FORAGING STRATEGIES AND EFFICIENCIES OF LACTATING NORTHERN AND ANTARCTIC FUR SEALS: IMPLICATIONS FOR REPRODUCTIVE SUCCESS

by

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Abstract

Efficient extraction of energy from the environment is key to the survival and reproductive success of wild animals. Understanding the ratio of energy gained to energy spent of different foraging strategies (*i.e.*, foraging efficiency) can shed light on how animals cope with environmental changes and how it affects population trajectories. I investigated how female foraging strategies during the breeding season impact the foraging efficiencies and reproductive successes of two fur seal species—one declining (NFS–northern fur seals, St. Paul Island, Alaska) and one increasing (AFS–Antarctic fur seals, Kerguelen Island, Southern Ocean). I also sought to develop new accelerometry-based methods to easily determine fine-scale energy expenditure at sea (VeDBA and flipper stroke metrics). Twenty lactating females of each species were captured and equipped with biologging tags to record GPS locations, depth and tri-axial acceleration. Energy expenditure for each foraging trip was measured using the doubly-labeled water method, and energy gained while foraging was determined from 1) diet composition (scat hard-parts and DNA) and blood stable isotope ratios; and 2) numbers of prey capture attempts (from head acceleration). Maternal investment in pups was determined from pup growth rates or from energy content of milk samples. Results showed acceleration metrics were only accurate at predicting energy expended by fur seals when time-activity budgets were taken into account (*i.e.*, time spent performing different types of activity). Foraging strategies of AFS females resulted in efficiencies of ~3.4, with more efficient females producing bigger pups at weaning that had greater chances of survival. NFS females employed two foraging strategies with very different efficiencies (~1.4 vs ~3.0) that were associated with different foraging habitats and diet qualities. However, NFS with the more efficient strategy (3.0) undertook longer foraging trips than the other NFS (1.4) or AFS (3.4), and thus fed their pups ~20% less frequently. As a consequence, the declining NFS (unlike the increasing AFS) had to compromise between the rate of energy acquisition and the pup feeding frequency. Such reductions in energy intake and time allocated to nursing pups can ultimately lower juvenile survival, and may explain the population decline of NFS in Alaska.

Preface

I designed the research protocols and conducted the field experiments described in Chapters 3 to 6, and performed all of the data analyses in all of the Chapters. I also prepared and wrote Chapters 2 to 6 as stand-alone manuscripts for publication. I benefited from comments and edits by co-authors Andrew Trites and Christophe Guinet (Chapters 2 to 6), John Arnould (Chapters 2, 3, 5 & 6), and Yves Cherel and Austen Thomas (Chapter 4). Laboratory measurements of oxygen and hydrogen stable isotope for the doubly-labeled water analyses (Chapters 2, 3, 5 and 6) were done at John Speakman's Isotope Laboratory in Energetics at the University of Aberdeen in Scotland. DNA-metabarcoding measures of northern fur seal scats were performed in collaboration with Austen Thomas (Chapter 4). Identification of scat hard part remains were performed by Pacific ID Inc., Victoria, BC, Canada for northern fur seal scats, and in collaboration with Yves Cherel at the CEBC, CNRS France for Antarctic fur seal scats (Chapters 4, 5, & 6). Northern fur seal milk samples were analysed at the SGS Canada Laboratories in Burnaby, BC, Canada (Chapter 6). All the work was approved under the US NMFS permit # 14329-01, the UBC animal care permit # A10-0364 and the ethical regulations approval from the French Polar Institute (IPEV).

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Lists of abbreviations

AFS	Antarctic fur seal
AIC	Akaike Information Critera
AICc	Second-order Akaike Information Critera
BM	Body Mass (kg)
BMR	Basal Metabolic Rate (MJ/d)
CI	Confidence Intervals
COT	Cost of Transport (J/m)
DBA	Dynamic Body Acceleration (m/s^2)
DD	Daily-Diary tag
DLW	Doubly-Labeled Water
DNA	Deoxyribonucleic Acid
EC	Energy Content (kJ)
ED	Energy Density (kJ/g)
EDTA	Ethylenediaminetetraacetic Acid
EE	Energy Expenditure (MJ)
ENSO	El Nino Southern Oscillation
ESS	Error Sum of Squares
FE	Foraging Efficiency
FL	Fish Length (cm)
FO	Frequency of Occurrence
GCDC	Gulf Coast Data Concept
gls	Generalized Least Square
GPS	Global Positioning System
hclust	Hierarchical Cluster Analysis
ID	Identity
IPEV	Institut Paul Emile Victor
LIENSs	Laboratoire du Littoral Environnement et Sociétés
lm	Linear Model
lme	Linear Mixed-Effects model

LRL	Lower beak Rostrum Length
MR	Metabolic Rate (MJ/d)
nlme	Non Linear Mixed-Effects models
nls	Non-Linear Least Squares
NFS	Northern fur seal
ODBA	Overall Dynamic Body Acceleration (m/s^2)
OL	Otolith Length (mm)
PrCA	Prey Capture Attempt
PCR	Polymerase Chain Reaction
PFZ	Polar Front Zone
RMA	Ranged Major Axis
RQ	Respiratory Quotient
RSS	Regression Sum of Squares
SD	Standard Deviation
SE	Standard Error
SRC	Standardized Regression Coefficients
SSFO	Split-Sample Frequency of Occurrence
UBC	University of British Columbia
US NMFS	US National Marine Fisheries Services
VeDBA	Vectorial Dynamic Body Acceleration (m/s^2)
X axis	Surge
X_{dyn}, Y_{dyn} and Z_{dyn}	Dynamic acceleration on axes X, Y and Z (m/s^2)
Y axis	Sway
Z axis	Heave

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My research involved months in the field in remote locations, and I could have never obtained such a dataset without the help of many field mates: John Arnould, Michelle Barbieri, Alistair Baylis and Rachel Orben all incredibly skilled in Alaska; and Nory El-Ksaby, Pacha of Kerguelen and field master extraordinaire, Jade Vacquie-Garcia, Laetitia Pons (who went out of her medical comfort zone to contribute to this project both in the field and in the lab!). Samantha Patrick, Aurelien Prudor, Pascal Grijol, Miguel and Tony 'Garage' among many other volunteers of the Mission 62 on Kerguelen Island. They were all amazing adventurers and dedicated individuals who spend months/years of their lives in hostile yet stunning territories to study wildlife in extreme environments. Special thanks to the Tafelzout tribe of Pointe Suzanne of course.

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To Erell and Vladik, the next generation

Chapter 1: General introduction

The effects of natural and anthropogenic environmental changes occurring in marine ecosystems are usually most noticeable on species occupying the top trophic levels, such as marine mammals and seabirds. These top predators are considered sentinels of the health of ecosystems and are often used as environmental indicators within the context of international marine conservation treaties (Boyd et al., 2006). Environmental changes linked to global warming have been occurring at a greater rate at high latitudes, affecting Arctic and Antarctic ecosystems more drastically than temperate or tropical ones (Watson et al., 1998; IPCC, 2007). Rapid population decline of marine mammals and seabirds as well as lower survival rates of new-borns and juveniles, and frequent reproductive failures have been observed in the Bering Sea and Arctic regions, concomitantly to changes in prey distribution and availability (Kock, 1992; Kitaysky and Golubova, 2000; Trites and Donnelly, 2003; Weimerskirch et al., 2003b; Jodice et al., 2006; Kitaysky et al., 2006). In the Southern hemisphere, changes in population dynamics of marine birds or mammals are likely linked to temperatures, sea-ice coverage or position of the Polar Frontal Zone (PFZ) that have varied in recent years (Barbraud and Weimerskirch, 2001; Siniff et al., 2008). Documenting such changes is important for understanding the processes that underlie the changes, and for developing sound and efficient management strategies for populations of animals in these marine ecosystems.

Survival and reproductive success of individuals, and thus the health of their populations, depends on the efficiency with which individuals extract energy from their environment per unit of time (MacArthur and Pianka, 1966). The more efficient they are, the more energy and time they can allocate between the competing needs of growth, reproduction, and body maintenance (Boggs, 1992). Animals have some flexibility to accommodate changes in environmental conditions. However, if energy intakes are ultimately sub-optimal, decisions regarding how energy is allocated will likely be modified. In long-lived animals, self-maintenance has priority over reproduction because fitness and lifetime reproductive success depend on longevity (Bouten et al., 1994). Hence, fluctuating energy resources are expected to first affect breeding performances before the survival of adults is compromised, but the extent to which reproduction is impaired by food availability

partly depends on the flexibility with which animals can acquire energy (foraging efficiency) and allocate it (physiological plasticity).

Understanding the responses of populations to environmental changes requires linking ecological factors with fitness, survival, and reproduction. One promising approach to study this is through bioenergetics that considers time budgets and energy balances of animals within an environmental context. This approach is ideal because it integrates biotic and abiotic influences, as well as external and internal factors that are easily translated from individual animals into population or community outcomes (Kooijman, 2000; Kooijman et al., 2004; Fischer et al., 2009; Sousa et al., 2010). In addition, individual animals are the unit of adaptability to changes in habitat conditions and are the drivers of population changes. Consequently, understanding the bioenergetic dynamics of individuals is needed to infer the potential success of an individual and ultimately the collective success of the population.

1.1 Study species and sites

As top predators breeding in high-latitude marine ecosystems with similar features, northern fur seals (*Callorhinus ursinus*) and Antarctic fur seals (*Arctocephalus gazella*) are ideal candidates to monitor and investigate the mechanisms and linkages between the environment, individual behaviours, energetics, fitness, and population dynamics. These are two closely related species of otariids that live at 50-60º latitude north in the Bering Sea for the northern fur seals and at 50-60º latitude south in the Southern Ocean for the Antarctic fur seals. They share physical, behavioural and ecological features, and have similar natural histories, maternal behaviours, and reproductive strategies (Gentry and Kooyman, 1986). They are the two northernmost and southernmost otariid species. As such, they experience the extreme seasonal variations in weather conditions that occur at high latitudes—which may explain why they are the only two species of otariids that have a short 4-month lactation period during the Austral and Boreal summers. Pups of both species wean abruptly, and are migratory and pelagic for the next 20–32 months of their lives.

The reproductive strategies of northern fur seals and Antarctic fur seals are energetically expensive, and rely exclusively on the mother's capacity to care for her pup

(Costa, 1993). Females nurse their offspring on land with alternate trips at sea to replenish their reserves. Lactation is one of the most demanding activities in their life cycles with energy demands increasing by 30% compared to non-breeders (Gentry and Kooyman, 1986; Arnould, 1997). Consequently, lactating females are likely to be more affected than other adults by sub-optimal foraging conditions. Both species are opportunistic feeders and can adapt to some extent to environmental changes (Guinet et al., 2001; Lea et al., 2002b; Reid et al., 2006; Zeppelin and Ream, 2006; Lea et al., 2008; Zeppelin and Orr, 2010). However, lactating females are limited in how far and for how long they can search for prey due to the fasting constraints of their young.

Figure 1.1: Picture of Northern fur seal male, females and pup during the breeding season 2011 on St. Paul Island (indicated by the yellow star and detailed on the close up map), part of the Pribilof Islands located in the Bering Sea, Alaska.

Pups wait on the rookeries for their mother's return, and rely on milk to grow and accumulate energy reserves. At weaning, pups of both species leave the breeding grounds and return several years later. Survival of pups and young of the year are linked to their growth rates and mass at weaning (Baker and Fowler, 1992; Boltnev et al., 1998; Hall et al., 2001; Lea et al., 2009). Weaned fur seals heavily rely on the reserves acquired during lactation to support their physiological needs at sea when they are inexperienced and ontogenetically immature—and can lose up to half their weaning body mass during their first year at sea (Trites and Bigg, 1996). Mortality rates are up to 60% in the first 2 years of life for northern fur seals (Trites, 1989; Gentry, 2002), but are hypothesized to have been lower prior to the population decline (Trites, 1989). In contrast, early mortality rates of Antarctic fur seals are around 30% (although it has never been precisely calculated from birth to first return on land, Boyd et al., 1995a; Wickens and York, 1997). Mortality rates of both species drop rapidly after the first 2 years at sea—the most critical period in their life histories (York, 1985). The nursing period is thus critical for mothers (via increased energy requirements) and pups (for their future survival).

Northern fur seals and Antarctic fur seals were heavily hunted in the 18th and 19th centuries, to the point that Antarctic fur seals were virtually extinct by the early 20th century. However, the northern fur seals breeding on the Pribilof Islands recovered once protected, and there were ~ 1.5 M animals from mid-1980s to mid-1990s when the decline resumed. Since then, pup production on St. Paul Island (the largest of the Pribilof Islands) has declined at ~ 6 % per year (Towell et al., 2006). They were listed as depleted under the Marine Mammal Protection Act in 1988 because population levels had declined to less than 50% of levels observed in the late 1950s, with no compelling evidence that carrying capacity had changed (NMFS, 1993). Although pre-sealing numbers are unknown, the Antarctic fur seal population has recovered rapidly since the end of their exploitation in the 1960s increasing by 6 to 14 % per year at South Georgia since 1990 (Arnould, 2002; Aurioles and Trillmich, 2008). Recovery rate has not been systematically assessed on Kerguelen Island, but pup production at the biggest colony is currently estimated at 6500 per year and increasing (Figure 2). Both species are subject to protection and conservation plans (Convention for the Conservation of Antarctic Seals, 1972; Pribilof Islands Area Habitat Conservation Zone, NMFS, 1993).

Figure 1.2: Picture of Antarctic fur seal male, females and pup during the breeding season 2011-2012 on Kerguelen Island (indicated by the yellow star and detailed on the close up map) located in the Sub-Antarctic Southern Ocean.

I studied two populations of fur seals located on St. Paul Island (northern fur seals, Figure 1.1) and Kerguelen Island (Antarctic fur seals, Figure 1.2). Both islands are located at similar high latitudes in the Arctic and Antarctic regions (49°S for Kerguelen Island and 56°N for St. Paul Island). The Pribilof Islands have an Arctic maritime climate with constant wind speed averaging 25–50 km/h year round. In contrast, the Kerguelen Archipelago is located in the "Furious Fifties" with winds blowing from the west at a remarkable average speed of 35 km/h and regularly reach 150 km/h. St. Paul and the Kerguelen Islands are both close to oceanographic discontinuities (*i.e.,* surrounded by relatively shallow waters with oceanic currents bringing up high nutrient concentrations and productivity in the close

vicinity) that are preferred foraging zones for top predators (Boyd and Arnbom, 1991; Georges et al., 2000).

The Kerguelen Archipelago is located on the Kerguelen plateau, with depths from 500 to 2000 m. The state of the sea is rough with wave heights of 12 - 15m being common, but the sea around Kerguelen is ice free. The Antarctic Polar Front where Antarctic surface waters moving northward sink below sub-Antarctic waters passes in the vicinity of the Kerguelen Plateau where it is responsible for mesoscale meandering, eddies, and ring formations. Upwelling from the Antarctic mixes with the warmer waters of the Indian Ocean stimulating oceanic primary production.

Like the Kerguelen Islands, St. Paul is located on the outer domain of the shallow continental shelf with depths < 200 m, 90 km North West of the Bering Sea shelf-break beyond which water depths are > 1000 m. The waters surrounding the island consist of discrete domains divided by oceanographic fronts. Coastal waters are generally ice free year-round around St. Paul, and marine currents present a steady clockwise flow, stronger south of the island and weaker to the east (Kowalik and Stabeno, 1999). These currents stir the relatively shallow, nutrient-rich waters that form the basis for the high productivity and biodiversity present. As around the Kerguelen Islands, the waters surrounding St. Paul Island have elevated productivity.

Major environmental changes have occurred in the Bering Sea and over the Kerguelen plateau in the last three decades. In the Eastern Bering Sea, water temperatures have risen by 2 - 3ºC, and the ice-associated, cold-water bodies have retreated north. This has resulted in lower nutrient input in the water columns, and changes in primary production and dynamics. Other changes associated with the rise in water temperatures are species distributions, both geographically and vertically to the water column, prey-predator trophic interactions, and large scale ecosystem dynamics (Anderson and Piatt, 1999; Napp et al., 2000; Overland and Stabeno, 2004). Major threats to the recovery of northern fur seals are due to heavy fishing of adult walleye pollock in the Bering Sea, or to potential impacts of climate change on the dynamics of the ecosystem and of the pelagic prey (Mace and Balmford, 2000). Major environmental changes starting in the mid-1970s altered the distribution and relative abundances of different species of fish in the Bering Sea (Anderson

et al., 1997; Anderson and Piatt, 1999) resulting in a switch from mainly high-energy prey to low-energy prey (Trites et al., 2007; Sinclair et al., 2008). Although fur seals in the central Bering Sea are declining, a small colony recently established on Bogoslof Island in the southern Bering Sea within the deep basin of the Bering Sea is increasing (Towell and Ream, 2011). This difference in dynamics and habitats suggests that local foraging conditions likely lie at the base of these changes (Trites et al., 2015). Reef rookery on St. Paul Island is one of the largest breeding sites for northern fur seals, and individual females are known to forage in different locations both on and off the Bering Sea shelf (Robson et al., 2004; Call et al., 2008), which might affect their foraging behaviours and efficiencies.

