using a tape measure. Females were weighed using a suspension scale (± 0.5 kg) while the mass of males was estimated from species- and sex-specific allometric relationship between body mass and morphometric measurements (standard length and axillary girth, Arnould & Warneke 2002). The longest whisker of each animal was
cut as close to the skin as possible and a blood sample was collected by venipuncture of an inter-digital vein in a hind-flipper. Red blood cells were separated from the plasma fraction and all blood samples were stored at -20ºC until isotopic analysis.

In the laboratory, whiskers were hand-washed in 100% ethanol and cleaned in an ultrasonic bath of distilled water for 5 minutes. Following Cherel et al. (2009), they were dried, measured and cut into 3 mm-long consecutive sections starting from the proximal (facial) end. Plasma and red blood cell samples were freeze-dried and ground into a fine powder. Since lipids can affect plasma δ¹³C values they were removed using a cyclohexane solvent (Cherel et al. 2005). The δ¹³C and δ¹⁵N values of each whisker section and blood samples were determined by a continuous flow mass spectrometer (Thermo Scientific, Delta V Advantage) coupled to an elemental analyser (Thermo Scientific, Flash EA 1112). Results are presented in the conventional δ notation relative to Vienna PeeDee Belemnite marine fossil limestone and atmospheric N₂ for δ¹³C and δ¹⁵N, respectively. Replicate measurements of internal laboratory standards indicated measurement errors < 0.10‰ for both δ¹³C and δ¹⁵N ratios.

Comparison of the spatial and isotopic niche

The 95% and 50% Utilisation Distribution (UD) probabilities were calculated for the 35 day period when male and female foraging trips overlapped. The Utilisation Distribution Overlap Index (UDOI) (Fieberg & Kochanny 2005) was then used to quantify the degree to which males and females shared foraging areas. Location data were filtered using a maximum swim speed of 8 m.s⁻¹ to remove erroneous locations (McConnell et al. 1992) and linearly interpolated every ten minutes. Smoothing parameters for the UD were calculated using the ad hoc method (Worton 1989) and bathymetry data were used as an habitat grid to avoid unrealistic UD probabilities.
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across land. The R packages trip and adehabitatHR (Calenge 2006) were used to perform these analyses.

Stable isotopes are increasingly used to studying the foraging ecology of wild animals (Kelly 2000, Newsome et al. 2007). The δ^{13}C values provide a proxy of a predator’s foraging habitat (Hobson 1999, Kelly 2000), and δ^{15}N values can be used to infer its trophic level (DeNiro & Epstein 1981). Different time-scales can be examined by using tissues with different turnover rates (Dalerum & Angerbjorn 2005). Although no turnover rates have been published for fur seals, plasma and red blood cells have half-lives of 4 and 28 days in black bear (*Ursus americanus*) (Hilderbrand et al. 1996), a carnivore of comparable size as Australian fur seal. In the present study, blood isotopic values were considered to be a proxy of the short- and medium-term foraging niche during the period just before seals were captured and tracked (winter). The otariid whisker is a continuously growing and metabolically inert tissue that retain its isotopic composition over time, such that serially sampled fur seal whiskers provide a chronology of δ^{13}C and δ^{15}N values over several years (Cherel et al. 2009, Kernaléguen et al. 2012, Vales et al. 2015).

Short-term sexual segregation was examined by comparing male and female plasma and red blood cells isotopic values using t-tests after checking the normality of the data and the equality of variances. Long-term niche differentiation was investigated by examining the isotopic signature of seals’ whisker. Otariid whiskers show sexual and inter-individual variation in growth rate (Kernaléguen et al. 2012, Rea et al. 2015) so that whiskers of similar length might not integrate a similar period of time. In order to compare groups and individuals over a similar time-frame, specific whisker growth rates were calculated for each individual. Isotopic signature of otariid whiskers often present regular annual cycles along their length (Hirons et al. 2001,
Cherel et al. 2009, Kernaléguen et al. 2012, Kernaléguen et al. 2015a, Rea et al. 2015) which allows for growth rate to be estimated for each whisker. The periodicity of $\delta^{13}$C and $\delta^{15}$N values was assessed, using the wavelet analysis following Kernaléguen et al. (2012). This analysis allowed us to detect: (i) if the isotopic signature of whiskers consist of a repeated periodic signal; and, more importantly (ii) if the period of the cyclic pattern is consistent along the length of the whisker (Cazelles et al. 2007, Cazelles et al. 2008). As whiskers were cut and not plucked, their most recently synthesized tissue remained under the skin. This part of the whisker (not analysed) corresponds to an unknown period of time depending on its length and the specific growth rate of the whisker. As a consequence, the first section of each whisker does not necessarily correspond to the same time. Isotopic values were time-synchronised by doing a phase synchronization for each individual between its isotopic time series and the time series of a reference individual randomly chosen.

Variation in long-term isotopic niche between males and females was assessed by comparing the mean and range of whisker isotopic values between both sexes. Linear mixed-effect models were used to test the influence of sex (fixed effect) and individuals (random effect) on $\delta^{13}$C and $\delta^{15}$N mean values. The use of mixed-effect models allowed to account for the repeated measurements on the same individuals and the time-correlation of whisker isotopic values (models included an auto-correlation factor) (Pinheiro & Bates 2000). Differences in the estimated mean $\delta^{13}$C or $\delta^{15}$N values for males and females were tested using ANOVA analyses. Comparison of the range of $\delta^{13}$C or $\delta^{15}$N data between the sexes was then performed using $t$-tests after checking the normality of the values and the equality of variances. Comparisons were made over a period of 2.5 years which corresponds to the time-period depicted by all whiskers.
Finally, the degree of individual specialisation in males and females was measured and compared using Roughgarden’s WIC/TNW index for continuous data (Bolnick et al. 2002). Roughgarden (1972) suggested that the population Total Niche Width (TNW, corresponding to the population variance) can be partitioned into the Within-Individual Component (WIC, intra-individual variance) and the Between-Individual Component (BIC, inter-individual variance), so that TNW = WIC + BIC. The WIC/TNW ratio is a measurement of the degree of individual specialisation: high values (approaching 1) indicate that individuals use the full range of the population resources, and low values (approaching 0) characterise specialist individuals. Each 3-mm long whisker section integrated an average period of time of 18 ± 5 and 38 ± 13 days for males and females, respectively (see Results) and was considered as one observation. Thus, WIC corresponded to the average variance between sections calculated at the whisker level and BIC to the variance between mean isotopic values of whiskers. The degree of individual specialisation was calculated on the most recent 2.5 years, a period of time depicted by all whiskers, so that all individuals contributed an equal weight to the analysis. The R package RInSp (Zaccarelli et al. 2013) was used to calculate individual specialisation indices. Significance of WIC/TNW was assessed using a nonparametric Monte Carlo technique to generate 10,000 replicate datasets under the null hypothesis that all individuals are generalists, from which P-values were calculated (Bolnick et al. 2002).

All results are presented as mean ± standard deviation and results were considered significant at the P < 0.05 level. All statistics were performed using R 3.0.3.
Results

Males were significantly larger than females (Table 4.1) and had an estimated mass twice higher than females (138 ± 24 and 64 ± 6 kg, respectively, t5.61=-7.41, P<0.001). Female foraging trips lasted on average 5.2 ± 6.5 d. Only half of the males returned to the breeding colony during the period they were tracked. The duration of the first trip performed by these three males was on average 22.5 ± 6.2 d. All individuals stayed within the continental shelf of central Bass Strait during the entire period they were tracked (35 days, from 4 June to 8 July) (Fig. 4.1). Accordingly, both sexes displayed restricted home ranges that were within 220 km of the breeding colony, and exhibited spatial overlap in home ranges, with a 95% UDOI of 36% (Fig. 4.1).

Figure 4.1 95% (plain line) and 50% (dotted line) utilisation distribution probabilities of males (black line) and females (red line), in June – early July (35 days). The black dot represents the breeding colony where seals have been captured and grey lines indicate the bathymetry (in 20 m intervals) to the edge of the continental shelf (200 m contour).
Table 4.1 Morphometric measurements and isotopic values of male and female Australian fur seals. Values are mean ± standard deviation.

<table>
<thead>
<tr>
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<th>Males</th>
<th>Females</th>
<th>Statistics (P values)</th>
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<tr>
<td>Length (cm)</td>
<td>175 ± 13</td>
<td>145 ± 4</td>
<td>t&lt;sub&gt;6.0&lt;/sub&gt;=−5.34 (0.002)</td>
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<tr>
<td>Axillary girth (cm)</td>
<td>126 ± 8</td>
<td>100 ± 5</td>
<td>t&lt;sub&gt;7.6&lt;/sub&gt;=−6.89 (&lt;0.001)</td>
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<tr>
<td>Mass (kg)</td>
<td>138 ± 24 *</td>
<td>64 ± 6</td>
<td>t&lt;sub&gt;5.6&lt;/sub&gt;=−7.41 (&lt;0.001)</td>
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<td><strong>δ&lt;sup&gt;13&lt;/sup&gt;C values (%)</strong></td>
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<tr>
<td>Plasma</td>
<td>-19.4 ± 0.2</td>
<td>-19.4 ± 0.1</td>
<td>t&lt;sub&gt;8.3&lt;/sub&gt;=0.36 (0.73)</td>
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<td>Red cells</td>
<td>-19.0 ± 0.2</td>
<td>-18.9 ± 0.3</td>
<td>t&lt;sub&gt;9.8&lt;/sub&gt;=−0.69 (0.51)</td>
</tr>
<tr>
<td>Whisker</td>
<td>-16.8 ± 0.1</td>
<td>-17.1 ± 0.2</td>
<td>F&lt;sub&gt;10,711&lt;/sub&gt;=9.32 (0.01)</td>
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<tr>
<td><strong>δ&lt;sup&gt;15&lt;/sup&gt;N values (%)</strong></td>
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<tr>
<td>Plasma</td>
<td>16.1 ± 0.4</td>
<td>15.6 ± 0.3</td>
<td>t&lt;sub&gt;9.8&lt;/sub&gt;=−2.33 (0.04)</td>
</tr>
<tr>
<td>Red cells</td>
<td>15.9 ± 0.2</td>
<td>15.5 ± 0.3</td>
<td>t&lt;sub&gt;9.4&lt;/sub&gt;−=2.90 (0.02)</td>
</tr>
<tr>
<td>Whisker</td>
<td>16.8 ± 0.3</td>
<td>16.3 ± 0.4</td>
<td>F&lt;sub&gt;10,711&lt;/sub&gt;=7.73 (0.02)</td>
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*Mass of males was estimated from species- and sex-specific allometric relationship between body mass and morphometric measurements (Arnould & Warneke 2002).

Males and females exhibited similar average δ<sup>13</sup>C plasma and red blood cell values (Table 4.1, Fig. 4.2). However, they consistently displayed a small but significant difference in their plasma and red blood cell δ<sup>15</sup>N values, with males having higher blood isotopic values than females (Fig. 4.2).

Male and female whiskers measured on average 210 ± 45 and 165 ± 30 mm, respectively. All seals exhibited constant periodic oscillations in δ<sup>13</sup>C and/or δ<sup>15</sup>N values along the length of their whisker. When both series (δ<sup>13</sup>C and δ<sup>15</sup>N) of a same individual were periodic (for five male whiskers), the period was similar for both δ<sup>13</sup>C and δ<sup>15</sup>N ratios. Whiskers recorded between 2.8 and 7.6 cycles, with an average of 3.5 ± 0.6 and 5.5 ± 1.5 cycles for males and females, respectively. Assuming cycles were annual (Hirons et al. 2001, Cherel et al. 2009, Kernaléguen et al. 2012, Kernaléguen et al. 2015a), average whisker growth rate was 0.17 ± 0.04 and 0.09 ± 0.03 mm·d<sup>−1</sup> for males and females, respectively.
Figure 4.2 Plasma, red blood cells and mean whisker δ¹³C and δ¹⁵N values of male (black) and female (grey) Australian fur seals sampled in winter. Values are mean ± standard deviation.

![Graph showing δ¹³C and δ¹⁵N values for plasma and red cells for males and females.]

Figure 4.3 Whisker δ¹³C and δ¹⁵N values of male (black lines) and female (grey lines) Australian fur seals over three consecutive years.

![Graph showing whisker values for each year from 2010 to 2013 for males and females.]