Although the Antarctic fur seal population on Kerguelen Island is currently healthy, they might face similar threats in the near future, as fisheries increase around the breeding areas and water temperatures increase due to climate change. These changes might result in the Antarctic Polar Front retreating southward, which would affect the availability of the main prey source for Antarctic fur seals (Hanchet et al., 2003; Lea et al., 2006; Learmonth et al., 2006). Significantly higher rates of reproductive failure have occurred in Antarctic fur seal colonies during warmer years (Lea et al., 2006). Antarctic fur seals are also thought to have lost considerable genetic diversity due to the historical population bottleneck (Wynen et al., 2000) and may now be at increased risk from disease outbreaks and environmental change. Under both scenarios, animals might have to employ new strategies to balance the compromise between the potential to gain energy against the actual time and energy spent foraging.

Differences in population trajectories provide an opportunity to compare how two closely related, and biologically and ecologically similar species respond and adapt to environmental changes, despite the inherent challenges of two-species comparisons. It also provides an opportunity to understand the mechanisms that underlie these different population responses.

1.2 Methodology

The rate with which climate is changing in the northern and southern hemisphere is unlikely to slow anytime soon. However, there is little understanding about how climate change will affect the physiology, behaviour and energetics of fur seals and other species—and how this will ultimately affect the dynamics of their populations. Animals modulate their behaviours over varying time scales, which need to be quantified and related to energetics to better understand the choices they will have to make. Consequently, understanding how animals respond to environmental changes requires information about their behaviours at sea and how it affects their foraging efficiency (*i.e*,. the energetic gains versus the energetic costs of such foraging strategies).

Traditionally, radio and satellite telemetry methods have been used to determine movement patterns and at-sea locations of fur seals. However, the resolution of the data has generally been too coarse to study fine scale behaviours of animals. Recently, the development of new remote sensors such accelerometers and magnetometers provide new insights into tri-dimensional body movements and behaviours. The resolution of the data is unprecedented and provides considerable information on animal behaviours at a fine scale never attained before. Combined with more traditional loggers such as time-depth recorders and satellite loggers, it is now possible to reconstruct the route of animals in 3 dimensions, measure distances and swimming speed, as well as allow segregating foraging trip into different types of activities such as transiting, grooming, resting and diving/feeding behaviours (*i.e.*, in time-activity budgets).

Types of behaviours displayed while foraging are associated with different energy costs, so defining and quantifying the behaviours that make up activity budgets is an important step in understanding the energetics of free-ranging marine mammals. Methods to measure energy expended by animals while foraging include heart rate monitors and doubly-labeled water (Lifson and McClintock, 1966; Butler et al., 1992; Butler, 1993; Speakman, 1997; Froget et al., 2004; Wilson et al., 2006; Young et al., 2011). However, these techniques can be invasive, very costly, and difficult to obtain in large free-ranging marine animals—especially with heart rate monitors (Nagy, 1980; Thorarensen et al., 1996; Ward et

al., 2002; Butler et al., 2004; Dalton et al., 2014b). In addition, the DLW method only provides an estimate of energy expenditure over an entire feeding trip. Consequently, there is a need to develop methods to determine energy expenditure at the activity level, which remains to be achieved in marine mammals.

Overall Dynamic Body Acceleration (ODBA) and Vectorial Dynamic Body Acceleration (VeDBA) are 3D body acceleration metrics that have been hypothesized to correlate with energy expenditure in various animal taxa (Wilson et al., 2006; Halsey et al., 2009a; Halsey et al., 2009b; Qasem et al., 2012). This method is based on the assumption that most of the energy spent while foraging is due to the cost of locomotion, and that there is a direct link between the energy needed to contract muscles (how muscular tissue converts metabolic energy to mechanical work) and the resulting movement of the body during locomotion from acceleration (the rate at which work is performed) (Gleiss et al., 2011). As acceleration can be recorded at a sub-second rate, it has the potential to resolve energy expenditure with fine temporal resolution, making it the only method able to determine the cost of short-lived behaviours. However relationships between acceleration and energy expenditure vary by species and by type of activity, and need to be individually calibrated for each case, and has seldom been tested on free-ranging animals (Halsey et al., 2008; Elliott et al., 2013; Wright et al., 2014).

In addition to affecting energy expenditure, foraging strategies impact foraging success of wild animals (*i.e.*, their energetic gains while foraging). Foraging success is inherently difficult to assess in elusive animals. It has traditionally been assessed from body mass or composition change during foraging trips. However, this metric does not consider that animals can lose weight even at satiation (ref) depending on types of prey they consume, or differences in energy allocation between conflicting physiological functions. Understanding energetic gains from foraging requires an understanding on both the diet composition of individuals and their success at capturing prey.

Assessing diets is thus important for understanding the balance between energy input from food, and the energy spent foraging. Diets of free-ranging animals are traditionally estimated by identifying the undigested hard-part remains of prey found in stomach contents, feces (scats) or regurgitates (Perez and Bigg, 1981; Perez and Bigg, 1986; Antonelis et al.,

1990). Taxon, size and relative number of prey ingested can be determined from hard-parts (Tollit et al., 2003), but the method is biased by differential digestion or retention rates of prey parts depending on species and sizes of prey consumed, and on species, sex, activity level, GI tract morphology and meal size of predator that lead to under- or over-estimation of prey occurrence (or size of prey consumed) in the diets (Bigg and Fawcett, 1985; Jobling and Breiby, 1986; Harvey and Antonelis, 1994; Tollit et al., 1997; Bowen, 2000; Arim and Naya, 2003; Gudmundson et al., 2006). More recently, molecular-based tools, such as DNA meta-barcoding, have been developed to overcome some of the limitations of hard-part analyses (Deagle et al., 2005; Casper et al., 2007a; Deagle and Tollit, 2007; Deagle et al., 2009; Deagle et al., 2010; Cristescu, 2014; Thomas et al., 2014), and allow species of organisms to be identified within a scat sample at a finer resolution than hard parts. However, this new DNA approach has its own inherent technical and interpretation biases (Casper et al., 2007a; Deagle et al., 2010; Thomas et al., 2014).

Both the hard-part and DNA-based methods provide diet composition only at the population level and only represent what animals consumed in the last few days (~ 48h, Orr and Harvey, 2001; Staniland, 2002; Deagle et al., 2005; Casper et al., 2007a). Carbon and nitrogen stable isotope concentrations in blood, hair and bone synthesize dietary have the advantages of providing information of the trophic level of the consumer and characteristics of its foraging habitat over longer timescales and at the individual level (Wada et al., 1991; Hobson and Welch, 1992). Consequently, scat-based methods and stable isotopes provide different but complementary insights into the diet and foraging habits of animals. Using a multi-methodological approach by pairing an individual's foraging strategy information from telemetry data with respective stable isotope analyses, and general scat based approaches can provide a more complete understanding of foraging strategies and diets, and disentangle spatial, trophic and energetic differences between individuals (Newsome et al., 2010).

Quantitative estimates of foraging success, or energetic gain, also requires determining numbers of prey captured and consumed by individuals. This was previously assessed from changes in body water pool (Costa, 1993), or with stomach temperature sensors (Grémillet and Plös, 1994; Kuhn and Costa, 2006), both of which present methodological and technical challenges in wild marine mammals. More recently, however,

high resolution tri-axial accelerometers have been used to measure numbers of prey capture attempts in free-ranging marine predators (Skinner et al., 2009; Suzuki et al., 2009; Viviant et al., 2010; Watanabe and Takahashi, 2013; Ydesen et al., 2014) from detection of head strikes during a capture attempt. Quantitative estimates of foraging energetic gain (from diet composition and number of prey capture attempts) paired with foraging costs and fine scale behaviours and movement at sea can thus provide an indication of how foraging strategies affect foraging efficiencies of animals within a specific habitat, which ultimately impact the energetic balance and fitness as individuals.

1.3 Research objectives and hypotheses

Given the on-going environmental changes occurring at a large scale in marine environments, there is a need to understand how animals will behaviourally and energetically respond to rapid shifts in their habitats, and how this will affect their capacities to survive and reproduce. Fortunately, recent technological and methodological advancements now allow multi-disciplinary approaches to be applied to individual animals to understand how collective responses can impact population trajectories. The main goal of my study was consequently to investigate how foraging strategies affect foraging efficiency of individual female fur seals during their breeding season, whether changes in their foraging efficiencies affected their maternal investment and reproductive success, and relate this back to environmental conditions. I also sought to develop new methods to easily determine fine-scale energy expenditure of fur seals at sea based on accelerometry.

My general hypothesis was that, despite the capacity to buffer environmental changes around their breeding grounds, female fur seals from the declining northern population would be expending greater foraging effort for a lower foraging success (due to lower prey accessibility and/or energetic quality) compared to females from the increasing population. They would therefore have less energy and time to allocate to reproduction, and would produce pups with lower growth rates. As mass at weaning is critical for survival during their first year at sea, this would lead to lower recruitment in the declining population. I also hypothesized that acceleration would be useful to determine energy expenditure when animals are under water, but not when they are at the surface given the conditions of the

marine environment and the limitations of accelerometry for uncontrolled studies in the wild (Halsey et al., 2011b).

To test these hypotheses, I investigated fine scale foraging behaviour of individuals using state-of-the-art biologging devices. I developed and tested methods and tools to effectively determine energy expenditure at sea and activity-specific metabolic rates that can be used in future energetic studies. I also investigated new methods to estimate diet composition of individuals and the rate with which fur seals attempt to capture prey, which together provide measures of energy gained while foraging. Finally, I combined morphometric, metabolic and isotopic data with location, depth, acceleration and dietary data to determine the linkages between foraging strategies, foraging efficiencies, and the capacity to invest in reproduction within and between fur seal species. This was complemented by data collected on pups during the same breeding season.

Overall, I investigated the foraging ecology of northern and Antarctic fur seals from an ecological-energetics perspective. Using such robust methods based on energetic-flows and thermodynamic laws to compare two similar species with opposite population trajectories provided an opportunity to study the mechanistic aspect of individual plasticity and their responses to their environment. It also adds an essential and yet often under-investigated individual-based bioenergetic piece to the puzzle by linking individual fitness to environmental conditions, and ultimately the response of populations to environmental changes. Multi-disciplinary studies integrating metabolic, energetic, biologging and modelling methods also provide greater clarity for explaining observed variations in foraging efficiency within and between species in a wider physiological and ecological context. My study was thus designed to yield results that could be easily incorporated within individual-based models and extended to a broad array of questions related to the impacts of environmental changes on the fitness and demography of animals, as well as the impacts of fur seals on prey stocks (and *vice versa*).

1.4 Thesis outline

My thesis is structured as follows. **Chapter 1** provides a general introduction to this study, background information, research questions and objectives, and working hypotheses. The subsequent five chapters consist of studies independently written for publication in peer-reviewed journals. **Chapters 2** and **3** investigate whether acceleration data can be used as a reliable indicator of energy expenditure or metabolic rates of marine mammals at sea, with **Chapter 2** focusing on Dynamic Body Acceleration, and **Chapter 3** on flipper stroke metrics. **Chapter 4** combines scat-based methods, DNA-based methods and isotopic methods to determine the diet of northern fur seals, which is needed to quantitatively measure energy gained while foraging as a function of foraging strategy (diet and stable isotopes of Antarctic fur seals were less thoroughly investigated and are mentioned as a side-note). **Chapters 5** and **6** build on the results of the previous chapters and explore how differences in foraging strategies affect foraging efficiencies and individual fitness of mothers via maternal investment in reproduction. **Chapter 5** focuses on Antarctic fur seals and empirically tests the relationship between individual foraging behaviours, foraging efficiencies and pup growth, while **Chapter 6** focuses on the different strategies observed within the northern fur seal population, and how this affects foraging efficiencies and indirectly reproductive success of individuals through trade-offs between the gain and expenditure of time and energy. **Chapter 6** also compares the foraging strategies of northern and Antarctic fur seals, and discusses whether they provide clues into why their reproductive success and population trajectories differ. Finally, **Chapter 7** provides a summary of the major findings and associated biases, and discusses future research directions.

Chapter 2: Accelerometers can measure total and activity-specific energy expenditure in free-ranging marine mammals only if linked to time-activity budgets

2.1 Summary

Energy expenditure is an important component of foraging ecology, but is extremely difficult to estimate for free-ranging animals, especially marine mammals. I investigated whether vectorial dynamic body acceleration (VeDBA) could accurately predict the energy expended by northern fur seals (*Callorhinus ursinus)* and Antarctic fur seals (*Arctocephalus gazella*) during single foraging trips or whether other dive or time-distance foraging parameters were better predictors. I also determined how well VeDBA could predict the energetic cost of the different foraging activities that made up each foraging trip (*i.e.,*diving, transiting, surface activity, and resting). To do so, I equipped 20 lactating females of each species with GPS, dive-behaviour data loggers and tri-axial accelerometers and simultaneously obtained estimates of field metabolic rates for each of 13 Antarctic fur seal and 12 northern fur seal females using the doubly-labeled water method. VeDBA was derived from tri-axial acceleration, and at-sea activities were inferred using dive depth, tri-axial acceleration and traveling speed to differentiate diving, transiting, resting and surface activities. Activity-specific metabolic rates were estimated using linear regression with individual time-activity budgets as independent variables and DLW measurements as the response variable. I found that VeDBA did not accurately predict the total energy expended by the fur seals to complete their full foraging trips ($R^2 = 0.36$). However, the accuracy of VeDBA increased significantly when I partitioned their foraging trips by activity, and used activity-specific VeDBA to estimate activity-specific energy expenditures ($R^2 > 0.85$). I was also able to accurately determine total energy expenditure at sea from activity-specific VeDBA paired with time activity budgets ($R^2 = 0.70$). My study confirms that acceleration, in combination with other behavioural knowledge, is a promising way to estimate energy expenditures of marine mammals, but shows that it needs to be based on the different activities that make up foraging trips and the time allocated to each of them rather than being derived as a single

measure of VeDBA applied to entire foraging trips. This activity-based method provides a cost-effective means to accurately calculate energy expenditures of fur seals using acceleration and time-activity budgets.

2.2 Introduction

Predators constantly make decisions on where to hunt, what to hunt, and for how long to hunt that collectively affects the efficiency with which they obtain energy and minimize foraging costs. It is this foraging efficiency, or the energy gain/cost ratio of foraging, that drives many aspects of the physiology, biology, and ecology of wild animals—which in turn affects their health, reproduction and survival. It is important to accurately estimate foraging costs and benefits to understand and predict survival and reproductive success at the individual and population levels (Boyd, 2002), or to calculate food requirements and understand predator-prey interactions (Lavigne et al., 1982; Winship et al., 2002; Halsey and White, 2010).

Heart rate monitors, accelerometers, and doubly labelled water have all been used to measure energy expenditure in vertebrates (Lifson and McClintock, 1966; Butler et al., 1992; Butler, 1993; Speakman, 1997; Froget et al., 2004; Wilson et al., 2006; Young et al., 2011). However, heart rates and DLW measurements can be invasive, very costly, have their own biological limitations and are often times impractical for large wild animals (Nagy, 1980; Thorarensen et al., 1996; Ward et al., 2002; Butler et al., 2004; Dalton et al., 2014b). They are difficult also to obtain for large sample sizes and across different temporal scales that are required in ecological studies if we are to better understand links between animals and changes in their environment. Accelerometry has the potential to provide valuable information over days, weeks or months at sea, and so simple measures of body movement (e.g., acceleration) are increasingly being used to estimate energy expended by animals. They however need to be truly tested in the field under natural meaningful conditions.

Overall Dynamic Body Acceleration (ODBA) and Vectorial Dynamic Body Acceleration (VeDBA) are 2 very similar metrics based on tri-axial acceleration of the body that can be linked to energy expenditure (Wilson et al., 2006; Halsey et al., 2009a; Halsey et

al., 2009b; Qasem et al., 2012). ODBA is the sum of the absolute values of the dynamic acceleration of the 3 body axis while VeDBA is the vectorial product of these same data. These measures of acceleration are based on the assumption that most of the energy spent while foraging is due to the cost of locomotion, and that there is a direct link between the energy needed to contract muscles and the resulting movement of the body during locomotion (Gleiss et al., 2011). ODBA and VeDBA have been tested and calibrated on various taxa, both marine and terrestrial, endotherm and ectotherm, during different activities (walking, flying, swimming etc., Fahlman et al., 2008; Halsey et al., 2008; Gleiss et al., 2009; Halsey and White, 2010; Gomez-Laich et al., 2011; Halsey et al., 2011a). They appear to have acceptable accuracy for determining energy expenditure, but relationships between acceleration and energy expenditure vary by species and by type of activity, and need to be individually calibrated for each case (Halsey et al., 2008; Elliott et al., 2013; Wright et al., 2014).

Establishing the relationship between ODBA and energy expenditure is particularly difficult for air-breathing divers due to a possible uncoupling of ODBA and gas exchange (Halsey et al., 2011b). Differences in resistance between air and water may also create different relationships between acceleration and energy expenditure and there may be effects of winds/waves at surface as well as water currents on acceleration that are not reflected in energy expenditure (Halsey et al., 2011b). Similarly, the effects of buoyancy, gliding, and other physiological functions (*i.e.,*thermoregulation, digestion etc.) that contribute to energy expenditure, but not to acceleration, may uncouple potential relationships between acceleration and energy expenditure (Gleiss et al., 2011; Halsey et al., 2011b).

Most validation and calibration studies of ODBA and VeDBA have been conducted in controlled environments over short periods, which might buffer the above limitations. For example, ODBA correlates with energy expenditure of semi-captive Steller sea lions (*Eumetopias jubatus*) trained to dive at sea (although with an R^2 of 0.47, Fahlman et al., 2008), but does not correlate with the daily metabolic rate and partial dynamic body acceleration of captive northern fur seals over a 5-day period (Dalton et al. (2014b). This suggests that the predictive power of ODBA may decrease with recording time over days and weeks increases due to animals engaging in a wider range of behaviours or experiencing

greater variability in environmental conditions. This may mean that ODBA and VeDBA are best applied to individual activities, rather than to the sum of all activities over extended periods.

Defining and quantifying the behaviours that make up activity budgets appear to be an important step in understanding the energetics of free-ranging marine mammals. Studies have attempted to determine time-activity budgets using a mix of acceleration, geolocation, altitude and depth data to visually discriminate behaviours (Yoda et al., 2001; Gomez-Laich et al., 2008; Insley, 2008), or have used supervised or unsupervised classification techniques such as Kmean clustering techniques (Sakamoto et al., 2009), K-nearest neighbour algorithms (Bidder et al., 2014) or decision-tree classifications (Nathan et al., 2012). Activities can be linked to specific energy expenditures within a global framework (Elliott et al., 2013; Gomez-Laich et al., 2013; Wright et al., 2014), but appear to be highly species-, environment- and activity-specific.

My primary goal was to determine whether behavioural or acceleration-based parameters could accurately predict the energy expended by 2 species of fur seals (northern and Antarctic fur seals) during individual foraging trips. Therefore, I tested whether ODBA or VeDBA alone yielded indices of energy expenditure that were comparable to simultaneous doubly-labelled water measurements of field metabolism for each species of fur seal. A secondary goal was to see whether better estimates of energy expenditure could be obtained by dividing the foraging trips into behavioural components (*i.e.,*diving, transiting, surface activity and resting). I also determined how well the indices performed at estimating the energy expenditure of the different behavioral activities that made up each foraging trip. Finally, I attempted to derive better predictions of energy expenditure from various acceleration- and behaviour-based parameters using multi-factorial models.

2.3 Material and methods

2.3.1 Data collection

Data were collected from 20 lactating northern fur seals at the Reef rookery on St. Paul Island (Bering Sea, 57°6'N - 170°17'W) during the breeding season from Aug-Sep

2011, and from 20 lactating Antarctic fur seal females at Pointe Suzanne, Kerguelen Island (Southern Ocean, 49°26'S - 70°26'E) during the breeding season from Jan-Feb 2012. Data were collected under the US NMFS permit # 14329-01, the UBC animal care permit # A10-0364 and the ethical regulations approval from the French Polar Institute (IPEV).

All females were captured using a hoop net and were mature adults with a confirmed suckling pup. The females were carried in the hoop nets a short distance to a restraint board where they were anaesthetized with isoflurane gas. Standard morphometric measurements of length and axial girth were made to the nearest 0.5 cm, and mass was recorded using a scale at ± 0.2 kg.

Measurements of daily energy expenditure (EE, kJ/day) were obtained using the Doubly-Labeled Water (DLW) method (Lifson and McClintock, 1966; Butler et al., 2004). This method has been previously validated by comparison to indirect calorimetry in a range of small mammals (Speakman and Krol, 2005), as well as on seals (Sparling et al., 2008). I took a first blood sample (3 to 8 ml) by veinipuncture of an inter-digital vein in a hind-flipper to determine baseline levels of ^{2}H and ^{18}O for each individual (Speakman and Racey, 1987 – method D). A known mass pulse-dose of DLW (622272 ppm ^{18}O, 384645 ppm ^{2}H) was then administered intravenously via a catheter on the other hind-flipper (0.3-0.6 g/kg body mass) and flushed with saline solution to ensure full injection into the blood stream. Syringes were weighed before and after administration (± 0.0001 g, Sartorius balance) to calculate the mass of DLW injected. The labelled isotopes were allowed to equilibrate with the body water pool for 2 h during which the seals were either kept under very light anaesthesia or kept in a quiet closed environment. Equilibration times have previously been determined by serial blood sampling to be less than 2 hours on fur seals (Costa, 1987; Arnould, 1995). At the end of this period, a second blood sample was taken.

During the DLW equilibration period, data loggers were glued to the dorsal mid-line fur using a 2-part Devcon 5-min epoxy glue. Daily Diary tags (DD, Wildlife Computers) recording tri-axial acceleration and tri-axial magnetic field at 16 Hz, and depth, light level, and water temperature at 1Hz were glued as close as possible to the projection of the center of mass on the back of the animal (roughly between the scapula). Fastloc GPS MK10 loggers (Wildlife Computers) were glued lower down the back from the DD tags. They recorded

GPS coordinates along the track of the animal at sea, as well as depth and water temperature at 1 Hz. Once the devices were securely attached and the second blood sample was taken at the end of the equilibration period, the females were released upon full recovery from the anaesthesia and allowed to rejoin the colony.

Individuals were recaptured after a single foraging trip and anaesthetized as previously described. A final blood sample was taken to determine isotope levels of ^{3}H and ^{18}O at the end of the foraging trip, and all the data loggers were removed by cutting the fur beneath them. A second set of morphometric measurements were also taken at this time.

2.3.2 Daily energy expenditure – doubly-labeled water method

All blood samples were collected in Monovette syringes (Sarstedt) coated with Li-Heparin and containing a plasma-red blood cell separator. Plasma was isolated from red blood cells either by centrifugation at 1000 g for 10 min (northern fur seals), or by natural gravity separation for 4 h when no electricity was available (Antarctic fur seals). Plasma samples were then flame sealed into 2 x 100 µL glass capillary tubes, and stored at room temperature until isotopic analyses were performed.

For isotopic analyses, plasma samples were vacuum distilled (Nagy, 1983) and the resulting distillate was used to produce CO_2 and H_2 (methods in Speakman, 2005 for CO_2 ; and Speakman and Krol, 2005 for H_2). The isotope ratios ^{18}O: ^{16}O and ^{2}H: ^{1}H were analysed using gas source isotope ratio mass spectrometry (Optima, Micromass IRMS and Isochrom µG, Manchester, UK). Samples were run alongside three lab standards for each isotope (calibrated to International standards) to correct delta values to ppm. Isotope enrichments were converted to CO_2 production for each individual using a two-pool model (*i.e.,*considering respective individual dilution spaces for ^{18}O and ^{2}H), best suited for larger animals including pinnipeds (Speakman, 1987; Schoeller, 1988; Sparling et al., 2008). Initial isotope dilution spaces were calculated using the plateau method (Halliday and Miller, 1977).

Several approaches can be taken to account for evaporative water loss when calculating metabolic rates from DLW concentrations (Visser and Schekkerman, 1999). I used 4 equations for my calculations: the equation 7.43 in Speakman (1997) that assumed evaporation of 25% of the water flux which minimizes error in a range of conditions and

were deemed most appropriate in a validation study on seals (Sparling et al., 2008); and the equations from Speakman (1993), Speakman et al. (1993) and Coward et al. (1985) that were recently shown to be the most accurate on captive northern fur seals in summer and fall when compared to metabolic rate measurements via respirometry (Dalton et al., 2014b). Finally, I converted CO_2 production rates into daily energy expenditure using a respiratory quotient (RQ = O_2 consumption / CO_2 production) of 0.80 as an estimate based on measurements performed in spring and summer (0.80) and fall (0.77) on northern fur seals (Dalton et al., 2014b) and on grey seals on a typical fish diet (0.76, Sparling et al., 2008).

The study individuals spent time on land after the post-equilibration sample and upon return to the colony before recapture and the final blood sample was collected. Energy spent during this 'non-foraging' time was part of the DLW measurement so energy expenditure at sea was calculated by subtracting on-land expenditure from the total estimate using previously determined values for lactating females in northern (4.67 W/kg, chapter 5 in Gentry and Kooyman, 1986) and Antarctic fur seals (4.56 W/kg in Costa and Trillmich, 1988) while on land.

2.3.3 Diving and foraging behaviour parameters

I used depth data recorded by the DD tags to determine diving behaviours, or depth data recorded by the fastloc MK10 when the Daily Diary tags malfunctioned. Any drift in the pressure sensors or error spikes were corrected prior to analyses using a zero-offset correction. Diving behaviours were quantified using a custom-made R program previously developed on Antarctic fur seals. Dives were defined as periods of time that animals spent under water below a minimum depth of 3 m and for a minimum of 4 s until they went back to the surface and I derived dive duration and maximum dive depth for each of them. The end of the descent phase was defined as the point at which the ascent rate was below 0.4 m/s and the start of the ascent phase was defined as the point at which the ascent rate exceeded 0.4 m/s. Bottom duration was the difference between the end of the descent and the beginning of the ascent.

Distances traveled on the surface of the ocean (horizontal distances) were calculated by measuring the linear distance between two successive GPS locations taking into account the curvature of the Earth using the Haversine formula (Sinnott, 1984). GPS locations have a

high spatial and temporal resolution (they were set to record a location every 5 min), so GPS tracks did not require interpolation or filtering (Tremblay et al., 2006). Part of the distance traveled under water while diving is inherently taken into account in the measured horizontal distance traveled. I approximated vertical distance traveled while diving by doubling the maximum dive depth of each dive (underestimate).

2.3.4 Time-activity budget

Fur seal behaviours were separated into 4 categories to determine time-activity budgets: 1) Diving for foraging; 2) resting and sleeping; 3) surface activity, grooming and slow travel; and 4) fast transiting at the surface. These 4 behaviours were identified using a custom-made classification-tree algorithm in R, parameterized as follows:

1. *Diving* and foraging time was defined as the period when animals were actively diving (see *Diving and foraging behaviour* parameters above) and included the post-dive intervals. Post-dive intervals were defined as the interval between two successive dives during which time the animal needed to return to the surface to replenish its oxygen stores and were estimated using the Bout-Ending Criterion (BEC) calculated with the maximum likelihood estimation method using the package diveMove in R (S. Luque). This validated method is considered to accurately measure the post-dive intervals of diving fur seals (Luque and Guinet, 2007).

2. *Resting* time was calculated by first applying a running variance over 3 s on the raw acceleration of each of the 3 axes. It was then defined as the time when the resulting acceleration variance signal was less than 2.5 m/s^2 for all 3 axes for more than 5 min (Figure 2.1). This acceleration threshold was determined visually and was similar for all animals. Very short spikes in variance (of maximum 5 s) in the middle of long periods of variances (30 min or more) below the threshold of 2.5 m/s^2 were considered to be due to the animal changing position while laying at surface and body orientation in the water (verified with the change in static acceleration) and were still considered in the resting time.

3. *Transiting* time was the period during which the animals were neither diving nor resting, and were moving at the surface at or faster than 1m/sec. Surface speed was

calculated from the distance between 2 successive GPS points and dividing it by the interval of time between them.

4. *Surface activities, grooming and slow travel* time occurred when the animals were neither diving nor resting, and were moving at the surface at a speed < 1m/s. Surface speed was calculated by determining the distance between two successive GPS points (see *Diving and foraging behaviour* parameters above) and dividing it by the interval of time between them.

Gaps in acceleration due to daily diary tag malfunction for northern fur seals were also quantified as a percent of the foraging trip duration (from 0.3 to 11.5 % of the datasets) that I accounted for in the calculation of ODBA and VeDBA by substituting average overall acceleration to the times when no data were recorded. Accuracy of the classification-tree model was visually verified over the entire foraging trip for all animals.

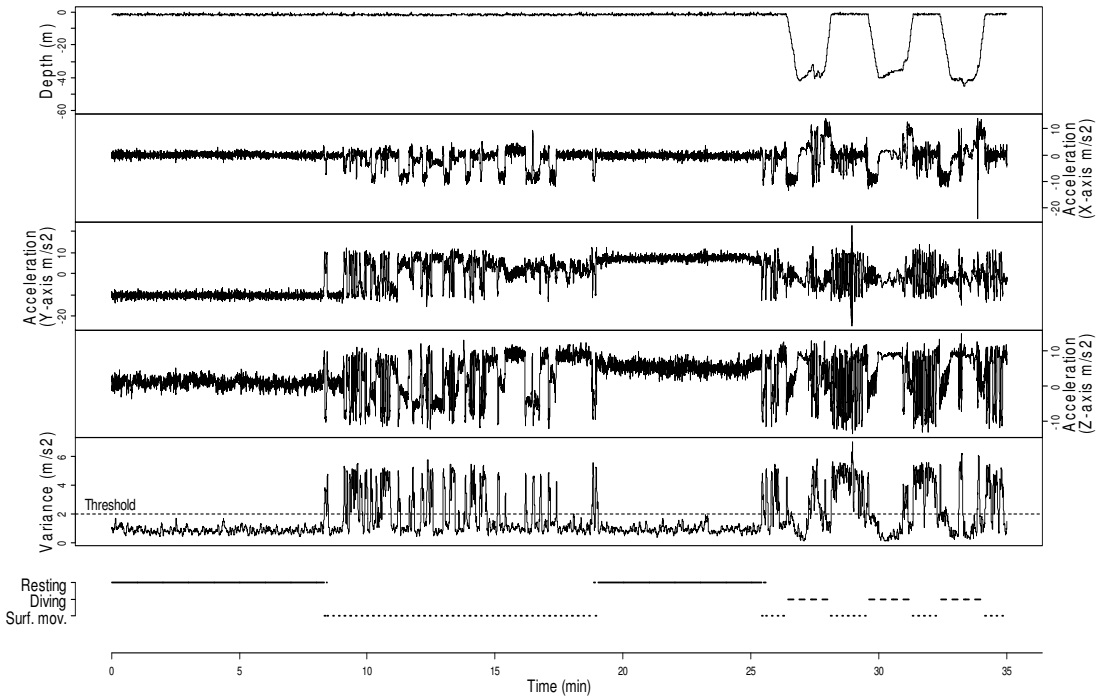

Figure 2.1: Example of depth profile, acceleration signals over the 3 axes, and combined running variance for 35 min for a female northern fur seal foraging in the Bering Sea.Variance was calculated over the 3 acceleration channels, variance thresholds showing the level below which the animal was considered to be sleeping or/resting (when the signal stayed below the threshold for more than 5 min at a time).

2.3.5 Dynamic body acceleration

Overall Dynamic Body Acceleration (ODBA, Wilson et al., 2006) and Vectorial Dynamic Body Acceleration (VeDBA, Gleiss et al., 2011) were calculated using the tri-axial acceleration data collected at 16Hz by the DD tag on the back of the animals. I performed the same analyses on both ODBA and VeDBA metrics, but I refer to these metrics as DBA for simplicity. Care was taken to standardize the positioning of the devices as close as possible to the center of mass of the seals to ensure accuracy of measurements between and within animals. The three axes X (surge, roll), Y (sway, pitch) and Z (heave, yaw), were first individually normalized using static data collected on all azimuths while the tags were still on a hard surface. The normalized signal was then filtered using a running mean of 2 s (Shepard et al., 2008; Fahlman et al., 2013; Dalton et al., 2014b) to dissociate the static acceleration (due to the positioning of the animal in space in respect to gravity) from the dynamic acceleration (X_{dyn}, Y_{dyn} and Z_{dyn}, due to the movement of the animal). I then calculated ODBA and VedBA using the following equations:

$$ODBA = |X_{dyn}| + |Y_{dyn}| + |Z_{dyn}|$$

$$VeDBA = \sqrt{X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2}$$

ODBA or VeDBA have been traditionally calibrated as indices of energy expenditure by averaging their values over the period of homogenous activities during which reference metabolic rates are measured (such as with respirometry or heart rate monitoring) (Fahlman et al., 2008; Clark et al., 2010; Halsey et al., 2011c). However, my estimation of metabolic rate from the doubly-labelled water method provided a single measurement for the foraging trip at sea (see below) of different durations, during which the seals displayed a wide range of behaviours. In the case of averaging, the mean values of DBA for animals engaged in similar behaviours (*i.e.,*with similar acceleration signals) should be similar regardless of whether the trip occurred over 2 days or 8 days. However, the longer trip would have higher total energy expenditure. Thus, measures of DBA were normalized for time spent at sea.

I normalized acceleration for time spent at sea by first integrating DBA over periods of 1 s using a linear interpolation (composite trapezoid rule; 'auc' function from the R package MESS, Author C. Ekstrom). Areas under the curves were then summed over the

entire foraging trip or over the period of specific activity types previously defined. Another normalized metric was to multiply the average DBA over their foraging trip by the time the animals spent at sea. Finally, calculated the 'noise–free' DBA defined as the dynamic body acceleration from which the residual acceleration caused by waves and wind at the surface was removed. I also normalized this metrics by multiplying the average over the foraging trip by the time the foraging trip lasted for each seal individually.