A small but significant difference was found in mean δ¹³C and δ¹⁵N whisker values between males and females (δ¹³C: -16.8 ± 0.1 and -17.1 ± 0.2‰, respectively, ANOVA: F₁₀,₇₁₁=9.32, P=0.01; δ¹⁵N: 16.8 ± 0.3 and 16.3 ± 0.4‰, respectively,)
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ANOVA: F_{10,711}=7.73, P=0.02) (Fig. 4.3). The range of whisker δ\textsuperscript{13}C isotopic values was higher in males than in females (1.1 ± 0.3 and 0.7 ± 0.2‰, respectively, t\textsubscript{8.4}=-3.59, P=0.006), while it was similar for δ\textsuperscript{15}N values (1.4 ± 0.2 and 1.3 ± 0.6‰, respectively, t\textsubscript{6.6} =-0.38, P=0.71, respectively). Both males and females exhibited significant individual specialisation. However, the degree of specialisation in males was very low (WIC/TNW=0.93, P=0.005) compared to females (WIC/TNW=0.41, P<0.001) when considering δ\textsuperscript{13}C values, and similar (WIC/TNW = 0.56 and 0.60, respectively, both P<0.001) when considering δ\textsuperscript{15}N values (Fig. 4.3).

**Discussion**

The foraging niche of the sampled male and female Australian fur seals greatly overlapped, both in terms of foraging habitat (tracking data and δ\textsuperscript{13}C values) and trophic level (δ\textsuperscript{15}N values). As both sexes exhibit strong size dimorphism and face very different breeding-related constraints, pronounced sexual segregation was expected. However, if individuals’ traits (e.g. morphology, dietary requirements, breeding constraints) is a major factor driving resource partitioning within a population, the local environment may also play a fundamental role. In the present study, the uniformity of Bass Strait (shallow benthic foraging habitat) is likely to limit the opportunities for sexual niche segregation to occur.

**Spatial segregation**

Tracking and δ\textsuperscript{13}C isotopic data indicated a great overlap between male and female foraging habitats in winter. All study individuals foraged within central Bass Strait, a region characterised by a typically low primary productivity, particularly during winter (Gibbs 1992). As expected due to their central place foraging mode, females
had a greater presence in the immediate area surrounding the breeding colony than males. As males do not provide any parental care, they were expected to disperse (Kirkwood et al. 2006) to forage in more productive areas and avoid intra-specific competition with females. Surprisingly, even though males do not have any land-based dependent offspring, half of them returned to the breeding colony within the tracking period, potentially to gain knowledge of breeding territories and impose themselves into the hierarchy among males for future reproductive seasons (Kirkwood et al. 2006).

The Australian fur seal is the most geographically restricted fur seal species, with a species distribution mostly limited to islands around the shallow Bass Strait region (Kirkwood et al. 2010). Numerous studies involving adult females have shown seals’ benthic foraging behaviour, limiting them to the continental shelf (Hindell & Pemberton 1997, Arnould & Kirkwood 2008, Hoskins et al. 2015). However, only a few studies have investigated the foraging ecology of males (Hindell & Pemberton 1997, Kirkwood et al. 2006, Knox et al. 2014) and male diving behaviour has been recorded in only one individual (Hindell & Pemberton 1997). Hence, it was not known if males could potentially display an epipelagic foraging behaviour and travel beyond the continental shelf. Even if restricted to the continental shelf, males could potentially have access to a wider range of foraging habitat than central Bass Strait. Indeed, Kirkwood et al. (2006) found that adult males (n = 9) from a nearby colony (Seal Rocks) foraged mostly within Bass Strait but 33% of individuals also moved along the Tasmanian and/or South Australian coasts.

The isotopic values of whiskers integrate the foraging ecology of the same individuals over several years, documenting seasonal and inter-annual variation. As expected from the tracking and blood isotopic data, the δ13C isotopic values of male and female whiskers strongly overlapped, reflecting the similar winter foraging habitats. However, the study males exhibited greater intra-individual variation in their
δ\textsuperscript{13}C values than females suggesting they exploited a greater variety of foraging habitats throughout the year. In several otariid species, males are known to travel great distances just after the mating period, some species undertaking a yearly migration (Loughlin et al. 1999, Cherel et al. 2009, Kernaléguen et al. 2012, Sterling et al. 2014). Whereas in the present study male Australian fur seals remained close to the breeding colony in winter, the whisker δ\textsuperscript{13}C values suggest they dispersed to different regions at other times of the year. In particular, they may move to more profitable areas just before and after the mating period, when they need to gain rapidly body mass in preparation to extreme fasting period (up to 60 days, Warneke & Shaughnessy 1985), and to recover their body condition, respectively (Kirkwood et al. 2006). Indeed, even if the sampled males might not be reproductively active, unsuccessful bulls and bachelor males congregate in the vicinity of the breeding territories and spend long periods of time ashore fasting during the mating period (Warneke & Shaughnessy 1985).

While intra-individual variation observed in male δ\textsuperscript{13}C whisker values is likely to reflect seasonal variation in foraging habitat, it could also denote potential seasonal variation of the isotopic signature of prey. Indeed, some prey are known to be migratory and enter into Bass Strait seasonally, potentially coming from different oceanographic regions characterised by different isotopic values. Furthermore, nutrient input of Bass Strait is primarily influenced by the Bonney Upwelling and three primary water masses, the South Australian Current Water, the East Australian Current Water and the sub-Antarctic Surface Water whose relative contributions vary across seasons and years (Lewis 1981, Sandery & Kämpf 2007). The baseline isotopic values of the trophic chains in these currents could differ such that the isotopic value of prey could vary over time. However, if males and females were foraging within the same habitat (i.e. within central Bass Strait) all year round, they should exhibit similar
variation in their δ\textsuperscript{13}C values. Hence, the potential temporal variation in the isotopic value of the food source cannot explain alone larger ranges of δ\textsuperscript{13}C values in males.

**Dietary segregation**

Males and females segregated in their δ\textsuperscript{15}N niche over the long-term (whisker isotopic data). Plasma and red blood cell δ\textsuperscript{15}N values were also higher in males, indicating isotopic niche variation occurs even when both genders forage in the same habitat and have access to the same available prey (central Bass Strait, in winter). Therefore, difference in nitrogen isotopic values is not explained by potential spatial variation of prey distribution or isotopic signature. However, difference in δ\textsuperscript{15}N values was small, with males and females overlapping in their isotopic niche. While this result suggests an overlap in the diet of the two sexes, it also reflects small variation in prey isotopic values. Indeed, in eastern Bass Strait, isotopic values of Australian fur seal prey species range between 11.5-13.9‰, with the main prey ranging between 11.5-12.8‰ (Davenport & Bax 2002). Hence, even small variation in nitrogen isotopic values is likely to have a biological significance. The isotopic values observed for females in the present study are consistent with previous diet studies based on scat/regurgitate content analyses (Hume et al. 2004, Littnan et al. 2007) and animal-borne video cameras (Kernaléguen et al. 2015c) indicating they feed mainly on benthic and benthopelagic fish (redbait (*Emmelichthys nitidus*), perch gurnards (Triglidae spp.), jack mackerel (*Trachurus declivus*), leatherjackets (Monocanthyidae spp.), red cod (*Pseudophysis bachus*)) and octopus (*Octopus* spp.). The nitrogen isotopic values of males suggest they are likely to consume similar prey items than females, but a higher proportion of higher trophic level prey (e.g. larger octopus (*Octopus* spp.), barracouta (*Thyristes atun*), small sharks (Carcharhiniformes), stingrays (Myliobatiformes spp.)).
The degree of trophic segregation was surprisingly low compared to other otariid species (Page et al. 2005a, Cherel et al. 2007, Kernaléguen et al. 2012) and what was expected in such a highly dimorphic species. Indeed, females are likely to be more limited in the prey size they can efficiently capture, handle and kill than their male counterparts. Conversely, their smaller body size may confer advantages over males with regard to manoeuvrability and the ability to capture small prey items (Fish et al. 2003). Males and females also differ in their quantitative and qualitative energetic requirements. Males have higher absolute needs to maintain their larger body size. For example, in the Antarctic fur seal (*A. gazella*), males can have up to twice the energy requirement of females: 3.8 tons of krill a year for an adult male compared to 1.9 tons for a female (Boyd 2002). Furthermore, as males are capital breeders and need large energy storage to prepare for long fasting periods during the mating season, they might be expected to primarily target prey of high lipid and protein content. In contrast, females are income breeders, forage throughout lactation and require different levels of lipid and protein for milk delivery (Arnould & Hindell 2002). Hence, both sexes should not necessarily share the same selection criteria in their respective foraging strategies and should accordingly show dietary differences. While the studied males were sexually mature and weighed approximately twice the mass of females, they were still not the size of prime territorial males. It is therefore possible that diet segregation will increase as body size continue to diverge with age (Bailleul et al. 2010).

**Gender-specific degree of individual specialisation**

Female Australian fur seals are known to exhibit long-term individual specialisation in terms of foraging habitat and diet, with the population being comprised of both specialist and generalist individuals (Kernaléguen et al. 2015c). Given that males and females appear to differ in their diet and foraging habitat during certain times of the
year (present study), both genders potentially experience contrasting levels of competition, resource availability or predation. As a result, the degree of individual specialisation might vary between the sexes (Kernaléguen et al. 2012, Elliott Smith et al. 2015). In particular, it has long been suggested that the accessibility of a greater diversity of resources (ecological opportunity, here foraging habitats) should favour individual specialisation, the variety of resources providing the raw material for inter-individual variation to occur (Roughgarden 1974, Araújo et al. 2011). Accordingly, recent studies have found higher inter-individual variation when resource diversity increases, either temporally (Herrera et al. 2008, Kernaléguen et al. 2015a) or spatially (Layman et al. 2007, Darimont et al. 2009, Evangelista et al. 2014). Hence, a higher degree of specialisation would be expected in males compared to females.

Surprisingly, the sampled males exhibited a similar degree of inter-individual variation in δ¹⁵N values and little difference in their δ¹³C values, when compared to females. When foraging in different habitats, males should encompass a spatial variation in prey assemblage and feed on a greater diversity of prey than females. However, male and female δ¹⁵N niche widths were similar and results suggest both sexes forage on a great variety of prey items, irrespectively of their foraging grounds. In accordance with the niche variation hypothesis which predicts that populations with wider niches exhibit more individual variability than populations with narrower niches (Van Valen 1965), the high diversity of δ¹⁵N niche was associated with a high degree of individual specialisation in both sexes.

The fact that males displayed very little inter-individual variation in their δ¹³C values suggests they all foraged in similar locations throughout the annual cycle. Considering males exploit a broader δ¹³C niche than females, a higher degree of specialisation was expected in males. This could indicate males go to specific productive habitats to feed. High density of prey would release intra-specific
completion that should induce a decrease in the degree of individual specialisation (Tinker et al. 2008, Elliott Smith et al. 2015, Kernaléguen et al. 2015a). However, this hypothesis assumes a high degree of competition in central Bass Strait. As for most cryptic species, it is difficult to quantify the degree of competition and its impact on the foraging behaviour in the Australian fur seal. The Australian fur seal is still slowly recovering from the severe over-exploitation of the commercial sealing era (1798-1825) and has not yet reached its carrying capacity (Kirkwood et al. 2010). Hence, this suggests food resource might not be a limiting factor, despite the relatively low productivity of Bass Strait (Gibbs 1992).

In summary, while strong niche segregation would be expected in such a sexually dimorphic species, the trophic niche of the sampled male and female Australian fur seals showed a substantial degree of overlap. Yet, males exploited a greater diversity of foraging areas and fed upon a higher proportion of prey of higher trophic level than females. Seasonal variation in the degree of resource partitioning was observed, emphasizing the importance of studying resource partitioning over multiple time-scales. The driving forces behind sexual dimorphism are still under debate (Isaac 2005). The two main hypotheses developed are the ecological divergence hypothesis, where the morphology of males and females have diverged as a consequence of variation in the utilisation of prey resources by the two sexes (Shine 1989), and the sexual selection hypothesis which predicts that dimorphism is a result of sexual selection that favour large, competitive males (or females) (Trivers 1972). Results of the present study suggest the Australian fur seal is an interesting model to investigate the mechanisms of sexual segregation. Indeed, the sampled males and females showed a strong sexual size dimorphism, yet, overlapped in their respective trophic niches. The species distribution of the Australian fur seal is almost exclusively restricted to the Bass Strait region, implying all populations should face a similar
4. Sexual Segregation in Australian Fur Seals

restriction in their foraging habitats. If the observed overlap between male and female foraging niches is a generalized pattern across all populations, this would support the sexual selection hypothesis as the two sexes differ in their morphology but exploit similar prey resources.
CHAPTER 5
Determinants of Individual Foraging Specialisation in Large Marine Vertebrates, the Antarctic and Subantarctic Fur Seals

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Abstract

1. The degree of individual specialisation in resource-use differs widely among wild populations where individuals range from fully generalised to highly specialised. This inter-individual variation has profound implications in many ecological and evolutionary processes. A recent review proposed four main ecological causes of individual specialisation: inter- and intra-specific competition, ecological opportunity and predation.