I assumed that the acceleration recorded when animals were resting and sleeping on the surface of the water was mostly caused by the movement of water (waves etc.) and was not produced by the seals. I consequently subtracted this 'residual' DBA from transiting and surface movement DBA to obtain 'noise-free' DBA ($DBA_{NoiseFree}$ in m/s^2*min) as follows:

$$\mathrm{DBA}_{\mathrm{NoiseFree}} = [T_{Transit.} \times (\mathrm{DBA}_{Transit.} - DBA_{Rest.})] + \left[T_{Surf.} \times \left(\mathrm{DBA}_{Surf.} - DBA_{Rest.}\right)\right] + (\mathrm{DBA}_{Dive} \times T_{Dive.})$$

where DBA_I are the average DBA (m/s^2) displayed during each type of activities *i* mentioned in section Time-activity budget and T_i are the time spent performing each activity *i*.

2.3.6 Statistical analyses

Foraging parameters – Statistical differences between 2 groups (for example between species, or between 2 activity types) were tested with two-sample *t*-tests ($\alpha = 0.05$) or Mann-Whitney tests depending on normality. Averages for dive parameters, such as for dive depths and dive durations, are nested within animals and were calculated using linear mixed effect models with no fixed effects (only the intercept is calculated) and with individual as a random effect to take into account that each animal performed a different number of dives.

DBA versus energy expenditure over full foraging trip – I tested whether VeDBA or ODBA could reliably predict total energy expenditure at sea in fur seals using general linear models (lm, 'stats' package, R 3.0.3) or general linear model using generalized least square that allows for unequal variances (gls, 'nlme' package, R 3.0.3) after verifying model assumptions. Metabolic rate and ODBA or VeDBA were mass-corrected for each animal by

dividing the values by individual body mass, as both of these parameters are known to depend on the mass of the animals (Kleiber, 1947; Gleiss et al., 2011). Relationships with energy expenditure for different measures of ODBA and VeDBA over the full foraging trip were investigated, including **1)** areas under the curve over the entire foraging trip, **2)** average ODBA/VeDBA normalized by time each animal spent at sea, and **3)** total 'noise-free' DBA to account for differences in foraging duration normalized by time each animal spent at sea (see *Time-activity budget*).

Activity-specific metabolic rate – Energy expenditure per type of activity was calculated by fitting the following model with general linear models (lm, 'stats' package, R 3.0.3):

Eq. 2.1 $$EE = C_{Transit} \times T_{Transit} + C_{Dive} \times T_{Dive} + C_{Surf} \times T_{Surf} + C_{Rest} \times T_{Rest}$$

where EE is the total energy expenditure in MJ, and the parameters T_i, are the time in d spent per activity (i), *i.e.,*diving (*Dive*), transiting (*Transit*), performing slow surface activities (*Surf*) and resting (*Rest*). This means that the parameter estimates C_i for each type of activity are in MJ/d and correspond to the rate of energy expenditure for diving, transiting, surface activity, and resting respectively. I consequently estimated the activity-specific metabolic rates by fitting Eq. 2.1 for all my seals to obtain the parameter estimates C_i. If EE was estimated for the total DLW time (including time on land between 2 captures), the term $C_{land} \times T_{land}$ was added to Eq. 2.1.

I forced the intercept through 0 because no energy is spent if no time passes. As R^2 values get overinflated in models without intercepts, I computed the R^2 as 1 - (RSS / ESS), where RSS is the regression sum of squares and ESS the error sum of squares of the models, as an additional mean of comparison of the variance between models.

Normality, homogeneity of variances, and correlation between different explanatory variables were verified to ensure accordance with the model assumptions, even though the parameters T_i are not theoretically independent from one another. The model (Eq. 2.1) was compared to the NULL model which considered only time at sea as the independent variable. In models with more than two parameters, the sample size per species became too small (n =

12 for NFS and n = 13 for AFS) and the power too low to obtain relevant statistics, so I pooled both species together.

Multivariate predictive models – I first tested whether all the activity-specific DBAs together were a good predictor of energy spent at sea using the same statistical methods described for full foraging trip. Measured energy expenditure and activity-specific DBA were all mass corrected, and were multiplied by respective time animals spent performing different activities. Second, I tested which other parameters would best predict energy expenditure at sea over a full foraging trip time-scale. These included foraging parameters (total distance traveled, travel rate, vertical distance traveled, dive rate, dive number), DBA parameters (DBA as area under the curve for total trip or for time spent displaying each type of activity), time-activity budget parameters (total time at sea or time displaying each type of activity), and morphometric parameters (mass and species).

All combinations of parameters were tested, and best models were selected based on the AICc (second-order information criterion or AIC adjusted for small sample size compared to the number of estimated parameters). I also computed AICc weights to obtain information about the model probability given the data and a set of models where one of the models is considered the best model for the situation at hand (log-likelihood of models normalized to be a set of positive AICc weights adding to 1, Burnham and Anderson, 2002). I also built models with energy expenditure corrected for mass of the animals (MJ/kg). In this case, I mass-corrected all DBA parameters, and did not include the mass of the animals in the list of tested explanatory variables. Finally, I compared estimated total energy expenditure from the best models to my DLW measurements to determine the accuracy of my method. All results are means ± SE.

2.4 Results

Three DD tags failed to record any data and 4 stopped recording before the end of the foraging trip. Seven females also came back on land with blood H and O isotopic levels too close to initial background levels to yield accurate metabolic rate measurements and were removed from further analyses. Consequently, sample size for analyses that only required

acceleration data or that only required energy expenditure data was n = 16 for northern fur seals and n = 17 for Antarctic fur seals. However, females missing acceleration data were usually not the ones also missing metabolic rate measurements. Consequently, sample size for analyses in which energy expenditure and acceleration data were combined was n = 12 for northern and n = 13 for Antarctic fur seals

Northern fur seal females weighed 37.9 ± 1.3 kg prior to departure (range 30.8 - 55.6 kg), and gained 1.1 ± 0.7 kg after a single foraging trip (which corresponds to 3.5 ± 1.8 % of their initial body mass). Female Antarctic fur seal were slightly smaller than northern fur seals with an average mass of 31.0 ± 0.8 kg (range 24.0 - 39.0 kg), and gained 0.6 ± 0.6 kg during a foraging trip (which corresponded to 2.2 ± 1.8 % of their initial body mass). Foraging trips lasted 7.96 ± 2.17 d (range 4.26 - 12.03 d) for northern fur seals, and 7.65 ± 3.88 d (range 2.34 - 15.47 d) for Antarctic fur seals (no inter-species difference $p = 0.750$). Both species travelled similar distances during their foraging trip ($p = 0.221$): 750 ± 50 km (range 391 - 1200 km) for northern fur seals and 635 ± 77 km (range 225 - 1295 km) for Antarctic fur seals.

2.4.1 Relationship between total energy expenditure and total DBA

Energy expenditures estimated from 4 different dilution equations are summarized in Table 2.1. Northern and Antarctic fur seals spent the same amount of energy while foraging at sea ($p > 0.09$). In addition, rate of energy expenditure per day was slightly, but not significantly greater for northern fur seals whether for the total DLW time or for the at-sea time (all $0.09 < p < 0.06$, and $0.08 < p < 0.06$). Rate of energy expenditure at sea was slightly higher than when time on land was taken into account for both species (although not significantly, all $p > 0.47$).

VeDBA performed slightly, but not significantly, better than ODBA in all tested models. Consequently, I only present results fitted with VeDBA and refer to this measure henceforth as DBA. Averaging dynamic body acceleration over the entire foraging trip (and for each type of activity, see below and in Table 2.2) showed that total average DBA was greater for Antarctic fur seals (0.411 ± 0.02 m/s^2) than for northern fur seals (0.312 ± 0.014 m/s^2, $p = 0.0004$).

Table 2.1: Energy expenditure estimated for 16 lactating northern (NFS) and 17 Antarctic fur seals (AFS) during a single foraging trip. Total time refers to the energy spent between two measurements of isotopic concentrations, and at-sea time refers to only the time when animal were at sea (see Appendices section). Values are mean ± SE.

		Speakman 1997 2-pool method		Speakman et al. 1993		Coward et al. 1985		Speakman 1993	
Energy expenditure		NFS	AFS	NFS	AFS	NFS	AFS	NFS	AFS
Total time	MJ/d	22.67 ± 1.38	19.19 ± 1.18	20.02 ± 1.27	17.02 ± 1.08	19.57 ± 1.35	16.15 ± 0.99	20.50 ± 1.28	17.41 ± 1.09
At-sea time	MJ/d	24.22 ± 1.58	20.39 ± 1.21	20.93 ± 1.47	17.72 ± 1.15	20.39 ± 1.65	16.66 ± 1.11	21.53 ± 1.48	18.20 ± 1.15
	MJ	179.93 ± 14.50	138.93 ± 18.88	155.10 ± 13.01	121.41 ± 17.06	150.78 ± 14.26	114.13 ± 16.30	159.68 ± 13.26	124.53 ± 17.35

Average DBA for the entire foraging trip (DBA_M) only explained ~ 36% of variability in energy expenditure at sea ($R^2 = 0.36$) using measures of energy expenditure from Speakman et al. (1993) equation. This relationship between DBA and energy expenditure improved somewhat when DBA was controlled for time animals spent at sea either by integrating DBA (DBA_I) by normalizing average DBA by the time at sea (DBA_{MT} average DBA), or by calculating 'noise-free' DBA over the entire foraging trip ($DBA_{Noise\text{-}Free}$ multiplied by time at sea). Under these scenarios, DBA_I or DBA_{MT} was able to explain ~ 60% of the variance in energy expenditure (Figure 2.2 B&C).

When fitted individually by species, the relationships between EE and DBA were significant for Antarctic fur seals, but not for northern fur seals. For Antarctic fur seals, EE (MJ/kg) = $(-0.19 \pm 0.68) + (3.10^{-6} \pm 4.10^{-7}) \times DBA_I$ (m/s/kg) ($R^2 = 0.80$, AIC = 45.5, slope $p = 3.10^{-5}$), while for northern fur seals, EE (MJ/kg) = $(3.00 \pm 1.15) + (1.10^{-6} \pm 1.10^{-6})$ DBA_I (m/s/kg) ($R^2 = 0.08$, AIC = 43.6, slope $p = 0.363$). The same general relationships were found using DBA_{MT} or $DBA_{Noise\text{-}Free}$. Rate of energy expenditure (in MJ/d) was never accurately predicted by acceleration, whether with averaged or integrated DBA (Figure 2.2 D, E, F), or over the entire foraging trip or by activity type (all $R^2 < 0.15$).

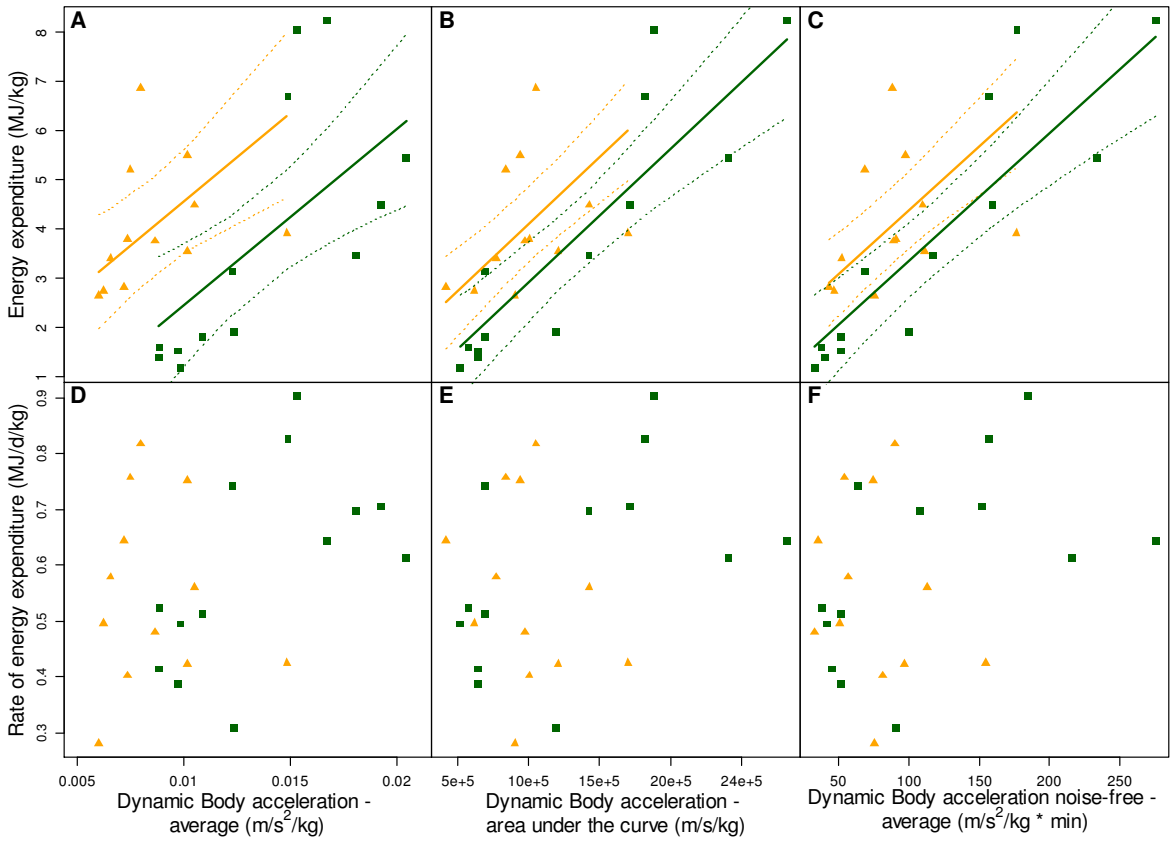

Figure 2.2: Relationships between energy expenditure (A, B and C) or rate of energy expenditure (Panels D, E and F) and the average dynamic body acceleration (A, D), the area under the curve of the dynamic body acceleration (B, E) over the entire foraging trip or the average DBA normalized by time spent at sea (C, F) for northern fur seals (yellow triangles, n = 12) and Antarctic fur seals (green squares, n = 13) during one single trip at sea. Each data point represents a single animal and was mass corrected. There were significant species-specific relationships between DBA and energy expenditure (general linear regressions with 95%CI dotted lines in A, B and C), but not between the DBA and the rate of energy expenditure (D, E and F). Equations were: Graph A: EE = (-1.17 ± 1.49) + (360.29 ± 103.51) × DBA_M (+ 2.11 ± 0.86 for NFS only), R^2 = 0.36, AIC = 102.1, slope *p* = 0.002, species *p* = 0.02. Graph B: EE = (0.21 ± 0.68) + (2.10^{-6} ± 4.10^{-7}) × DBA_I (+ 1.17±0.53 for NFS only), R^2 = 0.63, AIC = 88.2, slope *p* = 3.10^{-6}, species *p* = 0.039. Graph C: EE = (0.65 ± 0.65) + (0.027 ± 0.005) × $DBA_{NoiseFree}$ (+ 1.31 ± 0.53 for NFS only), R^2 = 0.56, AIC = 84.7, slope *p* = 5.10^{-5}, species *p* = 0.023.

2.4.2 Time-activity budget and activity-specific energy expenditure

Time-activity budgets revealed that the proportions of time allocated to transiting, diving, and surface activities / grooming were relatively evenly distributed between 25 and 35% average of the seals time at sea – range 20 – 45% between animals – for both species (Table 2.2). Conversely, fur seals spent only a small part of their time resting and sleeping at

the surface, (~ 6 - 10%). Northern and Antarctic fur seals allocated similar time to foraging (p = 0.328) and transiting to and from their foraging grounds (p = 0.063). However, Antarctic fur seals spent more time grooming and moving slowly at the surface (p = 0.013) and less time resting and sleeping (p = 0.040) than northern fur seals.

Models from Eq. 2.1 were fitted for each individual energy expenditure measures from the DLW measurement depending on the equation used (see Table 2.3), but I only report results from the best model with the lowest AIC and BIC values (Table 2.3, energy expenditure calculated with the equation from Speakman et al., 1993). Models involving time-activity budgets were better predictors of energy expenditure than models with only total time at sea or total time of DLW measurement (Table 2.3). As explanatory variables are in days at sea, and the response variable is in MJ, parameter estimates for each variable indicate the rate of energy expenditure (in MJ/d) for each type of activity.

The two major drivers of energy expenditure in fur seals were diving and transiting (lowest p values, Table 2.3). The seals used on average ~30 - 31 MJ/d diving, which was greater than the total rate of energy expenditure measured over the entire foraging trip (19.47 ± 1.05 MJ/d over all the seals). I also estimate that transiting at the surface required less energy than diving (~18 - 21 MJ/d), but required more energy than performing surface activities (~14 - 15 MJ/d). Outputs from Eq. 2.1 provided a negative parameter estimate for resting activity. However, standard errors for the term were more than 10-fold greater than the estimate itself, and values were not significantly different from 0. In addition, the p values associated with resting were > 0.05. I consequently excluded resting/sleeping time from Eq. 2.1. The simpler model did not fit the data better than the full model (Eq. 2.1; F-test p > 0.922) but had a lower AIC value (Table 2.3) and was thus considered the most parsimonious model. It was thus possible to calculate energy spent while performing each activity type (in MJ) by multiplying the parameter estimates from Eq. 2.1 (in MJ/d, see Table 2.3) by individual seal time-activity budgets (in d).

The relationship between time-activity budget and energy spent during the period between the two DLW measurements (*i.e.,*including energy spent during the time females were on land before and after their foraging trip in between capture and recapture) showed similar trends and parameter estimates compared to time-at-sea alone. Rate of energy spent

Table 2.2: Percentage of total time at sea and average VeDBA spent in 4 types of activity for 16 lactating northern fur seal and 17 lactating Antarctic fur seal during a single foraging trip. Activities included active foraging (diving + post dive surfacing), resting at the surface, transiting at a speed greater than 1 m/s, and slow surface movements (< 1 m/s) / grooming. Gap refers to the proportion of time when data were missing and could not be allocated to either of the 4 activity types. Values are means ± SE and asterisks show the values significantly different between species.

Activity	Proportion of at-sea time in each activity (%)		Average VeDBA during each type of activity (m/s^2)	
	NFS	AFS	NFS	AFS
Foraging/diving	28.6 ± 2.0	29.0 ± 0.7	0.297 ± 0.013	0.310 ± 0.018
Transiting	30.5 ± 1.8	26.4 ± 1.6	0.414 ± 0.013*	0.556 ± 0.026*
Surf mov.	28.8 ± 1.4*	36.3 ± 2.0*	0.456 ± 0.22*	0.605 ± 0.017*
Resting	10.9 ± 1.3	8.2 ± 1.7	0.125 ± 0.008*	0.155 ± 0.004*
Gap	1.1 ± 0.26	NA	NA	NA

Table 2.3: Parameters for general linear models describing the relationship between energy expended by fur seals per day to complete a single foraging trip (in MJ) as well as the cost of different foraging activities (time spent foraging, transiting, performing surface movements / grooming or resting). Note that "Total time" includes time at sea and time on shore tending to pups (*i.e.*,one foraging cycle), while "Time at sea" only accounts for the time away from land. Thus models were fitted with or without resting time.

Dependant variable	Parameter (d)	Estimate (MJ/d)	SE	p	R^2	AICc	Estimate	SE	p	R^2	AICc
EE at sea (MJ)	Time at sea	19.47	1.05	$<10^{-15}$	0.64	264.6					
EE at sea (MJ)	Diving	30.92	5.77	$<2.10^{-5}$	0.70	265.7	30.84	5.62	$<10^{-4}$	0.70	263.7
	Transiting	18.66	6.80	0.012			18.50	6.48	0.009		
	Surf. Mov.	14.95	7.93	0.073			14.47	6.18	0.028		
	Resting	-3.04	30.67	0.922							
EE total time (MJ)	Total time	18.58	0.88	$<10^{-15}$	0.65	265.4					
EE total time (MJ)	Diving	29.96	6.02	$<10^{-4}$	0.64	268.1	29.93	5.87	$<10^{-4}$	0.70	266.1
	Transiting	21.55	7.49	0.004			21.49	7.27	0.007		
	Surf. Mov.	13.85	8.24	0.105			13.49	6.36	0.045		
	Land	13.11	7.02	0.068			12.98	6.63	0.063		
	Resting	-2.34	32.69	0.942							

for time resting on land equalled the rate of energy spent at sea engaged in grooming and slow surface movements (13 - 14 MJ/d, Table 2.3).

2.4.3 Activity-specific DBA

When split by activity, DBA was the greatest when the animals were either transiting (0.414 ± 0.013 m/s^2 for NFS and 0.556 ± 0.026 m/s^2 for AFS) or active at the surface of the water (0.456 ± 0.22 m/s^2 for NFS and 0.605 ± 0.017 m/s^2 for AFS). DBA while diving was significantly lower than any surface activity (0.297 ± 0.013 m/s^2 for NFS and 0.310 ± 0.018 m/s^2 for AFS, $p < 10^{-6}$, no difference between species $p > 0.05$).

When animals were resting and sleeping at the surface, DBA should equal 0 as animals do not move but I found resting/sleeping DBA still significantly greater than 0 for both species ($p < 10^{-16}$), which means there was significant residual dynamic acceleration due to external factors (waves etc..) when the seals were lying on the water surface. I subtracted resting and sleeping DBA value from the transiting and surface movements DBA and found 'noise-free' DBA averages at the surface did not differ significantly from diving DBA for northern fur seals (0.278 ± 0.023 m/s^2 for transiting, and 0.321 ± 0.035 m/s^2 for surface movements, both $p > 0.316$), and for transiting for Antarctic fur seals (0.394 ± 0.035 m/s^2, $p = 0.08$) although surface-activity/grooming DBA was still slightly greater than diving DBA for AFS (and 0.428 ± 0.021 m/s^2, $p < 10^{-3}$).

Energy spent while performing each type of activity (MJ/kg) was significantly related to activity-specific DBA when standardized for time spent performing activities (acceleration multiplied by days spent performing activities Figure 2.3). DBA/EE relationships improved greatly when split by type of activity rather than over the full foraging trip (all $R^2 > 0.90$). Both species had similar mechanic-to-energy efficiencies while diving, but differences in slopes indicate that they differed while transiting or during surface activity. Regression slopes are lower during transiting and surface activity than while diving, and correcting for surface acceleration 'noise' decreased the mechanic-to-energy efficiency of seals. Specific equations for diving time, transiting and surface activity from Figure 2.3 included:

Eq. 2.2 $$EE_{Dive} \sim (0.10 \pm 0.10) + (91.99 \pm 4.42) \times DBA_{Dive} + (0.14 \pm 0.08 \text{ for NFS only})$$
$$R^2 = 0.94, \text{ slope } p < 2.10^{-16}$$

Eq. 2.3 $EE_{Transit} \sim (0.14 \pm 0.05) + (27.62 \pm 1.11) \times DBA_{Transit}$
$+ [(0.06 \pm 0.08) + (10.19 \pm 2.54) \times DBA_{Transit}$ for NFS only]
$R^2 = 0.96$, slope $p < 2.10^{-16}$

Eq. 2.4 $EE_{Surf} \sim (0.06 \pm 0.07) + (23.40 \pm 1.48) \times DBA_{Surf}$
$+ [(0.22 \pm 0.06) \times DBA_{Surf}$ for NFS only]
$R^2 = 0.90$, slope $p < 2.10^{-15}$

2.4.4 Predicting energy expenditure at sea from activity-specific DBA and behaviours

Total energy expenditure predicted by activity-specific DBA and time-activity budgets ($R^2 = 0.71$, AICc=91.1) was:

Eq. 2.5 $\text{Total EE} \sim (0.09 \pm 0.65) + (99.68 \pm 46.28 \text{ x } DBA_{Dive} \times Time_{Dive})$
$+ (3.54 \pm 19.80 \times DBA_{Transit} \times Time_{Transit})$
$+ (35.15 \pm 14.86 \times DBA_{Surf.} \times Time_{Surf.}) + [0.31 \pm 0.55$ for NFS only].

Where total EE is in MJ/kg, activity-specific DBA in m/s^2 and activity-specific time is in days ($R^2 = 0.70$ and AICc = 90.8). This model with no resting DBA was the most parsimonious model, but did not differ significantly than the model that took Resting into account (ANOVA, $p = 0.25$). Total energy expenditure estimated from activity-specific DBA and time-activity budgets correlated well with measured energy expenditure from the DLW method ($R^2 = 0.70$, Figure 2.4). Slope of the linear regression (1.00 ± 0.14) was not different from 1 ($p < 4.10^{-7}$) and the intercept ($1.10^{-15} \pm 0.56$) was also not different from 0. This means that there were no systematic differences between observed and simulated values, and that my model yielded appropriate estimates of total energy expenditure.

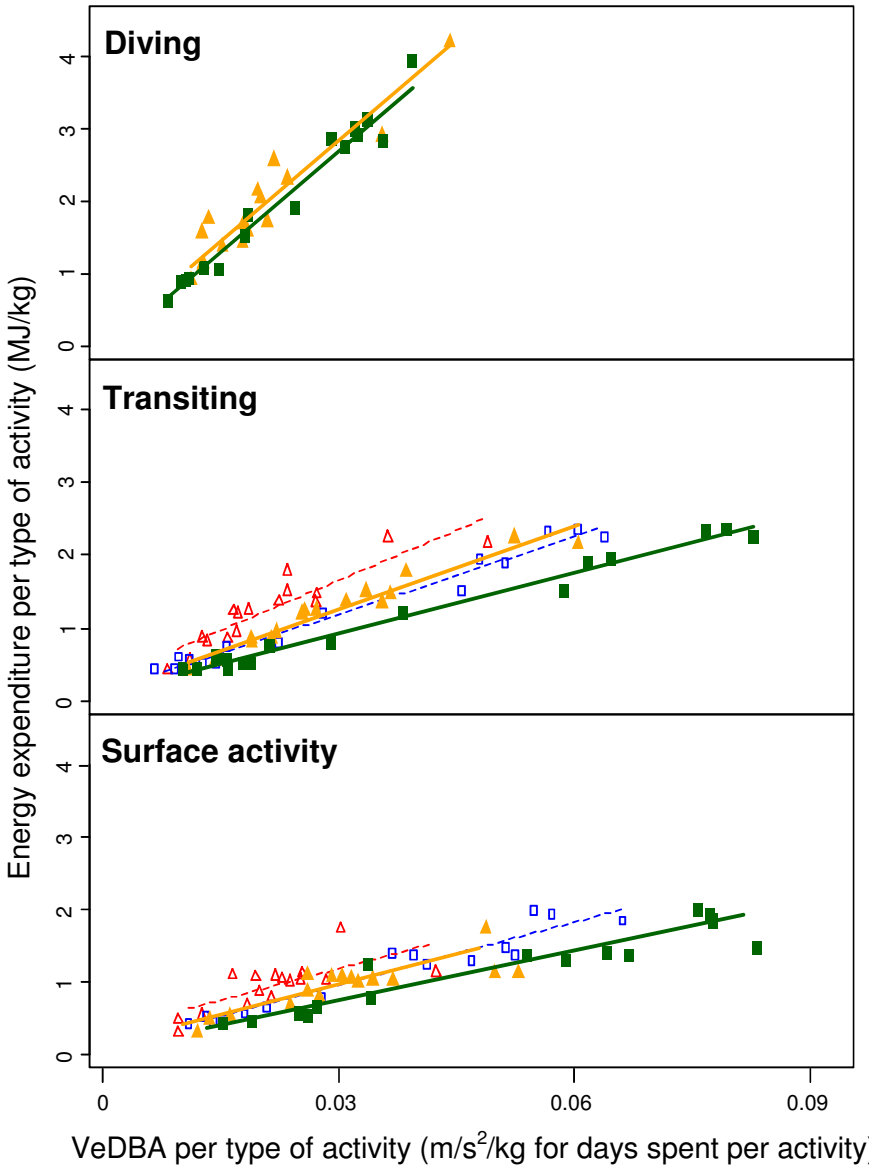

Figure 2.3: Relationships between activity-specific VeDBA standardized for individual time-activity budgets and body mass and activity-specific energy expenditure in MJ/kg for lactating northern fur seals (triangle symbols, n = 16) and Antarctic fur seals (square symbols n = 16) during a single foraging trip at sea. Filled symbols in middle and bottom graphs represents VeDBA at the surface while open symbols represent 'noise-free' VeDBA values corrected for environmental residual dynamic acceleration. Plain lines show the results of linear models that included species as an independent variable, and dotted lines are the 95%CI on the predicted values. Linear model for Diving activity: EE_{Dive} = (0.10 ± 0.10) + (91.99 ± 4.42) × DBA_{Dive} + (0.14 ± 0.08 for NFS only) (R^2 = 0.94, slope $p < 2.10^{-16}$), for Surface Transiting is $EE_{Transit}$ = (0.14 ± 0.05) + (27.62 ± 1.11) × $DBA_{Transit}$+ [(0.06 ± 0.08) + (10.19 ± 2.54) × $DBA_{Transit}$ for NFS only], R^2 = 0.96, slope $p < 2.10^{-16}$; and for Surface activity EE_{Surf} = (0.06 ± 0.07) + (23.40 ± 1.48) × DBA_{Surf} + [(0.22 ± 0.06) × DBA_{Surf} for NFS only]; R^2 = 0.90, slope $p < 2.10^{-15}$.

The model above is however not the best model I found. Best multivariate models (with a ΔAICc < 2, i.e. models that have approximately equal weight in the data) are shown in Table 2.4 (parameter estimates of all models from Table 2.4 are detailed in Table A.2 in the Appendices section). They all included indices related to transiting (area under the DBA curve while transiting (m/s) and/or time spent transiting in min) and diving (number of dives per trip (Dive.nb), dive rate per min (Dive.rate), and/or time spent diving in min). Best predictive models for energy expenditure at sea were:

Eq. 2.6 $$EE(MJ) \sim (1.616 \pm 1.417) - (3.10\text{-}7 \pm 7.10\text{-}8) \times Int.DBA_{Transit} - (0.041 \pm 0.010) \times Dive.nb + (0.026 \pm 0.006) \times Time_{Dive} - (2.10\text{-}6 \pm 8.10\text{-}7) \times Int.DBA_{Rest.} + (0.021 \pm 0.003) \times Total.Time$$

Eq. 2.7 $$EE(MJ/kg) \sim (2.314 \pm 0.629) - (3.10^{-7} \pm 3.10^{-8}) \times Int.DBA_{Transit}\,(/kg) - (0.178 \pm 0.044) \times Dive.rate + (9.10^{-4} \pm 1.10^{-4}) \times Time_{Dive} + (2.10^{-6} \pm 6.10^{-7}) \times Int.DBA_{Total}\,(/kg).$$

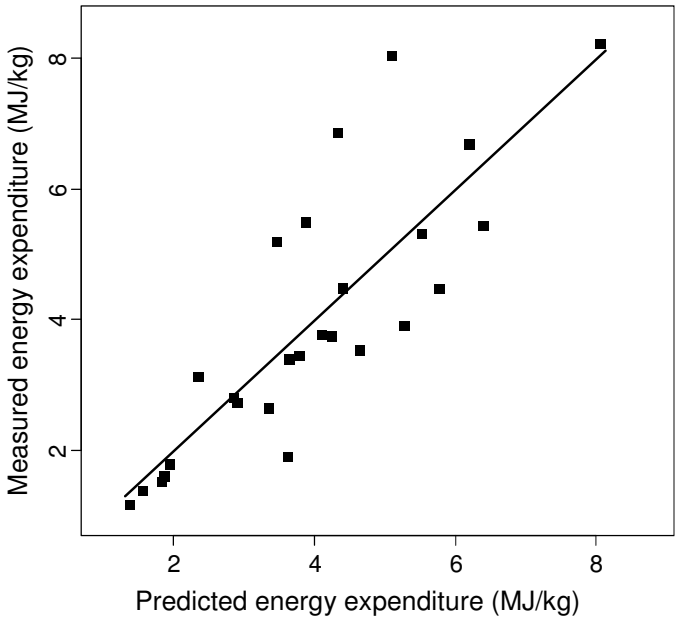

Figure 2.4: Comparison between measured energy spent at sea by lactating northern and Antarctic fur seals using the DLW method, and the predicted energy expenditure estimated using Eq. 2.5. The regression line has an intercept of $1.4 \times 10^{-15} \pm 0.56$, not different from 0, and a slope of 1.00 ± 0.13, not different from 1, $R^2 = 0.70$.

Table 2.4: Best predictive models for energy expenditure (mass-corrected or not) by lactating northern and Antarctic fur seals.Models were fit using general linear models and were selected using AICc. $Int.DBA_{Transit}$, $Int.DBA_{Rest.}$ and $Int.DBA_{Total}$ mean area under the curve of the dynamic body acceleration (integral) during transit time, resting/sleeping time or total time at sea. Dive.NB is the number of dives performed during the foraging trip; Dive.rate is the rate per min that animal dove over the foraging trip; and $Time_{Dive}$, $Time_{Rest}$, $Time_{Tramsit}$, $Time_{Surf.mov}$ and Total.Time indicate time spent in ech type of activity and total time spent foraging at sea. Only models with AIC less than 2 units above best model are shown. As a comparison, model from Eq. 2.5 for total energy expenditure (in MJ) as a function of activity-specific DBAs (EE ~ $DBA_{Dive} \times Time_{Dive} + DBA_{Transit} \times Time_{Transit} + DBA_{Surf.} \times Time_{Surf.}$ + Species) has a R^2 of 0.71 and an AIC of 91.1.