2. Using the isotopic signature of sub-sampled whiskers, we investigated to what degree three of these factors (inter- and intra-specific competition and ecological opportunity) affect the population niche width and the level of individual foraging specialisation in two fur seal species, the Antarctic and subantarctic fur seals (*Arctocephalus gazella* and *A. tropicalis*), over several years.

3. Population niche width was greater when the two seal species bred in allopatry (low inter-specific competition) than in sympatry or when seals bred in high density stabilized colonies (high intra-specific competition). In agreement with the Niche Variation Hypothesis (NVH), higher population niche width was associated with higher inter-individual niche variation. However, in contrast to the NVH, all Antarctic females increased their niche width during the inter-breeding period when they had potential access to a wider diversity of foraging grounds and associated prey (high ecological opportunities), suggesting they all dispersed to a similar productive area.

4. The degree of individual specialisation varied among populations and within the annual cycle. Highest levels of inter-individual variation were found in a context of lower inter- or higher intra-specific competition. Contrasted results were found concerning the effect of ecological opportunity. Depending on seal species, females exhibited either a greater or lower degree of individual specialisation during the inter-breeding period, reflecting species-specific biological constraints during that period.

5. These results suggest a significant impact of ecological interactions on the population niche width and degree of individual specialisation. Such variation at the individual level may be an important factor in the species plasticity with significant consequences on how it may respond to environmental variability.
Introduction

Traditionally, resource-use has been investigated at the species or population level and the Hutchinson’s concept of niche (Hutchinson 1957) has been seen as an attribute of the species or population as a whole. However, individual niche variation in resource-use is a widespread phenomenon in many vertebrate and invertebrate taxa (reviewed by Bolnick et al. 2003, Araújo et al. 2011). Individual specialisation occurs when individuals of similar sex and age class use a small subset of the population’s resources (Bolnick et al. 2003). This inter-individual variability has long been of particular concern in evolutionary studies as it provides the raw material for natural selection. More recently, it has also been shown to substantially affect the population and community dynamics (Hughes et al. 2008, Bolnick et al. 2011) and is recognized as playing a major role in many ecological processes.

The development of new indices that measure the degree of individual specialisation (Bolnick et al. 2002, Araújo et al. 2008) has enabled to investigate how the level of individual variation varies among populations and ecological contexts, providing new insights into the mechanisms of individual specialisation (e.g. Svanbäck et al. 2008, Darimont et al. 2009, Tinker et al. 2012). In a recent review, Araújo et al. (2011) identified four ecological causes of individual specialisation: inter-specific competition; intra-specific competition; ecological opportunity; and predation. These factors are likely to alter resource availability which, in turn, modifies the population niche width and the degree of inter-individual variation.

For example, in foraging ecology, Optimal Foraging Theory predicts that individuals should only feed on the most valuable resources that maximize the energy intake per unit handling time (MacArthur & Pianka 1966). If the more profitable prey become less abundant (increase of intra-specific competition) or the population has
access to a greater diversity of prey (decrease of inter-specific competition or predation, increase of ecological opportunities), individuals should broaden their diet to include a larger range of prey. Individuals may vary in their ability to find, handle and/or digest prey due to differences in morphology (Knudsen et al. 2007), physiology (e.g. digestive capacity (Afik & Karasov 1995), energy requirement (Belovsky 1978)) or behaviour (e.g. learned skills on how to capture/handle different types of prey (Estes et al. 2003)). As a consequence, individuals may vary in the profitability of alternative prey or ranking order (Svanbäck & Bolnick 2005). If individuals feed on different alternative prey, their respective diet will diverge as they increase their foraging niche. In reverse, if the less-preferred prey are items that were originally eaten by others, the degree of inter-individual variation will decrease as individuals broaden their diet (Svanbäck & Bolnick 2005, Tinker et al. 2012).

In addition, individuals might face functional trade-offs that limit the number of prey they can efficiently consume (Taper & Chase 1985, Afik & Karasov 1995, Robinson 2000). If individual niche is limited in size, expansion of population niche width, like in ecological release, will occur via an increase of inter-individual differences rather than all individuals increasing the range of resources they use. Accordingly, the Niche Variation Hypothesis (Van Valen 1965) states that populations with wider niches are more variable than populations with narrower niches.

A major limitation in investigating the determinants of individual specialisation is that estimating the individual variance requires repeated measurements on the same individuals, over a sufficient period of time to account for daily, seasonal or even multi-year variation of resource-use. Correspondingly, few studies have been conducted and in particular on long-lived species with large home ranges. The use of the isotopic niche as a proxy of the trophic niche enables to overcome this methodological limitation (Bearhop et al. 2004a, Araújo et al. 2007,
5. Determinants of Individual Specialisation

Newsome et al. 2007). For example, in otariids (fur seal and sea lion), the isotopic signature of continuously growing whiskers can provide a fine scale chronology of δ^13C (proxy of foraging habitat in marine environments, Hobson et al. 1994, Cherel & Hobson 2007) and δ^15N (proxy of trophic level, DeNiro & Epstein 1981) values over several years (Cherel et al. 2009, Lowther et al. 2011, Kernaléguen et al. 2012, Franco-Trecu et al. 2014).

Fur seals experience contrasting level of inter- and intra-specific competition and ecological opportunity. They represent thus an interesting model to investigate to what degree these ecological interactions affect the population niche width and the level of individual specialisation, in the marine environment. Firstly, in the Southern Ocean, two closely related species, the Antarctic (*Arctocephalus gazella*, Peters, 1875) and subantarctic fur seal (*A. tropicalis*, Gray, 1872), occur both in allopatry and sympathy during the pup-rearing period. The two species have a similar diet when foraging in the same water masses (Klages & Bester 1998, Robinson et al. 2002, Cherel et al. 2007). However, species-specific resource partitioning is observed in sympathy (Bailleul et al. 2005, Kernaléguen et al. 2012), suggesting an adaptation of the foraging behaviour to the co-occurrence of the competitor species. Secondly, fur seals have been intensively hunted during the 18th and 19th centuries, with commercial sealing resulting in local extinction of the two species. Many populations are still recovering with increasing sizes, suggesting they have not reached their carrying capacity yet (Bonner & Laws 1964). Other populations have stabilized and are very likely to experience a higher degree of intra-specific competition (Gilpin & Ayala 1973). Finally, lactating females are central place foragers during the pup-rearing period, they feed at-sea but need to come back regularly to the colony to suckle their single pup. After weaning, during the inter-breeding period, females are not as
spatially constrained; they can disperse and have potentially access to a greater diversity of foraging habitat and associated prey (ecological opportunity).

In the present study, the isotopic signature of serially sampled whiskers of Antarctic and subantarctic lactating females were determined to measure the population niche width and the degree of individual foraging specialisation under contrasting conditions of inter- and intra-specific competition and ecological opportunity. These ecological interactions together with predation correspond to the four ecological drivers of individual specialisation identified by Araújo et al. (2011). We predicted that: (i) population niche width should be lower in sympatry and that, in agreement with the NVH, the associated degree of individual specialisation should be also lower in sympatry than in allopatry; (ii) high density, stabilised populations should be characterized by a greater population niche width and higher inter-individual variations; and (iii) within a same population, the niche width and level of individual specialisation should vary within the annual cycle, and be lower during the pup-rearing than inter-breeding period.

**Materials and methods**

**Study sites**

Fieldwork was carried out on two species at three study sites in the Southern Indian Ocean (Fig. 5.1). Mare aux Elephant, Crozet Islands (46°22’S, 51°40’E, hereafter called Crozet), located in the subantarctic zone, between the subtropical and polar fronts, hosts sympatric populations of Antarctic and subantarctic fur seals during the pup-rearing period. These two populations are still recovering from past sealing and increasing in size (Guinet et al. 1994). Cap Noir, Kerguelen Archipelago (49°07’S, 70°45’E, hereafter called Kerguelen), located just north of the polar front hosts
allopatric breeding Antarctic fur seals with a population that is also increasing (long-term demographic unpublished data). Lastly, Mare aux Elephant, Amsterdam Island (37°50’S, 77°30’E, hereafter called Amsterdam), in the subtropical zone north of the subtropical front, hosts allopatric breeding subantarctic fur seals in a high density and stabilized population (Guinet et al. 1994) (Fig. 5.1).

**Figure 5.1 Location of Crozet, Kerguelen, Amsterdam and of the main oceanic fronts and zones in the southern Indian Ocean.** Abbreviations: SAFS: subantarctic fur seal, AFS: Antarctic fur seal, STF: Subtropical Front, PF: Polar Front, STZ: Subtropical Zone, SAZ: Subantarctic Zone and AZ: Antarctic Zone.

**Fieldwork and isotopic analysis**

During the 2002 pup-rearing period, 10 lactating females of unknown age were selected at random in each colony, captured using a hoop net, and restrained on a board while a whisker was cut as close to the skin as possible. Females from Crozet (and their corresponding whisker isotopic results) are the same individuals as those in the study by Kernaléguen et al. (2012). Seals breeding in Crozet were also weighed using
a suspension scale (± 0.1 kg). In the laboratory, whiskers were hand-washed in 100% ethanol and cleaned in distilled water for 5 minutes in an ultrasonic bath. They were dried, measured and cut into 3 mm-long consecutive sections starting from the proximal (facial) end, following Cherel et al. (2009). The δ¹³C and δ¹⁵N values of each whisker section were determined by a continuous flow mass spectrometer (Thermo Scientific, Delta V Advantage) coupled to an elemental analyser (Thermo Scientific, Flash EA 1112). Results are presented in the conventional δ notation relative to Vienna PeeDee Belemnite marine fossil limestone and atmospheric N₂ for δ¹³C and δ¹⁵N, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors < 0.10‰ for both δ¹³C and δ¹⁵N.

**Population niche breadth and inter-individual variability**

The degree of individual specialisation was calculated using Roughgarden’s WIC/TNW index for continuous data (Bolnick et al. 2002). (Roughgarden 1972) suggested that the population Total Niche Width (TNW, corresponding to the population variance) can be partitioned into the Within-Individual Component (WIC, intra-individual variance) and the Between-Individual Component (BIC, inter-individual variance), where TNW = WIC + BIC. The WIC/TNW ratio is a measurement of the degree of individual specialisation: high values (approaching 1) indicate that individuals use the full range of the population resources, and low values (approaching 0) characterise specialist individuals. Each 3 mm long section integrated an average period of time of 42 ± 15 days (see Results) and was considered as one observation. Thus, WIC corresponded to the average variance between sections calculated at the whisker level; and BIC to the variance between whiskers’ mean isotopic values (Fig. 5.2). If x_ij is the jth δ¹³C or δ¹⁵N value of the ith individual, then,
5. Determinants of Individual Specialisation

\[ TNW = \text{Var}(x_{ij}) \]
\[ WIC = E[\text{Var}(x_{j|i})] \]
\[ BIC = \text{Var}[E(x_{j|i})]. \]

Roughgarden’s indices for each population were calculated using the program IndSpec1 (Bolnick et al. 2002; http://www.esapubs.org/archive/ecol/E083/056/default.htm). In order to test the significance of WIC/TNW ratios, additional 1,000 replicate populations were generated under the null hypothesis that individuals are generalists which sample randomly from the population’s distribution. Replicate datasets were generated with IndSpec1 by resampling using a nonparametric Monte Carlo procedure (Bolnick et al. 2002). WIC/TNW has no published statistical proprieties (Bolnick et al. 2002, Araújo et al. 2011), so it was not possible to test whether two populations had significantly distinct WIC/TNW ratios. Population niche widths TWN were compared with a Fisher test after checking for the normality of the data.
5. Determinants of Individual Specialisation

Figure 5.2 Schematic diagrams illustrating (i) the calculation of (Roughgarden 1972) indices of individual specialisation (a and b, adapted from Bolnick et al. (2003)) and (ii) how these indices have been calculated from whisker isotopic values (c). (a and b) represent the population’s (thick curve) and individuals’ (thin curves) niches in a generalist and specialist populations, respectively. The Total Niche Width (TNW) is decomposed into its Within- and Between-Individual Components (WIC corresponding to the intra-individual variance and BIC corresponding to the inter-individual variance, respectively). Theoretical isotopic ratio ($\delta^{13}C$ or $\delta^{15}N$) along the length of two whiskers are represented in (c). TNW, BIC and WIC were calculated during the pup-rearing (in white) and the inter-breeding (in grey) periods separately. Analyses were performed on the 3 most recent years depicted in whiskers to account for the inter-annual variability and so each individual contributed equal weight in the analyses.