Eq.		Model	R^2	ΔAICc	AICc weight
2.8	EE(MJ) ~	$Int.DBA_{Transit}$ + Dive.NB + $Time_{Dive}$ + $Int.DBA_{Rest.}$ + Total.Time	0.89	0.00	0.260
2.9		$Int.DBA_{Transit}$ + Dive.NB + $Time_{Dive}$ + $Time_{Tramsit}$ + $Time_{Surf.mov.}$	0.89	0.72	0.181
2.10		$Int.DBA_{Transit}$ + Dive.NB + $Time_{Dive}$ + $Time_{Rest.}$ + Total.Time	0.88	1.50	0.123
2.11		$Int.DBA_{Transit}$ + Dive.rate + $Time_{Dive}$ + $Int.DBA_{Rest..}$ + Total.Time	0.88	1.80	0.105
2.12	EE(MJ/kg) ~	$Int.DBA_{Transit}$(/kg) + Dive.rate + $Time_{Dive}$ + $Int.DBA_{Total}$(/kg)	0.86	0.00	0.327

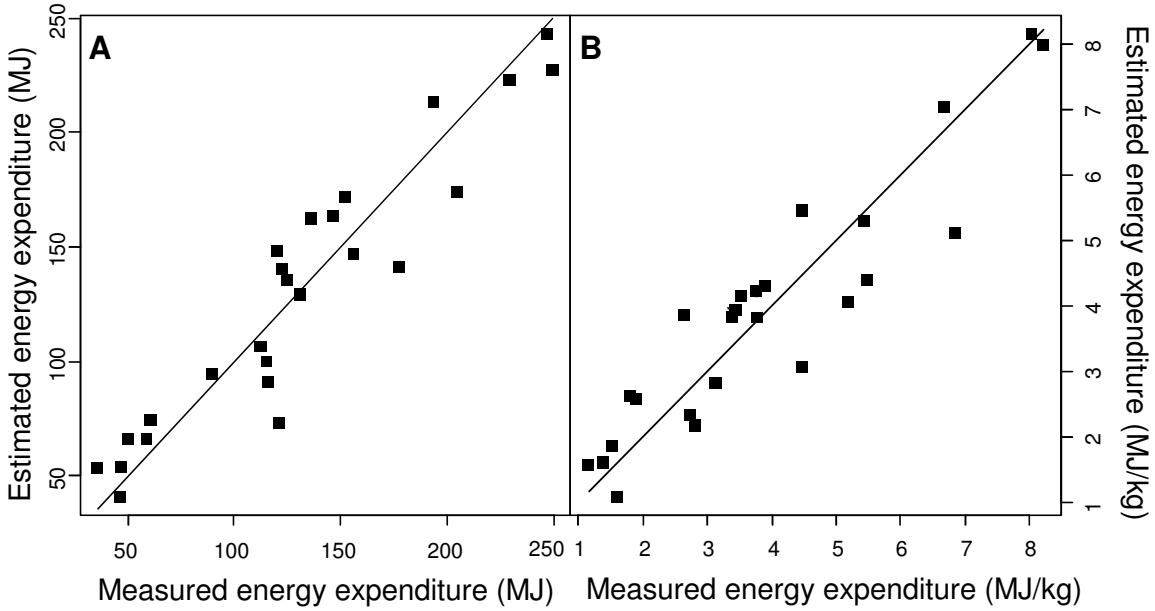

Figure 2.5: Relationship between estimated energy expenditure from best predictive models, and measured energy expenditure in MJ (graph A) or in MJ/kg (graph B) for lactating northern and Antarctic fur seals. Black squares show results from the two best predictive models: Eq. 6 (graph A) and Eq. 2.10 (graph B) from Table 2.4. Regression lines from best models (squares) are shown on both graphs (R^2 = 0.89 for A, and R^2 = 0.86 for B).

2.5 Discussion

I tested whether dynamic body acceleration and other behavioural parameters could accurately predict energy expended by fur seals, and found that DBA calculated independently of foraging behaviors or time activity budgets did a poor job of estimating energy expenditure of long foraging trips. However, activity-specific acceleration metrics could accurately predict energy used during specific types of behaviours at sea, and could be summed by types of activity (*i.e.,*diving, transiting, surface activity and resting) to accurately estimate energy expenditure of complete foraging trips. Even better estimates of energy expenditure were obtained by using multivariate models that include indices of duration and amplitude of effort (whether acceleration-related or not) of diving and transiting, as well as total foraging time.

My results confirm that acceleration has the potential to estimate energy expenditure in free-ranging animals but that it is only the case if the animals spend performing different types of activities—or time-activity budgets—are taken into account. DBA over a full trip is not an accurate predictor otherwise explaining only 36 % of the variation of EE (Figure 2.2A), an R^2 much lower than values reported for other species of vertebrates (0.47 for diving Steller sea lions, Fahlman et al., 2008; 0.84 in birds, Halsey et al., 2009a; 0.60 for swimming sharks, Gleiss et al., 2010; 0.56 for turtles, Halsey et al., 2011a)

2.5.1 Dynamic body acceleration

DBA (ODBA or VeDBA) is usuallyf study and comparing it to an independent measure of energy expenditure for a number of terrestrial and aquatic taxa (Halsey et al., 2009b). It has been argued that VeDBA estimates should be better than ODBA estimates if logger alignment cannot be standardized between individuals (Qasem et al., 2012). My models with VeDBA had slightly but not significantly lower AIC values (same as for European sea bass with implanted loggers, Wright et al., 2014), which indicates negligible differences in logger positions on the back of seals that cannot explain why DBA failed to accurately predict the total energy expended in my study.

Another explanation for the differences between my validation of DBA as a measure of energy expenditures with fur seals and studies of other species lies in the assumptions behind DBA as a proxy for energy expenditure, and sources of unmeasured error associated with free-ranging environmental conditions (Halsey et al., 2011b). Most studies have validated DBA in captive or semi-captive settings where conditions could be controlled (Wilson et al., 2006; Gleiss et al., 2010; Halsey et al., 2011a; Fahlman et al., 2013). However, free-ranging marine animals live in a dense medium under fluid environmental conditions. In addition, marine mammals such as fur seals spend a significant portion of their time at the water surface, where wind-related motions, mainly through wave action can interfere both with energy expenditure and the dynamic body acceleration signal. Considerable surface acceleration 'noise' occurs in the acceleration signal at the interface between the two mediums of different densities (air and water), which largely disappears when the animals dive.

I attempted to crudely quantify and account for environmental surface motion by averaging the dynamic acceleration at times when the animals were resting and sleeping at the surface. This 'acceleration noise' was slightly greater in the Southern Ocean for Antarctic fur seals (0.15 ± 0.004 m/s^2) than in the Bering Sea for northern fur seals (0.12 ± 0.009 m/s^2). However, environmental dynamic acceleration does not appear to explain much of the uncertainty in my global model given that the models that incorporated average 'noise-free' DBA did not perform significantly better than those with non-corrected DBA. Thus, it appears that surface noise augments body acceleration but that the influence is consistent between seals over their foraging trips (as shown by the very small standard errors mentioned above) and should thus not affect relationships. An interesting application of this would be to use acceleration signals during these time when seals are sleeping/resting as indices of ocean conditions in a given time and location.

Another difference between other validation studies and mine is the variation in the duration of measurements taken (*i.e.,*hours vs. days or weeks). In my case, the northern and Antarctic fur seals undertook foraging trips that averaged 7 - 8 days (range 2.5 - 15 days). A fur seal that makes a long foraging trip is likely to allocate energy differently compared to an animal that makes a short trip—yet averaging DBA over time does not account for such

differences. I suspect this is why none of my analyses that used metabolic rate as my reference measurement (in MJ/d, Figure 2.2D, E & F) yielded significant relationships with DBA, unlike the relationships reported for other studies.

I tried to account for foraging trip duration in two different ways. The first was to integrate the DBA signal (Figure 2.2B), and the second was to standardize the averaged DBA (or 'noise-free' DBA) by multiplying it by foraging time (Figure 2.2C). Both procedures improved the DBA/EE relationship between DBA and energy expenditure. Most notably, the R^2 increased to 0.63 in both cases, suggesting that difference in foraging trip durations might explain ~ 30% of the uncertainty in the initial model. It is equally noteworthy that time spent at sea ($R^2 = 0.64$) proved to be a much better predictor of energy expenditure over a foraging trip than was DBA (Table 2.3). However, it is debatable whether the improved predictions of energy expenditure that come by combining DBA and trip duration are sufficient given that the predictive power of such a combined model can only explain ~ 60% of the variation in the data.

Energy expended by fur seals could have been affected by a number of sources of errors that had no effect on DBA—or vice versa. For example, body condition of seals affects buoyancy, which in turn affects mechanical power and cost of transportation (through changes in buoyancy and gliding — Williams et al., 2000; Wilson et al., 2010), but would not affect DBA. In addition, fur seals typically transit by porpoising at the surface, which means that they switch from moving through air to moving through water in less than a second. Such changes in movement between mediums with highly different densities likely affect DBA in different ways, as would differences in gaits between swimming and porpoising movements. In addition, effects of 'barrel-wheel' turns while diving or surface grooming create centrifuge forces that remain part of the dynamic acceleration after low-pass filtering. This relationship between centrifugal acceleration and energy expenditure is likely to differ from the relationship between non-rotative acceleration and energy expenditure. However, the only way I could have estimated whether centrifugal force had a significant impact on the dynamic acceleration was with a gyroscope (Noda et al., 2012), which my data loggers did not contain.

In addition to the physical effects of moving through air and water, physiological functions can affect energy expenditure and DBA in different ways. For example, thermoregulation costs may increase while seals rest at the surface, or animals will incur costs of digestion, growth, and gestation that are independent of DBA. It has been suggested that the energy budgets of fur seals and other pinnipeds are largely a balance between basal metabolic costs, locomotion costs and feeding costs (Costa and Williams, 1999). Out of these expenses, digestion costs are non-negligible, and can increase the metabolic rate of seals by ~ 45% in Weddell seals, or ~ 55% in Steller sea lions (Rosen and Trites, 1997). A study with domestic chickens showed a clear increase in metabolic rate during digestion while DBA remained stable (Green et al., 2009). No differences have been reported in the relationship between DBA and energy expenditure for fasted and non-fasted Steller sea lions (Fahlman et al., 2013), but increase in metabolic rate due to feeding depends on the quantity of fish ingested (usually small in captive trials to keep animals working) and are usually deferred to resting time few hours apart from feeding (Sparling et al., 2007). It could thus be significant in free-ranging seals. Collectively, such studies point to an uncoupling between a significant portion of metabolic rate and the acceleration which could potentially contribute to the uncertainty in the DBA and energy expenditure relationship (Halsey et al., 2011b).

In addition to the inherent uncertainties associated with DBA measures of energy expenditure in free-ranging fur seals, there are also uncertainties with using the doubly-labeled water method (DLW) as my reference measure of energy expenditure. Some studies of specialist marine carnivores have suggested that the DLW method has high accuracy, but low precision (Speakman, 1993). For example, the DLW method applied to grey seals (*Halichoerus grypus*) subjected to simulated foraging conditions over 5-day periods yielded estimates of energy expenditure for groups or population averages that were similar to estimates derived from respirometry (Sparling et al., 2008). However, precision was quite low at the individual level (Sparling et al., 2008). Group error was 0.5% (based on the 2-pool equation from Speakman (1997) or the original calculations from Lifson and McClintock (1966)) when tested against 32 respirometry measurements on 9 individuals over 3 years). However, individual error was ~ ±40%. Similarly, a study of captive northern fur seals showed that the average error of the DLW method compared to respirometry measurements could be as low as ~ 0.8% but as high as ~ 27% depending on the calculation method used

and the time of year (lowest in the fall and highest in the summer, Dalton et al., 2014b). Consequently, the error associated with my reference measurement of energy expenditure is likely significant since I compared DLW to DBA measurements at the individual level (one DLW and one DBA point per animal).

I attempted to decrease the DLW-associated error by using estimates derived from the best equation provided by Sparling et al. (2008) as well as the 3 best equations derived by Dalton et al. (2014b), and chose the best fit for my data out of the 4 equations. I recognize that using DLW measurements as a reference measurement of energy expenditure comes with associated caveats, but was the only option available to us to study energy expenditure at sea for free-ranging fur seals. Either way, however, there seems to be no escaping the fact that DBA metrics are not an appropriate means to predict the total energy expended over the duration of a full foraging trip regardless of what means I might have used to establish the reference measurement of energy expenditure.

2.5.2 Time-activity budgets and activity-specific energy expenditures

DBA is not a good proxy for energy expenditure by fur seals over long periods of time and in field settings, and appears to also perform poorly for other species that engage in different behaviors that have markedly different energetic costs (Green et al., 2009; Halsey et al., 2011b; Dalton et al., 2014b). A study of free-ranging imperial cormorants (*Phalacrocorax atriceps*), for example, found that activity-specific DBAs were better predictors of energy expenditure during a foraging trip than overall DBA, especially if one activity type had a greater energetic cost than others (in this case flying, Elliott et al., 2013). Animals are known to incur different energetic costs for different activities, and different relationships are known to exist between DBA and energy expenditure for seemingly inconsequential activities as different gaits in humans (Halsey et al., 2008), different intensities of swimming in sharks (Gleiss et al., 2009) and different types of muscles involved in the movement of birds (Gomez-Laich et al., 2008). All told, this suggests that the poor ability of DBA to predict the energetic cost of the full foraging trips undertaken by my fur seals was due to differences in time-activity budgets (*i.e.,*how the animals partitioned their time at sea between diving, transiting, resting and surface activities).

Time budgets are the currency that defines foraging strategies and ultimately reflects the foraging efficiencies of animals when combined with energetics. In my study, both species of fur seals had surprisingly similar time-activity budgets despite inhabiting significantly different habitats. The lactating northern and Antarctic fur seals spent ~ 29% of their time diving, ~ 26 - 30% of their time transiting, and ~ 8 - 10% of their time resting and sleeping at the surface (Table 2.2). These activity time-budgets are consistent with previous findings showing northern fur seals spent 22-26% of their foraging trips diving, and Antarctic fur seals spent 35% of their time engaged in diving (Costa and Gentry, 1986; Insley, 2008). Similarly, northern fur seals rested for 17% of their time at sea, while Antarctic fur seals spent just 5% of their time resting (Costa and Gentry, 1986). However, this consistency between the activity time budgets of the 2 species of fur seals masks considerable variability between individual seals which differed by as much as a factor 2 - 2.5 times for time spent diving or foraging between seals. Such individual differences are bound to impact the energetic costs of foraging trips.

Overall, the average daily metabolic rate at sea (MR_{sea},Table 2.1) for both species of fur seals was 4.7 ± 0.3 × basal metabolic rate (BMR in kJ/d) calculated from Kleiber's equation (Kleiber, 1975). This calculated metabolic rate is consistent with values previously reported for Antarctic fur seals (4.59 ± 0.32 × BMR from Arnould et al., 1996) and California sea lions *Zalophus californianus* (5.2 × BMR from Boyd et al., 1995b; 4.8 × BMR from Ponganis et al., 1997). Consequently, total energy spent at sea over a foraging trip ranged from 38 to 259 MJ depending upon the duration of foraging trips and differences in the proportion of time the seals engaged in diving, transiting and resting.

The most expensive activity the fur seals engaged in was diving, which was 1.6 ± 0.1 × MR_{sea} (Table 2.3) — or roughly 7.5 × BMR, (7.0 ± 0.2 for NFS and 8.1 ± 0.2 for AFS). This high metabolism seems counter-intuitive given that diving in pinnipeds usually involves hypometabolism to preserve oxygen stores and extend dive duration (Sparling and Fedak, 2004). However, my values are close to previous measures of at-sea metabolic rates for northern fur seals (6.16 × BMR from Costa and Gentry, 1986) and Antarctic fur seals (6,7 × BMR from Costa et al., 1989), and for underwater swimming metabolic rate in southern sea lions and California sea lions (6.8× BMR from Boyd et al., 1995b; Dassis et al., 2012) –

although greater than metabolic measurements for Steller sea lions over one dive cycle in semi-captive conditions when animals stay stationary at a target at depth (4 × BMR, Gerlinsky et al., 2013). In my case, I derived my estimates of diving metabolism from a best fit model (Eq. 2.1), and not from direct measurements (which are virtually impossible to obtain from free-ranging animals). My estimates of metabolism also accounted for the total cost of diving (which included extended recovery that can occur over periods longer than a single dive cycle)—and show that diving remains the most expensive foraging activity despite the physiological mechanisms that pinnipeds have evolved to extend dive durations. Butler et al. (1995) also found that metabolic rate while diving was greater than when transiting in Antarctic fur seals. However, contrary to both my results, Arnould et al. (1996) found that energy expenditure at sea was negatively related to proportion of time spent diving in Antarctic fur seals, and thus concluded that the most costly activity was transiting rather than diving. They estimated time spent diving using depth recorded every 10 s. The finer scale and more detailed time-activity budget in my study might explain the difference in the results.

Transiting at the surface (surface movement ≥ 1 m/s) was 0.96 ± 0.10 × MR_{sea} which was less expensive than diving and roughly equivalent to the average daily metabolic rate at sea (0.9 ± 0.1 × MR_{sea} for NFS, and 1.1 ± 0.1 × MR_{sea} for AFS). Transiting fur seals usually porpoised at the surface or swam at depths equivalent to 3 times their body diameters, which would reduce drag forces and cost of transportation (Boyd, 2002; Hindle et al., 2010). Surface activities were less expensive than diving and transiting, and overall less expensive than average daily metabolic rate at sea (*i.e.,*0.77 ± 0.10 × MR_{sea}). My calculated metabolic rate on land (as well as the surface activity/grooming metabolic rate) was ~ 3.3 ± 0.1 × BMR which was very close to the 3.4 × BMR metabolic rate of female Antarctic fur seal females nursing on land (Costa and Trillmich (1988). It is also noteworthy that my calculated metabolic rates during surface activity/grooming and during time on land (Table 2.3) were roughly similar (13-14 MJ/d). This confirms that thermoregulation at sea is likely not an issue in fur seals—at least for most of their time at sea (Costa and Williams, 1999; Dalton et al., 2014a). Resting and sleeping at sea also had negligible metabolic costs for my fur seals (Table 2.3) due most likely to the low cost of doing so and the small proportion of overall at-sea time they spent resting (<10%).

The similarities between my field and modeled estimates of metabolism give confidence that my models provide accurate activity-specific metabolic rates. Similarly, the high correlations between the activity-specific energy expenditures and the activity-specific DBAs (all R^2 ~ 0.94) gives confidence that mean DBA is a much better proxy for energy expenditure when broken down by activity type. However, the relationships (*i.e.,*the mechanical to energy efficiency) varied by activity type. Changes in DBA affect mechanical power and thus energy expenditure more drastically while diving than while transiting or during surface activities (Figure 2.3). This means that small changes in measures of DBA can lead to larger changes in estimates of diving energy expenditure than of energy spent in surface behaviours.

The mechanical energy efficiency of fur seals differed between underwater activity (diving) and switching from water to air (transiting and surface activity). Similarly, the mechanical-to-energy efficiencies (*i.e.,*slopes of the DBA and energy efficiency relationships) of cormorants have been shown to differ between flying and all other activities (*i.e.,*resting at sea surface, diving and walking on land, Gomez-Laich et al., 2011; Elliott et al., 2013). Collectively, these findings indicate that the mechanical efficiency of different activities are constrained by the medium (air or water), but maybe more so by the mechanics and the types of muscles involved (*i.e.,*the force production to movement relationship of muscles and their contractile properties).

The difference I observed in activity-specific relationships between DBA and energy expenditure was likely due to the media through which they travelled (air/water intersection for transiting and surface activity versus exclusively water for diving) rather than changes in muscle groups involved. Densities of air and water differ by a factor of ~ 800, which undoubtedly affects DBA differently than it affects energy expenditure given that fur seals propel themselves using their fore-flippers. It seems however, that the effect of medium on DBA is inconsequential when DBA is partitioned by types of activity to predict the energy fur seals spent at sea.

The improved accuracy by incorporating activity levels (*i.e.,*swim speeds, frequency of dives, and time spent transiting and diving) to predicting energy expenditure compared to analyses over the full foraging trip may also reflect the fact that my calculations buffered

some of the errors associated with individual DLW measurements. I calculated energy expenditure from an average activity-specific metabolic rate from the energy that each animal spent per activity (in MJ) given their time-activity budget (in d) from the parameter estimates of Eq. 2.1 (in MJ/d, from best fit model between measured energy spent at sea and time-activity budgets of all individuals, results in Table 2.3), and not from an individual DLW measurements. As a consequence, the inherent individual variation and measurement error in DLW measurements was likely reduced in the average. This means that I could attribute ~ 20 - 35% of the uncertainty in the global model to errors in the DLW measurements and individual variability in time-activity budgets and foraging strategies (even if it was difficult to tease apart the respective effect of these two parameters).

The impact of factors other than activity levels might have on the total energy expenditure of fur seals is likely minimal given that otariids have high locomotion costs and operate close to their metabolic ceilings (Costa, 2007). For example, the uncoupling that likely exists between DBA and energy expenditures associated with such physiological functions such as digestion, thermoregulation, and growth might be minimal in the case of fur seals foraging at sea with much higher energetic costs due to locomotion. This shows that the time a seal decides to allocate to activities that have different metabolic rates is important for obtaining accurate estimates of energetic costs of foraging in fur seals.

2.5.3 Conclusions

Energy expenditure by fur seals over full foraging trips can be accurately determined from body acceleration, but only if it is done using activity-specific time budgets. The predicted energy expenditure derived from activity-specific measures of body movement (*i.e.,*DBA × activity budget) corresponded well with the DLW measured energy expenditures (Figure 2.4, $R^2 = 0.70$). Including other variables into the model that captured the intensity of activities such as number of dives per trip or total minutes spent diving significantly improved the ability to predict energy expended by the seals during foraging trips ($R^2 = 0.84$ - 0.89, Table 2.4 and Figure 2.5). However, I also incorporated elements of the time-activity budget in these multivariate models using proxies of diving and transiting effort (intensities)

that represent the most expensive parts of the foraging trip. I also included proxies to represent resting and slow surface movement, or total time at sea.

My predictive models reinforce the importance of separating animal behaviours into categories to obtain reliable estimates of energy expenditure. Interestingly, Skinner et al. (2014) found that DBA multiplied by distance traveled and by mass of the animal, and by vertical distance swam were together the best metrics to assess energy expenditure of northern fur seals at sea. This means that they also took into account metrics of effort (DBA, and of diving time). Acceleration is a useful tool for estimating the field metabolic rate of free-ranging fur seals, but it is essential to know how much time the animals spend diving versus transiting and being surface active. It is also important to know the intensity with which the seals perform these activities. Calculating total energy expended by fur seals should thus be done using either the activity-specific DBA paired with time-activity budget (*i.e.,*Eq. 2.5) or the multi-factorial models (Eqs. 2.6 and 2.7).

Being able to accurately calculate foraging costs helps to better understand the energetic requirements of free-ranging seals and other marine mammals, and whether they can be met in the wild. Knowing foraging costs also contributes to assessing the ecological impacts that marine mammals have on trophic webs, and how changes in time-activity budgets due to environmental changes will impact their fitness. Such knowledge is particularly important for the conservation and management of species that are easily impacted by ecosystem shifts and environmental changes, especially for fur seals that are already performing close to their metabolic ceilings, and may have limited scope to adapt to coming climate changes.

Chapter 3: Do flipper stroke rates and amplitudes accurately predict energy expenditure in foraging northern fur seals and Antarctic fur seals?

3.1 Summary

Flipper stroke rate and amplitude have been proposed as proxies to estimate the energy expended by seals and sea lions while foraging at sea, but have not been validated. I investigated how well metrics of flipper strokes correlate with energy expenditure in foraging northern fur seals (*Callorhinus ursinus*) and Antarctic fur seals (*Arctocephalus gazella*). Flipper strokes rates and amplitude were measured for 33 lactating females using dynamic bi-axial acceleration obtained from accelerometers deployed on the backs of the fur seals during diving or transiting because residual water movement at the surface clouded the detection of strokes during times of surface activity. I derived activity-specific energy expenditure by calculating time-activity budgets for single foraging trips (time spent diving, transiting at speeds >1m/s, surface activities and sleeping) and by measuring metabolic rate using the doubly-labeled water method. I found that flipper stroke count was a good predictor of energy spent while diving ($R^2 = 0.76$) and to a lesser extent while transiting ($R^2 = 0.63$), and that it performed better than flipper stroke amplitude. Fur seals spent 3.79 ± 0.39 J/kg per stroke while diving and a cost of transportation ~ 1.6 - 1.9 J/kg/m (and there was no difference between species), but the energetic cost per stroke and cost of transport differed when the seals were diving compared to when they were transiting and routinely porpoising at the surface. In terms of predicting energy spent during a complete foraging trip, I found that flipper stroke amplitude was a better proxy ($R^2 = 0.63$) than flipper stroke count. Flipper stroke amplitude (*i.e.,*an index of power delivered depending on the means of locomotion) encapsulated the type of locomotion or the gait used by the seal better than stroke count. In conclusion, the cost per stroke differed depending on the type of activity the seals were engaged in such that flipper stroke metrics were accurate at the activity level, but were not as accurate an index of energy expenditure over a full foraging trip compared to other acceleration-based proxies such as activity-specific VeDBA.

3.2 Introduction

Determining energetic costs of foraging is essential for understanding optimal foraging and the fitness of animals yet is difficult to attain. Over the years, different techniques have been developed to determine energy expenditure, such as direct or indirect calorimetry techniques, breathing rates (Le Boeuf et al., 2000), heart rates (Boyd et al., 1995b), and locomotion speed (Hind and Gurney, 1997). While they may be accurate in terrestrial or flying animals, they are usually either impossible to perform in the field or are overall poor predictors in most breath-hold divers species such as marine mammals because of confounding factors inherent to diving physiology and biomechanics (McPhee et al., 2003), changes in buoyancy and gliding (Costa and Gales, 2000), etc.

Cost of transport is defined as the energy needed to move a unit of mass over a distance, usually expressed in J/m or in J/kg/m. As most of the metabolic cost of foraging is thought to come from the cost of transport (Gleiss et al., 2011), proxies of energy spent have been developed to count and characterize stride', 'wingbeats', or—in the case of marine animals—'stroke' rates that are directly linked to the cost of underwater locomotion (Dassis et al., 2012; Maresh et al., 2014). Several methods, such as video images (Hays et al., 2007; Dassis et al., 2012; Dudley et al., 2014) or acoustic recordings (Insley, 2008) can be used to detect wing or flipper stroke rates in top marine predators. However, it is very difficult to assess the intensity of swimming effort (such as amplitude of the strokes) from the count of strides using these techniques. More recently, tri-axial acceleration has been used to investigate the cost of transport and has proven to be a cost-effective means to record data over long periods that can characterize both frequency and relative amplitude of strides as animals propel themselves through air and water (Gleiss et al., 2009; Adachi et al., 2014; Bishop et al., 2015).

In marine predators, the flipper or tail stroke rate can potentially be used to estimate foraging effort. Based on metabolic rates determine in Weddell seals (*Leptonychotes weddelli*) breathing through a hole in the ice at the end of dives, flipper strokes have been found to be a better predictor of energy expenditure during dives than the dive duration itself (Williams et al., 2004). Tail beats correlated with acceleration, which in turn correlated with metabolic rates in salmon (Wilson et al., 2013) and sharks (Gleiss et al., 2009; Gleiss et al.,

2010). Stroke rate has also been shown to vary with activity and dive phase in northern fur seals (Insley et al. 2007). It was also hypothesized for these animals that the cost per stroke multiplied by the average stroke rate of 0.5 Hz for 70% of the diving and traveling time would produce a reasonable correlation with the cost of locomotion (Insley, 2008). However, this needs to be verified under free-ranging conditions, and consideration must also be given to how the amplitude of the strokes affects swimming energetics given that power delivered with each stroke shapes energetics of locomotion (Booth, 2009).

Most studies on marine mammals have been performed either in captive controlled settings (Dassis et al., 2012) or on single types of activities such as continuously diving in species that spend little time at the surface (Williams et al., 2004; Maresh et al., 2014). Otariids such as northern fur seals and Antarctic fur seals are pelagic species that spend a significant portion of their time at sea at the surface where they transit, rest, and groom. The proportion of time spent performing surface activities also greatly affects total foraging effort of free-ranging animals (Chapter 2 and Elliott et al., 2013). Different modes for transport (swimming or porpoising) also affect locomotion costs, as does the media in which the animal evolved (air, water, land) (Gomez-Laich et al., 2013). There is consequently a need to assess whether flipper stroke metrics can accurately reflect energy expenditure of otariids under free-ranging conditions and how it might change with different types of behaviour or media (*i.e.,*air, water and the interface between the two).

My goals were to determine whether flipper strokes of fur seals could be accurately detected at any time and for different types of activities/gaits during foraging trips using accelerometry. I also sought to assess whether stroke rates or amplitude could accurately predict at-sea energy expenditure. Finally, I compared the accuracy of using flipper stroke metrics for quantifying the energetic costs of different types of activities that seals display at sea or over a full foraging trip, and relate it to cost of transport.

3.3 Material and methods

3.3.1 Data collection

All data were collected from 20 lactating northern fur seals at the Reef rookery on St. Paul Island (Bering Sea, 57°6'N - 170°17'W) during the breeding season from Aug-Sep

2011, and from 20 lactating Antarctic fur seal females at Pointe Suzanne, Kerguelen Island (Southern Ocean, 49°26'S - 70°26'E) during the breeding season from Jan-Feb 2012. Data were collected under the US NMFS permit # 14329-01, the UBC animal care permit # A10-0364 and the ethical regulations approval from the French Polar Institute (IPEV). All data collection methods are similar as the ones detailed in section 2.3.1 of Chapter 2. Three daily diary tags failed to record any data and 4 stopped recording before the end of the foraging trip. Consequently, sample size for acceleration data was n = 16 for northern fur seal and n = 17 for Antarctic fur seals. I also obtained inaccurate metabolic rate measurements for 7 females during their foraging trip, so they were discarded from further analyses. Consequently, sample sizes for energy expenditure were n = 16 for northern and n = 17 for Antarctic fur seals. Females missing acceleration data were usually not the ones also missing metabolic rate measurements, so sample size for analyses combining both parameters were reduced accordingly (n = 12 for NFS and n = 13 for AFS). All values provided in the result section are mean ± SE

3.3.2 Energy expenditure, diving and foraging parameters, and time-activity budgets

Methods for measuring energy expenditure during foraging trips at sea from the DLW method, for calculating diving and foraging parameters, and for deriving time-activity budget of individual animals from GPS, depth and acceleration data are similar to the ones detailed in Chapter 2. Please refer to sections 2.3.2 2.3.3 and 2.3.4 for further information.

3.3.3 Flipper strokes

Flipper strokes were detected and counted using only the X (surge) and Z (heave) accelerometer axes from back acceleration. Fur seals swim by flapping their fore-flippers which results in an up and forward movement clearly and synchronously visible the 2 signals. The dynamic accelerations X_{dyn} and Z_{dyn} were obtained using the same filtering method as mentioned in Chapter 2 and then added to increase the signal clarity compared to residual background noise. Each flipper stroke was detected by counting the spikes resulting from a deviation from the gravitational field above a specific threshold (Figure 3.1).

Thresholds were determined for each animal individually as the break point of a curve showing the number of flipper strokes detected for a range of thresholds going from 0.1 to 0.4 m/s^2. Thresholds ranged from 0.19 to 0.24 m/s^2 depending on individuals.

Maximum flipper stroke frequency is ~1 - 2 Hz in dolphins, Weddell seals, and elephant seals (Williams et al., 2000; Sato et al., 2003). However, it is known to vary with the size of the animal (Sato et al., 2007). Baikal seals which are closer in mass to fur seals than other investigated marine mammals (~45 kg) have a maximum stroke frequency of ~2.5 Hz during ascent and descent phase of dives (average ~0.25 - 1.75 Hz, Watanabe et al., 2006). Northern fur seals were found to have an average and maximum stroke rates of ~0.5 Hz and 0.89 Hz, respectively, using acoustic detection in diving females (Insley, 2008). However, these values were averaged and not recorded during chase time, so might be lower than the maximum flipper stroke frequency. I, therefore, considered that fur seals have an absolute maximum flipper stroke frequency of 2.5 Hz, same as the maximum stroke rate found in a species of similar mass, and any peak within 0.4 s was not considered a flipper stroke. As the dynamic acceleration is centered on 0, I also used the value at the highest point of the flipper stroke as a relative index of flipper stroke amplitude (*i.e.,*of swimming effort).

Flipper strokes where easily detected when animals were diving (Figure 3.1). However, oceanic/wave movements often clouded the acceleration due to the movement of the animal when the animals were at the surface. I was only able to detect flipper strokes when animals were at the surface travelling at a minimum of 1 m/s. Below this travel speed, the animal seemed to be either not stroking, or stroking with such a low amplitude that it was impossible to separate dynamic acceleration signal coming from oceanic movements or animal movements (Figure 3.1).

Consequently, I only measured flipper strokes at depth or at the surface when the animal was moving at or faster than 1 m/s between 2 GPS points. Accuracy of peak threshold and flipper stroke detection were verified visually on ten 5-min periods randomly chosen over the entire foraging trip for each seal. Relationship between flipper strokes and distance traveled was also verified for each animal at depth and while transiting at a speed ≥1 m/s at the surface (example for 2 NFS and 2 AFS on Figure 3.2) to validate the detection method.

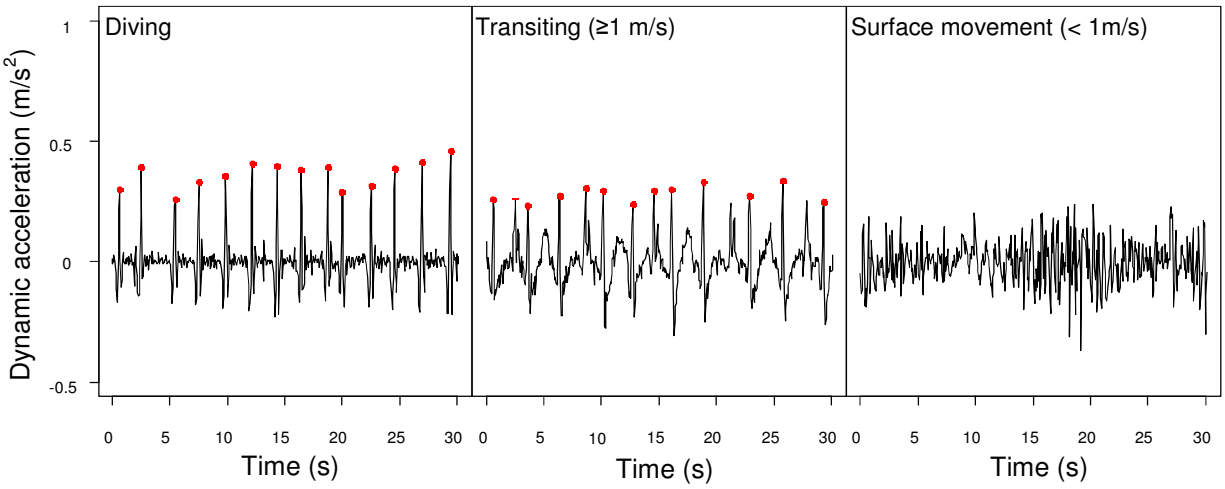

Figure 3.1: Example of detection of flipper strokes from the dynamic acceleration on the X and Y accelerometer axes while diving, while transiting at the surface at speeds > 1m/s, or while performing slower movements at the surface at speeds < 1m/s.