Population isotopic niche width and the degree of individual specialisation were calculated during the pup-rearing season (December to March for Antarctic fur
seals; December to August for subantarctic fur seals); and during the inter-breeding period (April to November and September to November for Antarctic and subantarctic fur seals, respectively) separately (Fig. 5.2). Whisker isotopic values were assigned to one of each period by placing the annual breeding cycles along the length of each whisker (conversion of the whisker length into a time-scale). In many cases, isotopic signature of otariid whiskers present regular annual cycles along their length (Hirons et al. 2001, Cherel et al. 2009, Kernaléguen et al. 2012). Periodicity of $\delta^{13}C$ and $\delta^{15}N$ values was first assessed using the wavelet analysis following Kernaléguen et al. (2012). This analysis allowed us to detect: (i) whether the isotopic signature of whiskers consisted of a repeated periodic signal; and, more importantly (ii) whether the period of the cyclic pattern was consistent along the length of the whisker (Cazelles et al. 2008). In addition, isotopic ratios of whole blood collected at different stages of the breeding cycle of females (unpublished data) allowed us to identify the summer and winter signatures in whiskers. A blood sample was collected during the pup-rearing period on the same individuals, when the whisker was taken. Additional blood samples were collected on random females in December 2002, when females returned to the colony after their winter trip, at Crozet (on both species) and Amsterdam; and in August 2002, on subantarctic fur seal females at Crozet and Amsterdam.

The temporal integration of whiskers varied greatly between individuals (from 2.7 to 7.3 years, see Results). The population niche width and the degree of individual specialisation were calculated only on the 3 most recent years depicted in whiskers to account for the inter-annual variability and so each individual contributed equal weight in the analyses. However, whiskers of two subantarctic fur seals breeding at Amsterdam integrated only 2.7 and 2.8 years. One Antarctic fur seal from Crozet exhibited extremely low $\delta^{13}C$ values at the distal end of its whisker, most likely
reflecting an ontogenic shift. Since the aim of this study was to compare the foraging ecology of lactating females, the isotopic data corresponding to the third year of this specific whisker were not taken into account in the variance analyses.

**Results**

*Body condition and whisker isotopic results*

Antarctic and subantarctic fur seal females breeding at Crozet weighed on average 34.5 ± 4.4 kg (range: 27.4 - 41.0 kg) and 28.1 ± 4.5 kg (range: 23.6 - 38.0 kg), respectively. Mean whisker length was 132 ± 38 mm, corresponding to an average of 44 ± 13 isotopic measurements per individual. In total 1,760 samples were analysed. Overall isotopic data of whiskers were spread over a large range, with $\delta^{13}C$ and $\delta^{15}N$ values varying from -25.8 to -14.3 ‰ and from 8.4 to 15.1 ‰, respectively (Table 5.1). Wavelet analyses indicated that all seals exhibited significant periodic oscillations along the length of their whisker in $\delta^{13}C$ and/or $\delta^{15}N$ signals (Fig. 5.3). Importantly, in all individuals, the cycle duration was constant along the length of each whisker and similar in both $\delta^{13}C$ and $\delta^{15}N$ ratios, supporting the assumption of a constant whisker growth rate in otariid species (Hirons et al. 2001, Cherel et al. 2009, Kernaléguen et al. 2012). Whiskers recorded an average of 4.8 ± 1.0 years and each 3 mm section integrated an average period of time of 42 ± 15 days (Table 5.1).
### Table 5.1 Whisker $\delta^{13}$C and $\delta^{15}$N values, C/N mass ratios, overall length, time-integration of 3 mm long section and number of cycles recorded in whiskers.

Values are means ± standard deviation. Abbreviations: Antarctic FS: Antarctic fur seal, subantarctic FS: subantarctic fur seal.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Length (mm)</th>
<th>$\delta^{13}$C (‰) ± SD [range]</th>
<th>$\delta^{15}$N (‰) ± SD [range]</th>
<th>C/N mass ratio</th>
<th>Section (day)</th>
<th>Number of cycles [range]</th>
</tr>
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<tbody>
<tr>
<td>Antarctic FS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crozet</td>
<td>10</td>
<td>145 ± 45</td>
<td>-17.1 ± 1.1 [-25.8; -16.1]</td>
<td>10.6 ± 0.6 [8.4; 12.4]</td>
<td>2.86 ± 0.04</td>
<td>40 ± 11</td>
<td>5.1 ± 1.2 [3.2; 7.3]</td>
</tr>
<tr>
<td>Kerguelen</td>
<td>10</td>
<td>97 ± 24</td>
<td>-18.1 ± 0.7a [-21.6; -16.8]</td>
<td>10.4 ± 0.5a [8.4; 11.7]</td>
<td>2.83 ± 0.04</td>
<td>59 ± 17</td>
<td>5.0 ± 0.9 [4.0; 6.5]</td>
</tr>
<tr>
<td>subantarctic FS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crozet</td>
<td>10</td>
<td>133 ± 27</td>
<td>-16.7 ± 0.4b [-18.2; -15.7]</td>
<td>10.5 ± 0.6b [8.6; 12.4]</td>
<td>2.88 ± 0.02</td>
<td>36 ± 9</td>
<td>4.2 ± 0.9 [2.7; 6.5]</td>
</tr>
<tr>
<td>Amsterdam</td>
<td>10</td>
<td>152 ± 34</td>
<td>-15.2 ± 0.4 [-16.0; -14.3]</td>
<td>13.4 ± 0.7 [11.4; 15.1]</td>
<td>2.87 ± 0.03</td>
<td>35 ± 7</td>
<td>4.7 ± 0.9 [3.0; 6.5]</td>
</tr>
</tbody>
</table>

*Two samples were removed because they corresponded to the suckling period of one female when she was pup.

*Fourteen samples were removed because they corresponded to the suckling period of two females when they were pups.

### Figure 5.3 Whisker $\delta^{13}$C (open circles) and $\delta^{15}$N (filled circles) values of one representative females of each population.

Pup-rearing and inter-breeding periods are represented in white and grey, respectively. The proximal end (time zero), i.e. the youngest part of the whisker, appears on the right of plots. Abbreviations: AFS: Antarctic fur seal, SAFS: subantarctic fur seal.
**Population niche breadth and inter-individual variability**

During the pup-rearing period, $\delta^{13}C$ total niche width (TNW) of Antarctic females was similar between the allopatric and sympatric sites ($F_{59,90} = 0.87$, $P = 0.53$), while the $\delta^{15}N$ TNW was greater by a factor of two in allopatry than in sympatry ($F_{59,90} = 0.53$, $P < 0.001$) (Table 5.2, Fig. 5.4). Significant individual specialisation occurred in both populations (all $P < 0.03$) but varied in magnitude depending of the level of interspecific competition. The degree of individual specialisation was greater in allopatry considering both $\delta^{13}C$ and $\delta^{15}N$ values ($\delta^{13}C$ and $\delta^{15}N$ WIC/TNW indexes of 0.52 and 0.49, respectively in allopatry and 0.80 and 0.73 in sympathy).

| Table 5.2 Population isotopic niche breadth and intra- and inter-individual variations in $\delta^{13}C$ and $\delta^{15}N$ values during the pup-rearing and the inter-breeding periods, based on whisker’s isotopic signature during 3 years. The Total Niche Width (TNW) is decomposed into its Within- and Between-Individual Components (WIC corresponding to the intra-individual variance and BIC corresponding to the inter-individual variance, respectively). Roughgarden’s WIC/TNW index (1972) provides a measurement of the degree of individual specialisation of the population, low and high values characterise specialist and generalist individuals, respectively. Abbreviations: Antarctic FS: Antarctic fur seal, subantarctic FS: subantarctic fur seal. |
|----------------------------------|----------------|---------------|----------|----------------|----------------|---------------|----------|----------------|----------------|----------------|
|                                  | $\delta^{13}C$ | $\delta^{15}N$ |          | $\delta^{13}C$ | $\delta^{15}N$ |          |
|                                  | TNW  | WIC  | BIC  | WIC/TNW | TNW  | WIC  | BIC  | WIC/TNW |
| Pup-rearing Antarctic FS Crozet  | 0.12 | 0.09 | 0.02 | 0.80     | 0.08 | 0.06 | 0.03 | 0.73    |
| Kerguelen                        | 0.13 | 0.07 | 0.08 | 0.52     | 0.16 | 0.08 | 0.08 | 0.49    |
| Inter-breeding Antarctic FS Crozet | 0.52 | 0.37 | 0.19 | 0.70     | 0.26 | 0.24 | 0.02 | 0.93    |
| Kerguelen                        | 0.28 | 0.19 | 0.10 | 0.67     | 0.23 | 0.19 | 0.05 | 0.82    |
| Pup-rearing subantarctic FS Crozet | 0.14 | 0.08 | 0.08 | 0.57     | 0.27 | 0.20 | 0.08 | 0.73    |
| Amsterdam                        | 0.15 | 0.13 | 0.02 | 0.85     | 0.54 | 0.33 | 0.21 | 0.61    |
| Inter-breeding subantarctic FS Crozet | 0.13 | 0.05 | 0.09 | 0.37     | 0.25 | 0.15 | 0.09 | 0.63    |
| Amsterdam                        | 0.17 | 0.09 | 0.07 | 0.57     | 0.48 | 0.25 | 0.26 | 0.52    |
Subantarctic fur seals from Crozet and Amsterdam had a similar $\delta^{13}$C TNW during the pup-rearing period ($F_{238,243} = 0.96, P = 0.73$), while the $\delta^{15}$N TNW was twice higher in Amsterdam than in Crozet ($F_{238,243} = 0.50, P < 0.001$). Subantarctic females also exhibited significant individual foraging specialisation ($P < 0.001$ for all WIC/TNW ratios). The degree of individual specialisation was lower in Amsterdam than in Crozet when considering $\delta^{13}$C values (WIC/TNW indexes of 0.57 and 0.85 in Crozet and Amsterdam, respectively). However, an opposite trend was found when considering $\delta^{15}$N values (WIC/TNW indexes of 0.73 and 0.61 in Crozet and Amsterdam, respectively).

The overall population niche breadth TNW of Antarctic females from Crozet and Kerguelen increased during the inter-breeding season (increase in at least one isotopic ratio, $F_{90,183} = 0.22$, $F_{90,183} = 0.47$ for Crozet $\delta^{13}$C and $\delta^{15}$N TNW, respectively, both $P < 0.002$; and $F_{59,135} = 0.33$, $P < 0.001$ and $F_{59,135} = 0.69$, $P = 0.10$ for Kerguelen $\delta^{13}$C and $\delta^{15}$N TNW, respectively). Concurrently, the degree of individual specialisation was lower during the inter-breeding period, for both isotopic ratios and populations, with the exception of WIC/TNW $\delta^{13}$C ratio of females breeding at Crozet.

In contrast, subantarctic fur seals exhibited a similar TNW during both periods ($F_{72,238} = 1.10$ and $F_{72,243} = 0.89$ for Crozet $\delta^{13}$C and $\delta^{15}$N TNW, respectively, both $P > 0.60$; and $F_{72,238} = 0.33$ and $F_{72,243} = 0.69$ for Amsterdam $\delta^{13}$C and $\delta^{15}$N TNW, respectively, both $P > 0.50$). Greater inter-individual differences were found during the inter-breeding period, for both isotopic ratios and populations. All WIC/TNW indices were significants during the inter-breeding period (all $P < 0.003$) except for the $\delta^{15}$N WIC/TNW index of Antarctic fur seals breeding at Crozet ($WIC/TNW = 0.93, P = 0.20$).
Discussion

Isotopic signature of whiskers highlighted significant individual foraging specialisation in fur seal populations. The degree of inter-individual variation varied depending on the intensity of inter- and intra-specific competition and over the breeding cycle, as the diversity of accessible foraging grounds differed. However, potential effect of confounding factors such as oceanographic differences between the sites could not be ruled out due to the lack of replication. The effect of predation could
not be tested as no accurate data are currently available on the density of predator species or rates of predation.

Since individual foraging specialisation plays a major role in many natural processes, it is important to better understand how ecological interactions influence the amount of inter-individual variation (Araújo et al. 2011). However, this question has been little documented, especially in the wild and on species with large home ranges (Tinker et al. 2008, Darimont et al. 2009). A major limitation is the difficulty in acquiring repeated diet data on the same individuals to account for temporal variability in foraging behaviour. In that context, sub-sampling whiskers provided a unique opportunity to address this question in fur seals as they provided longitudinal isotopic data at a fine scale over numerous years.

**Inter-specific competition**

As expected, the overall isotopic niche breadth (TNW) of Antarctic fur seals was much greater in allopatry (Kerguelen) than in sympaty (Crozet, during the pup-rearing period). The increase occurred via δ^{15}N values (a proxy of the trophic level) which exhibited double the variation in Kerguelen, whereas the variation in δ^{13}C values (a proxy of the foraging habitat) was similar between the two populations. This niche expansion, also known under the name of “ecological release”, has been extensively described in many island vertebrates (e.g. Van Valen 1965, Diamond 1970, Prodon et al. 2002). The underlying hypothesis is that populations from species-poor habitats (e.g. islands) have access to a larger range of resources that would be depleted or monopolized in a highly competitive environment (e.g. mainland).

Previous tracking and isotopic studies have shown a spatial segregation in foraging niche between the two sympatric species at Crozet (Bailleul et al. 2005,
Cherel et al. 2007, Kernaléguen et al. 2012). Hence, a smaller δ¹³C TNW was also expected at Crozet. Isotopic δ¹³C values of marine organisms exhibit a latitudinal gradient in the Southern Ocean, allowing discrimination of foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010). However, δ¹³C values at the base of the trophic chain are not linearly related to latitudes but display stepwise changes, with little variation within a given water mass and abrupt changes at frontal zones (François et al. 1993, Trull & Armand 2001). In accordance with tracking studies (Bonadonna et al. 2001, Guinet et al. 2001, Bailleul et al. 2005), δ¹³C values showed that females from both islands foraged exclusively in one water mass during the pup-rearing period, the subantarctic zone. A limit of the isotopic method is that if resource pools differ little in isotopic values, consumers will have similar isotopic composition even if they differ substantially in their foraging habitats and prey.

Antarctic fur seal females breeding at Crozet and Kerguelen are known to feed primarily on myctophid fish (Cherel et al. 2007, Lea et al. 2008). Based on the isotopic values of females (this study) and their known diet from scat analyses (Cherel et al. 2007), higher δ¹⁵N TNW in allopatry is likely to reflect the consumption of a higher proportion of squid, and/or of myctophids with higher δ¹⁵N values (Cherel et al. 2010). The co-occurrence of the competitive species in Crozet might also impact the species composition of fur seals’ diet. For example, the main prey of Antarctic females breeding at Kerguelen (Cap Noir colony), Gymnoscopelus fraseri, is also the primary component of the diet of subantarctic, but not Antarctic females at Crozet, where the latter species feed mainly upon G. piabilis (Cherel et al. 2007, Lea et al. 2008). However, the isotopic method might fail to distinguish diet based on different fish species as they may have similar δ¹⁵N signatures.
Niche expansion can occur either when all individuals exploit a wider range of resources (increase of individual niche width) or when each individual keeps using a small range of available resources but diverge from each other (increase of among-individual differences). The Niche Variation Hypothesis (NVH) proposed by Van Valen (1965) supports the latter scenario and states that populations with wider niches are more variable than populations with narrower niches. Our data were in agreement with this prediction. The increase of $\delta^{15}$N TNW in allopatry was achieved by higher inter-individual variations while individual niche breadth remained unchanged. However, the effect of potential confounding factors could not be ruled out because of the lack of replication due to the challenge of studying wild marine species. Interestingly, the degree of individual specialisation, measured by the ratio WIC/TNW (see methods), was similar for both isotopic ratios: 0.52 and 0.49 in allopatry, and 0.80 and 0.73 in sympathy. As expected, during the inter-breeding period, when seals from Crozet are no-longer in sympatry, differences between the two populations decreased and results converged toward a similar level of individual specialisation.

An underlying question in individual specialisation is why individuals vary in their foraging strategy. If individuals were ecologically similar, they should all adopt the same optimum strategy to maximize their energy intake and, ultimately, their fitness (MacArthur & Pianka 1966, Schoener 1971). However, conspecific individuals differ in many traits including their morphology, age, social status, behaviour or physiology (Bolnick et al. 2011). For instance, in this study, fur seals varied in body size which is an important factor in their diving capacity as it determines their aerobic dive limit (Kleiber 1961). Larger females can dive longer and deeper (Costa et al. 2001), and have potentially access to a wider range of resource. Age is another component influencing foraging behaviour in pinnipeds (McDonald et al. 2009, Arnould et al. 2011). The age of the sampled females was not known, but can
potentially range from 3 to 20 years-old (Lunn et al. 1994). Furthermore, while females were all providing a pup the year of the study, they might not have been pregnant or lactating the previous years. Reproductive status can affect nutritional or energetic requirements which, in turn, modify individual’s optimum diet (Belovsky 1978).

Like elsewhere in the Southern Ocean, Antarctic and subantarctic fur seal populations at Crozet and Kerguelen are continuing to recover from the over-exploitation of the commercial sealing during the 18th and 19th centuries (Bonner & Laws 1964, Guinet et al. 1994). In contrast, the population of subantarctic fur seals at Amsterdam have stabilized (Guinet et al. 1994). As this population has reached its carrying capacity, the intra-specific competition level should accordingly be higher in the Amsterdam population than at Crozet (Gilpin & Ayala 1973). In addition, Authier et al. (2011) have reported that the probability of breeding success has decreased in Amsterdam as the population has stabilised, most probably as a consequence of increasing competition. Therefore, the impact of inter-specific competition in the subantarctic fur seal (sympatry in Crozet, allopatry in Amsterdam) may be masked by effects of contrasted level of intra-specific competition between the two populations and has not been investigated in this species. Since the absolute level of competition (inter- and intra-specific competition combined) should be much higher in Amsterdam, intra-specific competition should be the main ecological interaction explaining variations between the two populations.

**Intra-specific competition**

Overall isotopic niche breadth in subantarctic fur seals was much greater in Amsterdam than in Crozet, where the population is still increasing. This difference was also influenced primarily by $\delta^{15}$N values which exhibited double the variation in
5. Determinants of Individual Specialisation

Amsterdam than in Crozet. Variation in δ¹³C values within the two populations were alike and similar to that of Antarctic fur seal populations. Such a wider population niche is expected in a higher intra-specific competitive environment. Indeed, as the intra-specific competition intensifies, preferred prey resources become less abundant and Optimal Foraging Theory predicts that individuals should broaden their diet to include less-preferred prey (MacArthur & Pianka 1966). Consistent with this theory, individual δ¹⁵N niche breadth of subantarctic fur seals was higher in Amsterdam than in Crozet.

Inclusion of inter-individual phenotypic variation in classical Optimal Diet Theory reveals that intra-specific competition should also affect the strength of individual specialisation (Svanbäck & Bolnick 2005). If individuals differ in their prey rank preferences or the profitability of alternative prey, models predict their diet should vary in different directions as competition intensifies. For example, if individuals have different “preferred prey” (distinct preferences model), they might include in their diet secondary prey that were originally eaten by other conspecifics. As a consequence, the diet of individuals should become more similar as they feed on a larger diversity of prey. In contrast, if individuals have the same preferred prey (first choice) but vary in their ranking order of alternative prey (competitive refuge model) or vary in the profitability of these prey (willingness of adding novel prey, shared preferences model), the level of inter-individual variation should increase with the predator density up to a certain level, where individuals add all alternative prey and become generalist (Svanbäck & Bolnick 2005).

Empirical and experimental studies, mostly conducted in freshwater fishes, have consistently found a positive relationship between the population density and the degree of individual specialisation (e.g. Svanbäck & Persson 2004, Svanbäck &
Bolnick 2007, Huss et al. 2008). Similarly, in the present study, subantarctic fur seals exhibited a higher level of individual specialisation in their $\delta^{15}N$ values when breeding in higher density. Subantarctic fur seal females are also myctophid fish eaters, although females breeding at Crozet and Amsterdam feed on different species reflecting variation in prey distribution in their respective foraging zones (Beauplet et al. 2004, Cherel et al. 2007). As for the Antarctic species, a greater diversity in $\delta^{15}N$ values most probably reflected a higher range of prey size or type (squid and/or myctophid fish).

In contrast, $\delta^{13}C$ values revealed a higher degree of individual specialisation in Crozet, even though both populations exhibited a similar $\delta^{13}C$ TNW. Isotopic values indicated that females foraged exclusively in one water mass, the subantarctic or subtropical zone, during the whole pup-rearing period. As expected, subantarctic females breeding at Crozet had also a similar TNW that Antarctic females foraging in the same water mass. Higher inter-individual variation is predicted by models under certain circumstances (e.g. distinct preferences model, Svanbäck & Bolnick 2005). However, the lack of variation between the two populations’ TNW together with the small isotopic $\delta^{13}C$ variation in the environment suggest that results are more likely to be a methodological artefact. However, further studies in contrasted geographic and isotopic environments are required to better address this question.

**Ecological opportunity**

During the pup-rearing period, lactating females are central place foragers, alternating at-sea foraging trips with periods on land to suckle their pup. Following the lactation period, during the inter-breeding period, females are not constrained by the need to feed their pup. Consequently, their foraging grounds and associated prey are much less
spatially limited. With lactation periods varying substantially between Antarctic (4 months) and subantarctic (10 months) fur seals, their inter-breeding periods, and the opportunity for exploiting a greater diversity of foraging resources, also differ between the two species.

Whiskers isotopic values exhibited synchronous annual cycles in $\delta^{13}C$ and $\delta^{15}N$ values indicating temporal variation in foraging strategy. Individuals fed in different foraging habitat throughout the year and changed accordingly their diet. As a consequence, population and individuals niche breadths were not only determined by the diversity of resource used at a time but were also influenced by the duration of the studied period (pup-rearing or inter-breeding period). Accordingly, subantarctic females from both locations had a smaller individual niche breadth during the short inter-breeding period (2 months) than during the longer pup-rearing period (10 months). Similarly, individual niche widths of Antarctic fur seals were higher during the inter-breeding (8 months) than pup-rearing (4 months) period.

The index of individual specialisation was less influenced by this artefact as it is calculated as a ratio (individual to population variance, WIC/TNW, see Methods). Subantarctic fur seals exhibited among the highest levels of specialisation found in the present study during the inter-breeding period, when they were no longer central place forager and could disperse. The degree of inter-individual variation was consistently higher than during the pup-rearing period. This result is in agreement with recent studies which have consistently found higher dietary inter-individual variation when resource diversity increases, either temporally (Herrera et al. 2008) or spatially (Layman et al. 2007, Darimont et al. 2009, Evangelista et al. 2014). Higher levels of individual specialisation were always associated with higher population niche breadth. In the present study, $\delta^{13}C$ and $\delta^{15}N$ TNW were similar during the pup-rearing and
inter-breeding periods. However, pup-rearing TNW also included higher intra-individual temporal variation of foraging behaviour. Hence, results also suggested individuals used relatively a greater diversity of resource during the short inter-breeding period, both in terms of foraging grounds and diet.

In contrast, Antarctic females showed less inter-individual variation during the inter-breeding period, except for the δ\textsuperscript{13}C values of females breeding at Crozet. In contradiction with the Niche Variation Hypothesis (Van Valen 1965), the increase of TNW was mainly achieved by higher individual niche breadth, suggesting that females dispersed to the same productive area after weaning. The inter-breeding period (when females gain condition in preparation for the next lactation period) lasts 8 and 2 months in the Antarctic and subantarctic fur seal, respectively. Consequently, the shorter period available to the latter species may lead to increased inter-individual divergence in foraging area or prey selection to avoid competition. Moreover, the difference in the duration of the inter-breeding period between the two species might also affect the calculation of individual specialisation indices. Estimations of population and individual niche width variances are dependent of the sample size (amount of time averaging) and may have different asymptotic properties as it increases. So it is possible that the longer inter-breeding period for the Antarctic fur seals results in more time averaging and thus a lower estimate of individual specialisation (Bearhop et al. 2004a). However, the latter hypothesis may not explain the opposite trend found in the two species.

Interestingly, isotopic niche of Antarctic females from both sites greatly overlapped during the inter-breeding period, indicating females exploited the same resources in the same water mass. Simultaneously, difference in the degree of individual specialisation between females breeding at Crozet and Kerguelen decreased
5. Determinants of Individual Specialisation

during the inter-breeding period, and $\delta^{15}N$ WIC/TNW ratios were similar in both populations. These results confirmed the level of individual specialisation is mainly driven by the local environment, even at a short-term scale, and does not seem a characteristic of a population.

In summary, the results of the present study highlighted the importance of examining variation in several aspects of the ecological niche (spatial, dietary and temporal, as determined by whisker stable isotopes) as contrasting trends may be observed depending on the parameter investigated. In accordance with Araújo et al. (2011) predictions, for the two Antarctic fur seal populations, levels of inter-individual variation were similar during the inter-breeding period, when their isotopic niches overlapped and were presumed to experience a similar degree of competition and ecological opportunity. However, during the pup-rearing season, when both populations were constrained to contrasting levels of inter-specific competition, the degree of individual specialisation diverged, confirming an effect of competition on the level of inter-individual variation. Higher levels of inter-individual variation were found in lower inter- and higher intra-specific competition environments. The influence of ecological opportunity, however, differed between the species and was primarily influenced by the local environment and specific biological cycle and constraints of the two species.
Reproductive Consequences of Individual Trophic Specialisation: is it What You Eat or How Much?

A version of this chapter has been submitted as:

Kernaléguen L, Cherel Y, Guinet C, Arnould JPY Reproductive consequences of individual trophic specialisation: is it what you eat or how much?

Open Science – in review
Abstract

Individual specialisation is widespread among wild populations. While its fitness consequences are central in predicting the ecological and evolutionary trajectories of populations, they remain poorly understood. Long-term individual foraging specialisations occur in male Antarctic (Arctocephalus gazella) and Australian (A. pusillus doriferus) fur seals. Strong selective pressure is expected in these highly dimorphic and polygynous species, raising the question of the fitness payoffs associated with different foraging strategies. We investigated the relation between individual isotopic niche (a proxy of foraging specialisation), body size and condition, and an index of reproductive success (harem size) in territorial males. Individuals varied greatly in their skin and fur isotopic values reflecting a range of foraging strategies within the two populations. However, in both species, isotopic niche was not correlated to body size, condition or mating success ($R^2 / \rho < 0.06$). Furthermore, no foraging niche was predominant in either species, which would have indicated a substantial long-term fitness benefit of a particular strategy via a higher survival rate. These results suggest that the fitness consequences of a foraging strategy depends not only on the quality of prey and feeding habitat but also on an individual’s hunting efficiency and skills.
6. Fitness Consequences of Individual Specialisation

**Introduction**

Within a population, individuals vary in many traits including their morphology, physiology, breeding status or learned abilities such that their optimal foraging strategy may differ, potentially leading to individual specialisations (Bolnick et al. 2003). While individual variation in resource-use has been widely documented (Bolnick et al. 2003), less is understood about the consequences of such specialisation. In environments where food is limited, foraging efficiency determines the quantity and quality of energy that can be allocated to growth, reproduction and survival. Furthermore, when targeting different resources, individuals might be exposed to different levels of threat such as predation (Darimont et al. 2007) or pathogen exposure (Johnson et al. 2009). Hence, different feeding strategies could result in different fitness payoffs (Marra et al. 1998, Vander Zanden et al. 2014).

In sexually dimorphic polygynous mating systems, only the largest, most dominant males have access to females such that breeding success can vary dramatically between individuals. For example, as few as 3% of male northern elephant seals (*Mirounga angustirostris*) can be responsible for up to 92% of the mating observed within a breeding season (Le Boeuf & Reiter 1988). As large body size provides advantages in male-male conflicts for the defence of territories or females, there is strong selection for increasing male size. Indeed, pinnipeds display the greatest size dimorphism in vertebrates, with males weighing up to 10 times the mass of females in some species (Authier et al. 2012). Recent studies have demonstrated long-term individual dietary specialisation in male Antarctic (*Arctocephalus gazella*) and Australian (*A. pusillus doriferus*) fur seals (Cherel et al. 2009, Kernaléguen et al. 2012, Kernaléguen et al. 2015b). As territorial bulls are expected to be subject to strong selective pressure toward efficient foraging behaviour,
they provide a unique opportunity to test the fitness consequences of individual specialisation. Therefore, the aim of the present study was to test the relationship between males’ foraging strategy and reproductive success and body condition in these two fur seal species.

**Methods**

The study was conducted at the Antarctic fur seal Pointe Suzanne colony (49°26’S, 70°26’E), Kerguelen archipelago, during the 2013 mating season. Pointe Suzanne is a low-density colony spread along ~1km of coastline which consists of a narrow beach bordered by a small cliff surrounded by a plateau. Approximately 25% (n=12), 100% (n=38) and 100% (n=24) of males seen within the same location for several consecutive days in the beach, plateau and hinterland, respectively, where individually paint-marked, using a brush fixed on a 2.5 m long pole. A relative index of mating success for each male was estimated from the total number of females present within the male’s harem during its tenure duration (i.e. cumulative number of females during male’s tenure duration). Number of females present in each harem was daily counted, from the 5th of December when the first pup was born, until the end of the mating season (31st of December). However, harem sizes could not be monitored from the 14th to the 21st due to logistic reasons.

Skin and fur biopsy samples were obtained from 69 and 73 males, respectively, using an 8 mm biopsy head. Biopsies were performed manually, with the biopsy head attached to a 2 m long pole. Length and body condition (Surface/Length) indices at arrival was assessed for 53 males using laser-metrics. Two parallel laser-pointers (30 mW Aussie Made Rifle Pistol Green Lasers Pointers, Telescopes and Astronomy, Ohalloran Hill, WA, Australia) were mounted 200 mm apart on a digital camera. Laser
parallelism was checked before each photograph session at a distance of 25 m. All photographs were taken at distances <10 m, while males were in the prone position and perfectly perpendicular to the laser beams. Straight length index, from nose to tail, and the surface of males were estimated on photographs using the two laser beams as a scale, in Adobe Photoshop CS6.

Fieldwork was conducted on the Australian fur seal on Kanowna Island (39°10'S, 146°18'E), during the 2012 mating season. The Kanowna Island colony is a heterogeneous area varying primarily in elevation (i.e. access to water) (Lourie et al. 2014). Seven zones of contrasted quality have previously been described, covering 53% of the colony. The boundary of harems are not distinguishable in this higher density colony such that harem size was calculated as the ratio between the number of females and territorial males within each zone (Lourie et al. 2014). Males were individually identified from natural marks (e.g. scars, fur coloration). An index of relative mating success was calculated from 39 males across six zones, corresponding to 49% of territorial males breeding within these zones. Census of bulls and females were performed every three days, from the 6th of November until the 16th of December. Unusual high movement of females were observed on the 13th of December due to uncharacteristic early morning hot temperatures. Hence, data for this specific day were excluded. A hair sample was collected from these territorial males using an 8 mm biopsy head attached to an arrow launched by a crossbow (Sanlida Chase Wind 90 lbs).

The stable isotope niche of a predator provides a proxy of its foraging ecology, with $\delta^{13}C$ and $\delta^{15}N$ values documenting individual foraging habitat and trophic level, respectively (Kelly 2000). While skin documents the feeding habits over the last few weeks prior to males arriving at the colony, fur is a metabolically inert tissue and
reflects the isotopic signature of the diet during the last moult, 7-8 months prior to the breeding season. Prior to analysis, lipids were removed from skin samples using a cyclohexane solvent and only guard hairs were analysed. Replicate measurements of internal laboratory standards indicated isotopic measurement errors <0.10‰ for both isotopic ratios. Groups were compared using one-way ANOVA or Kruskal-Wallis test, and the percentage of isotopic niche overlap was calculated as the overlap of the standard ellipse area corrected for unbalanced sample sizes (SEAc) of each group, using the Bayesian ellipse-based metrics SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011), using the SIAR package in R (Jackson et al. 2011). Correlation were tested using Pearson or Spearman’s rank correlation, according to the normality of data. Statistics were performed using R3.0.3.

Results

Territorial male Antarctic fur seals varied greatly in size and body condition (Table 6.1). Males tended to be smaller in the hinterland ($F_{2,50}=2.86$, $P=0.066$) but of similar length and condition in the beach and plateau (Table 6.2). Tenure duration and the index of mating success were similar in the beach and plateau, and lower in the hinterland where harems are usually smaller and unstable (Table 6.2). Males occupied a large isotopic niche (Table 6.1), with no variation in skin or fur isotopic values between zones (all $F_{2,66}<2.66$, $P>0.17$, with pairwise SEAc overlap ranging from 89 and 92% and 68 and 88% for skin and fur samples respectively). There were no relationships between length or body condition and male tenure duration or their index of mating success (all $p<0.03$, $P>0.27$, n=53). Similarly, skin and fur $\delta^{13}C$ and $\delta^{15}N$ values were not correlated to length, body condition (all $R^2<0.06$, $P>0.07$, n=53), or index of mating success (both $p<0.01$, $P>0.33$, n=69/73, Figure 6.1).
Table 6.1 Index of mating success, isotopic values, and body size and condition of territorial male Antarctic and Australian fur seals. Results are mean ± SD (range).

<table>
<thead>
<tr>
<th></th>
<th>Antarctic fur seal</th>
<th>Australian fur seal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tenure duration (d)</td>
<td>27.9 ± 14.4 (4; 41)</td>
<td>34.0 ± 6.3 (12; 39)</td>
</tr>
<tr>
<td>Overall number of females</td>
<td>52.7 ± 43.7 (0; 147)</td>
<td>94.3 ± 54.6 (44.6; 218.2)</td>
</tr>
<tr>
<td>Fur δ¹³C (%)</td>
<td>-22.6 ± 0.9 (-24.9; -20.2)</td>
<td>-16.5 ± 1.0 (-18.4; -12.2)</td>
</tr>
<tr>
<td>Fur δ¹⁵N (%)</td>
<td>10.4 ± 0.8 (8.4; 12.4)</td>
<td>16.1 ± 0.7 (14.2; 17.8)</td>
</tr>
<tr>
<td>Skin δ¹³C (%)</td>
<td>-21.6 ± 1.2 (-24.0; -19.0)</td>
<td></td>
</tr>
<tr>
<td>Skin δ¹⁵N (%)</td>
<td>12.8 ± 0.8 (10.9; 14.7)</td>
<td></td>
</tr>
<tr>
<td>Length (cm)</td>
<td>147 ± 9 (121; 167)</td>
<td></td>
</tr>
<tr>
<td>Body condition index (cm)</td>
<td>24 ± 2 (19; 28)</td>
<td></td>
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</table>

Table 6.2 Reproductive success index, isotopic values and body size and condition of territorial male Antarctic fur seals breeding on the beach, plateau and hinterland.

<table>
<thead>
<tr>
<th></th>
<th>Beach</th>
<th>Plateau</th>
<th>Hinterland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tenure duration (d) *</td>
<td>--</td>
<td>30.8 ± 13.8 a</td>
<td>16.8 ± 10.3 b</td>
</tr>
<tr>
<td>Overall number of females *</td>
<td>64.8 ± 36.2 a</td>
<td>67.1 ± 45.1 a</td>
<td>23.8 ± 29.4 b</td>
</tr>
<tr>
<td>Fur δ¹³C (%)</td>
<td>-22.5 ± 1.0</td>
<td>-22.5 ± 1.0</td>
<td>-22.8 ± 0.8</td>
</tr>
<tr>
<td>Fur δ¹⁵N (%)</td>
<td>10.2 ± 0.7</td>
<td>10.6 ± 0.9</td>
<td>10.2 ± 0.7</td>
</tr>
<tr>
<td>Skin δ¹³C (%)</td>
<td>-21.7 ± 1.3</td>
<td>-21.5 ± 1.2</td>
<td>-21.7 ± 1.2</td>
</tr>
<tr>
<td>Skin δ¹⁵N (%)</td>
<td>12.6 ± 1.0</td>
<td>12.8 ± 0.8</td>
<td>12.7 ± 0.8</td>
</tr>
<tr>
<td>Length (cm)</td>
<td>149 ± 5</td>
<td>149 ± 9</td>
<td>142 ± 11</td>
</tr>
<tr>
<td>Body condition index (cm)</td>
<td>24 ± 2</td>
<td>24 ± 2</td>
<td>23 ± 2</td>
</tr>
</tbody>
</table>

Significant differences between zones are indicated (*, P<0.05), with subscripts representing homogenous subsets.

Tenure duration results are not reported for the beach as males were not sampled uniformly during the mating season, artificially increasing the average tenure duration of males breeding in this zone.
Figure 6.1 Skin and fur $\delta^{13}C$ and $\delta^{15}N$ values of territorial males in relation to their index of mating success.
Male Australian fur seals varied greatly in harem size, tenure duration and fur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Table 6.1). The index of mating success was not correlated with individual isotopic niche (both $p<0.02$, $P>0.41$, $n=38/39$) (Figure 6.1). Fur isotopic values were similar across all zones (both $H_7<8.9$, $P>0.26$, with pairwise SEAc overlap ranging from 47 and 100%, Table 6.3) indicating body size and condition, assessed by the location of breeding territories (Lourie et al. 2014), were not related to isotopic niche.

### Table 6.3 Fur isotopic values of male Antarctic fur seals holding a territory in six of the seven zones described by Lourie et al. (2014).

<table>
<thead>
<tr>
<th>Zone</th>
<th>Fur $\delta^{13}\text{C}$ (%)</th>
<th>Fur $\delta^{15}\text{N}$ (%)</th>
</tr>
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<tbody>
<tr>
<td>Zone 1</td>
<td>-16.9 ± 1.0</td>
<td>16.0 ± 0.7</td>
</tr>
<tr>
<td>Zone 2</td>
<td>-16.6 ± 0.1</td>
<td>16.1 ± 0.6</td>
</tr>
<tr>
<td>Zone 3</td>
<td>-16.4 ± 0.7</td>
<td>15.8 ± 1.0</td>
</tr>
<tr>
<td>Zone 4</td>
<td>-16.4 ± 0.9</td>
<td>16.2 ± 0.9</td>
</tr>
<tr>
<td>Zone 5</td>
<td>-14.4 ± 3.1</td>
<td>16.2</td>
</tr>
<tr>
<td>Zone 6</td>
<td>-16.5 ± 0.7</td>
<td>16.2 ± 0.7</td>
</tr>
</tbody>
</table>

### Discussion

While the skin and fur samples only measured two narrow time-periods in trophic niche, previous studies in these species have indicated short-term inter-individual variation in blood isotopic values were correlated with long-term specialisation revealed in whisker isotopic signatures (Cherel et al. 2009, Kernaléguen et al. 2012, Kernaléguen et al. 2015b, Kernaléguen et al. 2016). As expected (Cherel et al. 2009), territorial male Antarctic fur seals occupied a wide isotopic niche. While part of the isotopic variation may be attributed to inter-individual physiological variation, $\delta^{13}\text{C}$
values were characteristic of males foraging along a latitudinal gradient, from
Antarctic to subtropical waters. δ^{15}N values were highly correlated to δ^{13}C values,
indicating males altered their diet depending on their foraging habitat and the
associated prey. Results indicate bulls fed most likely on the Antarctic krill (*Euphausia
superba*) in Antarctic waters where this resource is highly abundant and switched to
myctophid fish and oceanic squids when foraging in northern areas (Cherel et al.
2009). Despite Australian fur seals having a much reduced habitat range than Antarctic
fur seals (Arnould et al. 2011, Kernaléguen et al. 2015b), territorial males of this
species also exhibited a wide isotopic niche. Interestingly, the range of isotopic values
was much larger than previously shown for adult females and, more importantly, small
but sexually mature males (Arnould et al. 2011, Kernaléguen et al. 2015b,
Kernaléguen et al. 2016), suggesting ontogenetic variation in foraging niche associated
with reproduction in males.

Body size is expected to confer an advantage in male-male conflicts and fasting
abilities in dimorphic, capital breeding, males (Le Boeuf & Reiter 1988). Accordingly,
larger male Australian fur seals hold territories in higher quality habitats which are
characterised by earlier occupancies, greater female densities and harem sizes, and are
occupied by larger breeding females (Lourie et al. 2014). Surprisingly however,
contrasted results were found for Antarctic fur seals. Males tended be to smaller in the
hinterland where harems are smaller and unstable. However, tenure duration and the
index of mating success were not correlated to body size or condition. This could be
due to the Pointe Suzanne being a low density colony and that competition for
territories is low enough that individual differences in motivation and personality or
that some level of female mate choice influence male mating success (Bones 1991).

Males of such highly polygynous, sexually dimorphic species are expected to
be subject to strong selective pressure toward efficient foraging behaviour. Hence, a
clear and strong pattern would be expected if specialisations differed in their respective fitness payoffs. However, individual foraging niche was not correlated to length, body condition, or mating success, in either species. It is possible that the consequences of specialisation occur at an earlier stage in the males' life (i.e. survival) and that territorial males across the colonies may already represent a reduced set of good quality individuals. However, territorial males of both species occupied a very large isotopic niche, indicating that a wide range of foraging strategies allows males to reach breeding age. Furthermore, no foraging niche was predominant in either species (Fig. 6.1), which would have indicated a substantial long-term fitness benefit of a particular dietary strategy via a higher survival rate (Authier et al. 2012). Alternatively, the use of a fairly high number of habitats has the consequence of diminishing consumer density in a given habitat, reducing potential inter-individual competition for trophic resources.

Contrasted results have been found on the reproductive consequences of individual specialisation in different taxa and ecological contexts (Marra et al. 1998, Woo et al. 2008, Authier et al. 2012, Vander Zanden et al. 2014). The main drivers maintaining individual variability appears to play an important role in predicting the occurrence of a relation. Where dietary specialisation is a heritable factor, natural selection should only maintain the most efficient strategies in the population, and all specialisations should confer similar fitness payoffs (Authier et al. 2012). In contrast, variation in fitness consequence would be expected where social dominance maintains sub-optimal strategies in the population (Marra et al. 1998), or when individual specialisation is driven by disruptive selection or fluctuating selection on specialists in time or space (Van De Pol et al. 2010, Cucherousset et al. 2011).

While the majority of studies investigate the impact of diet and habitat selection, fitness consequences might not vary depending on the type of resources used
but on the individual’s behaviour and hunting abilities. Indeed, the main driver of individual specialisation is individual variability, notably in morphology, physiology, experience or skills (Bolnick et al. 2003). As conspecifics differ in traits and characteristics, it is expected that the fitness payoff of a specific foraging strategy should vary between individuals, and that a range of foraging niches should confer fitness advantages depending on individual characteristics. Accordingly, in the present study, males occupying the same isotopic niche varied greatly in their body size, condition and mating success. This suggests that the fitness consequence of a foraging strategy depends not only on the quality of prey and feeding habitat, but also on an individual’s hunting efficiency and skills (i.e. not only what an individual eats but also how much).
General Discussion
Within population niche differentiation plays a major role in many ecological and evolutionary processes (Roughgarden 1972, Hughes et al. 2008, Bolnick et al. 2011). In particular, individual variability influences species diversity, species interactions and the role a population plays in its ecosystem, the resilience of a population toward perturbations, and provides the raw material for natural selection (Crutsinger et al. 2006, Lankau & Strauss 2007, Fridley & Grime 2010). Although resource partitioning is widespread among various taxa (Polis 1984, Shine 1989, Smith & Skulason 1996, Bolnick et al. 2003, Araújo et al. 2011) and has major implications, its causes and consequences remain poorly understood. Hence, using fur seals as model species, the overall objectives of this thesis were to report the incidence of within population resource partitioning, investigate the intrinsic and extrinsic factors driving niche segregation, and study the fitness consequences of individual specialisation.

**Intrinsic drivers shaping foraging niche segregation**

Populations consist of phenotypically diverse individuals. This phenotypic variability has long been proposed to explain niche differentiation within populations (Roughgarden 1972). As individuals differ in their morphology, age, sex, breeding status, physiology, competitive abilities, learned experiences and skills, the profitability of specific food types may vary such that individuals may have different optimal diets (Bolnick et al. 2003, Svanbäck & Bolnick 2005, Tinker et al. 2009). In most studies, these intrinsic factors are assumed to be the main causes of resource partitioning as they provide a potential mechanism explaining the observed niche differentiation.

For example, dramatic variation in body size between juvenile and territorial male Antarctic fur seals (*Arctocephalus gazella*) are likely to explain variation in their
respective foraging niche (Chapter 3). In particular, large bulls have the physiological requirements to reach the bottom of the continental shelf, while juveniles have lower oxygen storage due to their smaller body size and cannot dive and forage efficiently on the benthos (Chapter 3, Green 1997, Staniland & Robinson 2008). Variation in body size and shape can also explain variation in diet between female Australian fur seals (*Arctocephalus pusillus doriferus*) (Chapter 2, Arnould et al. 2011). Indeed, body shape influences a seal’s manoeuvrability and, ultimately, its efficiency at chasing and capturing different prey items (Fish et al. 2003). Similarly, variation in growth rate and breeding strategy are proposed to explain differences in the ontogenetic trajectory of the two sexes in the Antarctic fur seal (Chapter 3). The earlier maturing and breeding sex (females) shows a rapid ontogenetic shift and shares the same foraging niche as adults as soon as the age of 2, while males exhibit a more progressive variation in resource-use (Chapter 3). Differences in reproductive ecology can also explain sexual segregation in adults. For example, as females regularly return to the colony to suckle their pup, their foraging range is restricted, potentially leading to smaller spatial niche than their male counterparts (Chapter 4).

However, while intrinsic factors provide a potential explanation of within population variability, it is essential to test these predictions (Chapter 3). Size dimorphism and variation in breeding constraints are commonly proposed as the main factors explaining sexual niche segregation in many fur seal species (Chapter 4, Green 1997, Hindell & Pemberton 1997, Boyd et al. 1998, Loughlin et al. 1999, Campagna et al. 2001, Page et al. 2005b, Page et al. 2005a, Kirkwood et al. 2006, Page et al. 2006, Cherel et al. 2007, Staniland & Robinson 2008, Cherel et al. 2009, Kernaléguen et al. 2012, Franco-Trecu et al. 2014, Knox et al. 2014). However, under these assumptions, male and female pups should share the same ecological niche at weaning, when size dimorphism is minimum (<15%, Lunn et al. 1993) and seals do not face any breeding
constraints. Sexual niche segregation should mirror the progressive size divergence between the sexes and strengthen as adults start breeding. In contrast to these predictions, male and female Antarctic fur seals segregate as soon as weaning (Chapter 3). Niche variation is of a similar amplitude as observed in full-size breeding adults and is maintained throughout the whole development of seals. These results indicate size dimorphism and differences in breeding strategy are not the main factors driving sexual niche segregation, highlighting the importance of testing the actual role factors play in shaping resource partitioning. However, investigating the mechanism of niche differentiation raises methodological issues.

Niche segregation is, indeed, likely to be caused by a combination of factors, and disentangling the effect of each parameter is often difficult in empirical studies. Ideally, the study system should allow one variable to vary, while all other potential factors remain constant. Comparison between populations or sub-groups of a population can potentially provide such possibility. For example, a case study where neonatal young Nubian ibexes (*Capra ibex nubiana*) were naturally confined in a predator-free area has demonstrated variation in foraging behaviour of female ibexes. Females feeding on their own while their young remained in this safe environment were foraging in different habitats than females feeding with their young, supporting the predation-risk hypothesis (Kohlmann et al. 1996). Experimental studies are another way to control variables and test their relative influence in driving niche differentiation. Castrated males provide a good opportunity to manipulate breeding status and size of male individuals and quantify the effect of these factors in the emergence of sexual niche variation (Ruckstuhl et al. 2006). Other experimental studies have demonstrated a fitness benefit associated with niche differentiation, providing a basis explaining resource partitioning (Croft et al. 2006, Ruckstuhl 2007). For instance, in the shoaling fish threespine stickleback (*Gasterosteus aculeatus*),
be behavioural synchrony cost is lower, and growth rate higher, when an individual is associated with fish of similar body size, in accordance with the activity budget hypothesis (Ruckstuhl 2007).

Alternatively, investigating the ontogeny of segregation enables determining at which life-stages, associated with which life-history traits, niche differentiation occurs (Chapter 3). Accordingly, studies have identified the timing of niche segregation, highlighting potential drivers such as differences in body size (Shine et al. 1998, Vincent et al. 2004), growth rate (Stewart 1997), social interactions (behavioural dominance hypothesis, Marra 2000, Catry et al. 2004) or trade-offs between growth and survival and/or exploration and local knowledge (Chapter 3). Meta-analyses can also highlight general patterns across populations and species. For example, a comparative analysis on size monomorphic and dimorphic species across a broad range of ungulate species has enabled to test the existence of a consistent pattern linking sexual size dimorphism and segregation (Mysterud 2000).

**Extrinsic drivers shaping foraging niche segregation**

Within population niche segregation is a plastic trait that can vary in time and space. For example, the degree of individual specialisation of female Antarctic fur seals varies through year, as females forage in different habitats during the breeding and inter-breeding periods (Chapter 5). Furthermore, females from two populations (breeding in Crozet and Kerguelen, respectively) exhibit a similar degree of individual specialisation during the inter-breeding period, when they forage in the same habitat, upon the same resources. However, the level of individual niche variation of the two populations varies during the breeding period when females exploit different feeding
grounds, illustrating the influence of the local environment on the level of specialisation (Chapter 5).

Prey availability plays a major role shaping resource partitioning (Svanbäck & Bolnick 2005, Araújo et al. 2011, Svanbäck et al. 2011). Indeed, the optimal diet of an individual depends on its efficiency at detecting, capturing, handling and digesting prey (intrinsic factors), as well as the encounter rate and energetic content of alternative prey (extrinsic factors) (MacArthur & Pianka 1966). Hence, the super abundance of a resource can mask any potential resource partitioning, at the individual or species levels (Cherel et al. 2007). Similarly, when the diversity of resources is limited, the environment might not provide the ecological opportunity for individuals to segregate (Chapter 4, Chapter 5, Darimont et al. 2009, Araújo et al. 2011, Robertson et al. 2015). Accordingly, female subantarctic fur seals (Arctocephalus tropicalis) exploit a greater diversity of resources and exhibit a higher level of individual specialisation during the inter-breeding period, when they are not as spatially restricted in their foraging ground compared to the breeding season (Chapter 5). Similarly, the Australian fur seal, which is highly restricted in its foraging habitat due to its benthic foraging mode, shows very limited sexual niche differentiation (Chapter 4) when compared to epi-pelagic foraging fur seal species (Chapter 3, Page et al. 2005b, Staniland 2005, Kernaléguen et al. 2012, Franco-Trecu et al. 2014).

Various factors can influence prey availability. Among the abiotic factors, temperature, precipitation, solar radiation, wind velocity and humidity greatly impact the productivity of terrestrial and marine ecosystems, influencing prey abundance at higher trophic levels (Polis 1999). Among the biotic factors, Araújo et al. (2011) identified four main ecological interactions shaping the level of individual specialisation: inter- and intra-specific competition, ecological opportunity and predation. These factors have long been known to influence population niche width
(Diamond 1970, Roughgarden 1972, Bolnick 2001). For instance, during an interspecific competition release, populations are expected to broaden their ecological niches, and occupy the empty niche of the missing species. However, less is known how these ecological factors influence individual niches (Araújo et al. 2011). During competition release, every individuals in the population might extend the range of resources they use which would not impact the degree of individual specialisation. Alternatively, individual niche breadth might be constrained, for instance by functional trade-offs (Estes et al. 2003, Svanbäck & Eklöv 2003, Tinker et al. 2009), and increase of population niche might be achieved by an increase of among-individual variation. The niche variation hypothesis supports the latter scenario and states that populations with wider niches are more variable than populations with narrower niches (Van Valen 1965). Accordingly, recent studies have shown a positive relationship between population niche breadth and degree of individual specialisation (Bolnick et al. 2007, e.g. Araújo et al. 2008, Svanbäck et al. 2008, Araújo et al. 2011, Svanbäck et al. 2011, Tinker et al. 2012). Similarly, ecological opportunity, inter- and intra-specific competition affect Antarctic and subantarctic fur seal population niche width. In all but one case, populations with a wider niche exhibit a greater level of individual specialisation (Chapter 5).

Svanbäck and Bolnick (2005) integrated these extrinsic and intrinsic factors into an Optimal Diet Theory and conceptualised variation in population and individual niche width under various levels of intra-specific competition. As forager density increases, preferred prey become scarce and individuals are expected to broaden their diet and include secondary prey. Individuals might vary in their prey ranking order and/or benefit to add novel prey due to individual variability in phenotypic traits or experience. Accordingly, the degree of specialisation should increase if individuals share the same preferred prey (first choice) but vary in their ranking order of alternative
prey (competitive refuge model) or vary in the profitability of these prey (shared preferences model). In reverse, if individuals vary in their preferred prey (distinct preferences model), they might include in their diet secondary prey that were originally eaten by other conspecifics which would result in a decrease of individual variation (Svanbäck & Bolnick 2005). These models propose a mechanistic basis for diet variation and establish a theoretical framework linking prey availability, phenotypic variability and the level of individual specialisation.

Resource availability fluctuates greatly in time. It is, thus, essential to investigate the incidence of niche differentiation over an appropriate time-scale (Chapter 2, Novak & Tinker 2015). In particular, long-term studies might not account for potential temporal variation in individual diet (due to variation in prey abundance but also energy requirement, breeding constraints, physiology over time). Accordingly, pooling diet data over a long period of time raises time-averaging issues and tends to under-estimate the strength of niche segregation (Chapter 2, Novak & Tinker 2015). For example, cabbage butterflies (*Pieris rapae*) preferentially target the first flower encountered during the day (Lewis 1986). As the search image changes every day, they appear to be generalist over a period of several days, whereas they exhibit substantial individual specialisation at a daily time-scale. Similarly, the isotopic niche of female Australian fur seals varies over the seasons, such that some females occupy a distinct niche at all time, but their overall niche greatly overlap (Fig. 2.4.d, Chapter 2).

Conversely, short-term studies are prone to stochastic sampling errors as they might not be representative of the full range of resources individuals exploit (Chapter 2, Bearhop et al. 2004a, Novak & Tinker 2015). For instance, generalist individuals might exhibit high degrees of specialisation if they encounter a patch of a specific prey just before the sampling period. When not recording the intra-individual variation in
resource-use, short-term studies are likely to over-estimate differences between individuals and artificially increase the apparent degree of individual specialisation of a population (Bearhop et al. 2004a). The method used and time-scale over which individuals are monitored can affect our estimation of within population niche segregation. It is, thus, essential to explicitly take into account time in studies (Chapter 2, Novak & Tinker 2015). Ideally, time-scale should be in accordance with the study system (i.e. species biology and prey temporal fluctuation). When methodology is constrained, it is crucial to take into consideration the potential bias associated with the method used.

**Fitness consequences of individual specialisation**

When foraging on different set of resources, individuals may vary in the quantity and quality of energy gained that can be allocated to growth, reproduction and survival, such that different diets may provide contrasting fitness payoffs (Marra et al. 1998, Bearhop et al. 2004b, Vander Zanden et al. 2014). Furthermore, direct diet-specific risk factors may apply as foraging individuals are commonly a vulnerable target for predators and parasites (Darimont et al. 2007, Johnson et al. 2009). Individuals might also vary in their respective degree of specialisation (Chapter 2, Bolnick et al. 2002, Araújo et al. 2008, Araújo et al. 2010, Tinker et al. 2012), which might also lead to variation in fitness benefits. For example, life-span of southern elephant seals (*Mirounga leonina*) is not related to their foraging habitat but increases when individuals exhibit an early ontogenetic shift and are consistent in their foraging areas (Authier et al. 2012).

However, while the existence of fitness consequence of individual specialisation has received some theoretical and empirical support (e.g. Post 2003,
Gunnarsson et al. 2005, Cucherousset et al. 2011, Vander Zanden et al. 2014, Robertson et al. 2015), other studies have found no evidence of a relationship between individual niche and fitness indices (e.g. Chapter 6, Lea & Dubroca 2003, Watanuki et al. 2003, Votier et al. 2004, Woo et al. 2008, Ceia et al. 2012). For example, while strong selective pressure toward foraging efficiency are expected in dimorphic polygynous species, foraging niche is not correlated to individual mating success or body size and condition in territorial male Antarctic and Australian fur seals (Chapter 6). The absence of relationship between individual niche and fitness is likely to be more widespread among populations than currently documented, with negative results being underrepresented in published studies.

Several factors might explain such variation in the fitness consequences of individual specialisation. The ecological context, such as resource abundance, degree of competition, and occurrence of extreme climatic events can influence the strength, incidence, and even the direction of the relationship between foraging strategies and their fitness payoffs (Van De Pol et al. 2010, Robertson et al. 2015). For instance, annual fitness is slightly higher for generalist Eurasian oystercatchers (Haematopus ostralegus ostralegus) than for specialist birds during most years, but substantially lower during rare but extreme cold winters (Van De Pol et al. 2010). Hence, studies conducted over one year could potentially lead to opposite conclusions depending on the environmental conditions during the study period.

The drivers maintaining individual niche variability might also influence the consequences of specialisation (Marra 2000, Cucherousset et al. 2011). Indeed, if a foraging strategy is conferring a substantial fitness advantage, it should be highly selected within the population, limiting the degree of individual variability over time (Chapter 6, Authier et al. 2012). When variation in phenotypic traits leads individuals to vary in their foraging strategy, individuals are also expected to vary in the fitness
payoffs of a particular strategy, and, conversely, individuals occupying different niche
can potentially gain a similar fitness benefit from their respective strategy. This would
weaken or even remove any relationship between individual fitness and its foraging
niche (Chapter 6, Woo et al. 2008). In contrast, in various migratory bird species,
larger dominant birds exclude sub-ordinates from high quality winter habitats. Where
social dominance maintains sub-optimal strategies in the population, a consistent
relationship between winter ecological niche and the subsequent reproductive success
has been reported (Marra et al. 1998, Marra 2000, Bearhop et al. 2004b, Norris et al.
of individual specialisation has been observed when individual specialisation is driven
by disruptive selection and/or fluctuating selection on specialists in time or space (Van
De Pol et al. 2010, Cucherousset et al. 2011).

A major limitation in investigating the consequences of individual
specialisation is the difficulty to disentangle the causes and consequences of
specialisation. For example, variation in body size and shape in the Australian fur seal
might explain why females forage on different resources (Chapter 2). Alternatively,
size difference might be a consequence of specialisation, with contrasted diet
providing different payoffs. Another major limitation is the estimation of individual
fitness. Fitness is the life-span contribution to the gene pool of the next generation,
which is extremely difficult to quantify. Fitness indices used in studies often consider
only one fitness-related aspect (e.g. reproductive success, survival or body condition),
over one season (Chapter 6, Marra et al. 1998, Bearhop et al. 2004b, Cucherousset et
al. 2011). However, strong trade-offs exist between reproduction, growth and survival
such that considering only one aspect might not be representative of the actual fitness
payoffs of a foraging strategy (Main & Coblentz 1996, Darimont et al. 2007).
Furthermore, consequences of individual specialisation are likely to vary over time, as

**Perspectives and future research direction**

Causes and consequences of niche differentiation appear to be tightly related. Consequences of specialisation seem to be influenced by the main factors driving resource partitioning and the ecological context. Conversely, the ultimate cause for individuals to exploit different resources should be that it confers them a fitness benefit. Hence, comprehensive studies that integrate both the intrinsic causes and consequences of niche segregation, as well as the influence of the local environment, should provide a better understanding on the underlying mechanisms driving individuals of a same population to occupy distinct niches.

The first studies investigating within population niche segregation were mostly qualitative, documenting the fact that individuals of a same population can potentially occupy different ecological niches (Shine 1989, Bolnick et al. 2003). More recent studies have adopted a more quantitative approach, allowing to compare the degree of niche differentiation among populations and species (Araújo et al. 2011). This has enabled intrinsic causes of niche segregation to be identified, such as individual or sexual variation in phenotypic traits (e.g. morphology, physiology, digestive abilities) or emergent traits (e.g. competitive abilities, social status, parasite resistance). The emergence of individual variation in these traits can be stochastic, environmentally induced or genetic (Bolnick et al. 2011). An important future direction is, therefore, to determine these ultimate causes of niche differentiation as they greatly influence the heritability of these traits as well as the temporal consistency of niche differentiation.
These, in turn, have a dramatic influence on the extent individual niche variation impacts the evolutionary trajectory of a population and shapes population dynamics and community structure (Hughes et al. 2008, Bolnick et al. 2011).

Populations exhibiting a certain level of individual specialisation are likely to be composed of both generalist and specialist individuals. Network analyses allow describing the organisation of resource partitioning among individuals (Araújo et al. 2008, Pires et al. 2011, Tinker et al. 2012) and recent studies have highlighted a consistent nestedness pattern across various taxa (co-existence of specialist and generalist individuals, with the resources used by specialists being ordered, predictable subsets of the resources used by generalist individuals) (Araújo et al. 2010, Tinker et al. 2012, Dáttilo et al. 2014, Chapter 2). Such variation in the degree of specialisation has also substantial implications in the consequences of individual specialisation in evolutionary and ecological processes. Indeed, this adds a level of complexity in species and population interactions which should, ultimately, be integrated into theoretical models of population demography, species interaction and adaptation.


Bolnick DI, Svanback R, Araujo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences 104:10075-10079


Bridcut EE, Giller PS (1995) Diet variability and foraging strategies in brown trout (Salmo trutta): an analysis from subpopulations to individuals. Canadian Journal of Fisheries and Aquatic Sciences 52:2543-2552


Cherel Y, Hobson KA, Guinet C (2015) Milk isotopic values demonstrate that nursing fur seal pups are a full trophic level higher than their mothers. Rapid Communications in Mass Spectrometry 29:1-6


Gilpin ME, Ayala FJ (1973) Global models of growth and competition. Proceedings of the National Academy of Sciences 70:3590-3593


Hirons AC, Schell DM, St Aubin DJ (2001) Growth rates of vibrissae of harbor seals (Phoca vitulina) and Steller sea lions (Eumetopias jubatus). Canadian Journal of Zoology 79:1053-1061


in assessing individual foraging specialisation in Australian fur seals. Oecologia In press


156


158


Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86:3-15


Tinker MT, Mangel M, Estes JA (2009) Learning to be different: acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations. Evolutionary Ecology Research 11:841-869


« Peut-être qu’ainsi j’apprendrai à ne plus poser de questions. Est-ce qu’on interroge la mer ? Est-ce qu’on demande des comptes à l’horizon ? Seuls sont vrais le vent qui nous chasse, la vague qui glisse, et quand vient la nuit, les étoiles immobiles, qui nous guident »

J.M.G Le Clézio, Le Chercheur d’Or
“Maybe, this way, I shall learn not to ask questions anymore. Does one ask questions of the sea? Does one ask justifications of the horizon? The wind that chases us; the wave that glides; only those are real, and when the night comes, so are the fixed stars, that guide us”

J.M.G. Le Clézio, The Prospector