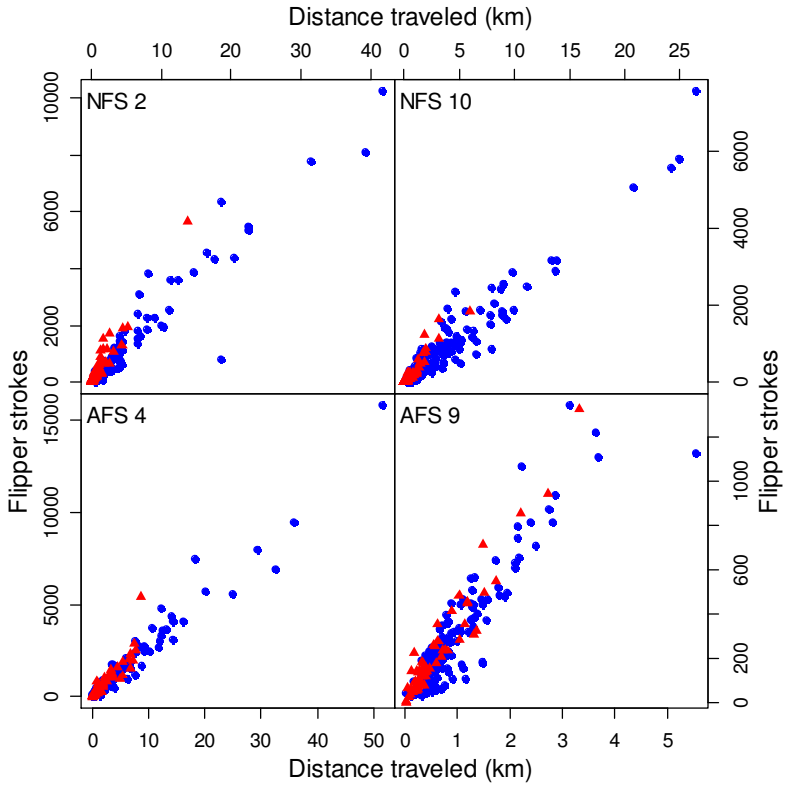

Figure 3.2: Number of flipper strokes detected per distance traveled either vertical distance while diving (red triangles) or horizontal distance while transiting (blue circles) for 2 northern fur seals (NFS 2 and NFS10) and 2 Antarctic fur seals (AFS 4 and AFS 9) between 2 GPS locations during a foraging trip. Transiting at the surface is defined as periods of time when animals travel at speeds > 1m/s between 2 GPS locations.

3.3.4 Statistical analyses

The number of flipper strokes or cumulated stroke amplitude (indicative of swimming effort) swam during dives or between 2 GPS locations were calculated using linear mixed effects models with animal ID nested in species. Fixed effects were horizontal distances for number of flipper strokes while transiting at the surface and vertical distance for flipper strokes while diving. Autocorrelation in the data was corrected using an autoregressive moving average structure (lag 1) and a power structure for any deviance of heterogeneity of variances.

Relationships between energy spent during total trip (or while diving and transiting) and number of flipper strokes or cumulated stroke amplitude were estimated using general linear models (lm, 'stats' package, R 3.0.3) or general linear model using generalized least squares that allows for unequal variances (gls, 'nlme' package, R 3.0.3) upon verification of model assumptions. These methods minimize the squared residuals in the dependent variable.

Cost of transportation (COT) was estimated using 2 separate methods. First COT was estimated from the slope of the relationship between diving energy expenditure and vertical distance traveled using a using general linear model (lm, 'stats' package, R 3.0.3) as mentioned above (in J/kg/m). I also calculated cost of transportation by multiplying the energetic cost per stroke (*i.e.,*3.79 J/kg/stroke) by the number of strokes necessary to travel one meter (stroke/m) for each individual.

Finally, I tested which associations of parameters (cumulative or average stroke amplitude, number of flipper strokes while diving, while transiting or total) would best predict energy expenditure at sea over a full foraging trip time-scale. I tested all variable combinations and selected best models based on the AICc (second-order information criterion or AIC adjusted for small sample size compared to the number of estimated parameters). I also computed AICc weights to provide information on the model probability given the data and a set of models where one of the models is considered the best model for the situation at hand (Burnham and Anderson, 2002).

3.4 Results

Mass of the animals, flipper length and width, foraging parameters, energy expenditure during total foraging trip or during diving or transiting are detailed in Table 3.1. Both species had similar trip duration, distance traveled and time spent diving versus transiting but AFS performed on average more dives of shorter duration. They also had similar at-sea metabolic rates and spent on average similar amount of energy for foraging and for transiting. However, individuals spent more energy while diving than while transiting (Table 3.1). During these times, fur seals beat their flippers 21.5 ± 2.3 times per dive (22.6 ± 3.6 for AFS and 20.3 ± 2.7 for NFS, $p = 0.759$), which corresponds to 0.41 ± 0.03 Hz while diving (0.44 ± 0.06 for AFS and 0.37 ± 0.03 for NFS, $p = 0.004$). Similarly, rate of flipper stroke at the surface when animals were transiting (surface speed > 1 m/s) was 0.44 ± 0.02 Hz (0.53 ± 0.03 for AFS and 0.35 ± 0.02 for NFS, $p < 3.10^{-4}$). Rates of flipper strokes were similar between surface transiting and diving within species (all $p > 0.2$). Rates of flipper stroke while diving and transiting were negatively related to body mass (smaller animals have a greater stroke frequencies, $p < 0.01$) but differences remained significant between species even when rates were mass corrected (all $p < 1.10^{-5}$).

Antarctic fur seals beat their flippers on average 270 ± 14 times and northern fur seal only 190 ±19 times to travel a distance of 1 km at the surface of the water ($p < 10^{-4}$). Both species used the same number of flipper strokes to swim 1 km under water, *i.e.,*496 ± 30 (478 ± 35 for AFS and 514 ± 48 for NFS, $p = 0.418$). Traveling at the surface of the water used fewer flipper strokes than traveling the same distance underwater while diving. There was also no significant inter-species difference in mass corrected number of flipper strokes

The average flipper stroke amplitude (indicative of the average swimming effort) while diving was 0.61 ± 0.03 m/s^2 (0.75 ± 0.02 m/s^2 for AFS greater than 0.46 ± 0.01 m/s^2 for NFS, $p < 7.10^{-12}$). This was overall greater (all $p > 0.05$) than the average swimming effort while transiting at the surface 0.45 ± 0.01 m/s^2 (0.48 ± 0.01 m/s^2 for AFS greater than 0.43 ± 0.01 m/s^2 for NFS, $p < 0.007$). This translated into a cumulative swimming effort per min of diving (sum of flipper stroke intensities, 16.4 ± 1.6 m/s^2 per min for all seals, or 22.6 ± 1.5 m/s^2/min for AFS and 10.26 ± 1.0 m/s^2/min for NFS, $p < 10^{-4}$) greater than per min of

transiting at the surface (11.9 ± 1.0 m/s^2 per min for all seals, or 15.0 ± 1.1 m/s^2/min for AFS greater than 8.7 ± 0.5 m/s^2/min for NFS, $p < 10^{-3}$).

The number of flipper strokes during diving was a good indicator of energy expenditure while diving ($R^2 = 0.76$, AIC = 46.4, $p < 2\ 10^{-10}$, Figure 3.3) according to:

$$3.1 \quad EE_{Dive} \sim (0.16 \pm 0.22) + (3.79\ 10^{-5} \pm 3.96\ 10^{-6}) \times Stroke.Count_{Dive} + (0.30 \pm 0.17 \text{ for NFS only}$$

where EE is the energy spent while diving (in MJ/kg) and $Stroke.Count_{Dive}$ is the total number of flipper strokes detected during diving.

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Table 3.1: Morphometric, metabolic and foraging parameters for northern and Antarctic fur seals during a single foraging trip at sea. Values are mean ± SE and * show between species significant differences ($p < 0.05$).

Parameters	Northern fur seals		Antarctic fur seals	
Mass (kg)	37.9 ± 1.3		31.0 ± 0.8	
Fore flipper length (cm)	39.4 ± 0.9*		34.3 ± 0.3*	
Fore flipper width (cm)	12.5 ± 0.2*		11.1 ± 0.1*	
Trip duration (d)	7.96 ± 2.17		7.65 ± 3.88	
Distance traveled (km)	750 ± 50		635 ± 77	
Number of dives	2551 ± 323*		3949 ± 597*	
Dive depth (m)	19.4 ± 2.4		19.9 ± 2.7	
Dive duration (s)	62.8 ± 7.3*		42.6 ± 4.5*	
Time spend diving (%)	28.6 ± 2.0		29.0 ± 0.7	
Time spent transiting (%)	30.5 ± 1.8		26.4 ± 1.6	
Time spend diving (h)	53.9 ± 4.7		47.7 ± 6.0	
Time spent transiting (h)	59.9 ± 5.9		45.9 ± 7.7	
At-sea metabolic rate (MJ/d)	20.9 ± 1.5		17.7 ± 1.1	
At-sea metabolic rate (MJ/d/kg)	0.56 ± 0.04		0.59 ± 0.04	
Total energy expenditure (MJ)	155.1 ± 13.0		121.4 ± 17.1	
Total energy expenditure (MJ/kg)	4.2 ± 0.4		4.1 ± 0.6	
	Diving	**Transit**	**Diving**	**Transit**
Energy expenditure (MJ)	69.28 ± 24.22*	46.20 ± 18.37	61.34 ± 30.78*	35.39 ± 23.74
Energy expenditure (MJ/kg)	1.89 ± 0.81	1.24 ± 0.51	2.00 ± 1.03	1.15 ± 0.75
Flipper stroke Frequency (Hz)	0.37 ± 0.03	0.35 ± 0.02	0.44 ± 0.06	0.53 ± 0.03*
Average swimming effort per stroke (m/s^2)	0.46 ± 0.01	0.43 ± 0.01	0.75 ± 0.02*	0.49 ± 0.01
Cumulative swimming effort (m/s^2/min)	10.26 ± 1.0	8.70 ± 0.52	22.60± 1.51*	15.01 ± 1.13

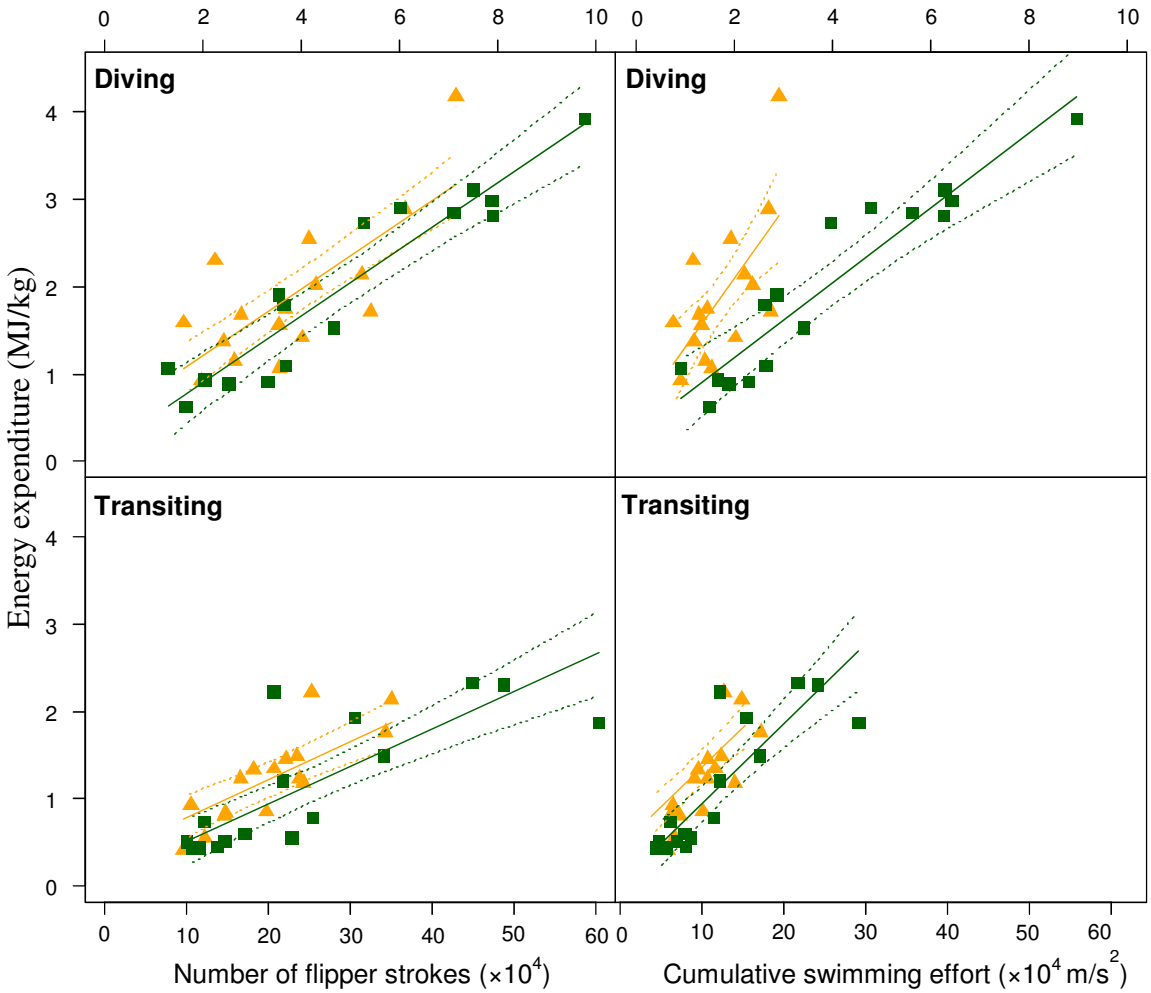

Figure 3.3: Relationships between number of flipper strokes during diving or while transiting at the surface (speed ≥ 1m/s) and activity-specific energy expenditure (in MJ) for northern fur seals (orange triangles, n = 16) and Antarctic fur seals (green squares n = 16).Plain lines show the results of linear models that treated species as an independent variable, and dotted lines are the 95% CI on the predicted values. Results from linear models while diving are: EE_{Dive} = (0.15 ± 0.22) + ($3.8.10^{-5}$ ± 4.10^{-6}) × $Stroke.Count_{Dive}$ + (0.29 ± 0.17 for NFS only) (R^2 = 0.76, slope p < 2.10^{-10}) and while transiting at the surface: $EE_{Transit}$ = 0.08 ± 0.18) + (4.10^{-6} ± 6.10^{-7}) × $Stroke.Count_{Transit}$ + (0.28 ± 0.14 for NFS only) (R^2 = 0.63, slope p < 1.10^{-7}). Activity-specific cumulative swimming effort was also related to activity-specific energy expenditure whether while diving: EE_{Dive} = (0.34 ± 0.26) + (4.10^{-5} ± 6.10^{-6}) × $Swim.Effort_{Dive}$ + [(0.17 ± 0.45) + (3.10^{-5} ± 2.10^{-5}) × $Swim.Effort_{Dive}$ for NFS only)] (R^2 = 0.72, AIC = 53, slope p < 5.10^{-8}) or while transiting: $EE_{Transit}$ = (0.03 ± 0.17) + (9.10^{-6} ± 1.10^{-6}) × $Swim.Effort_{Transit}$ + (0.42 ± 0.14 for NFS only) (R^2 = 0.67, AIC = 33, slope p < 3.10^{-8}).

Based on this this, the energetic cost per flipper stroke at depth was 3.79 ± 0.39 J/kg/stroke for all seals (3.77 ± 0.47 J/kg/stroke for AFS and 3.84 ± 0.91 J/kg/stroke for NFS similar between the 2 species, $p = 0.74$).

The relationship was also significant during transiting time at the surface, but slightly less accurate ($R^2 = 0.63$, AIC = 36.4, slope $p < 10^{-7}$, Figure 3.3):

3.2 $EE_{Transit} \sim (0.08 \pm 0.18) + (4.28\ 10^{-6} \pm 6.07\ 10^{-7}) \times Stroke.Count_{Transit}$
$+ (0.28 \pm 0.14$ for NFS only).

Finally, activity-specific cumulative swimming effort (from stroke amplitude) correlated to activity-specific energy expenditure while diving and transiting ($R^2 = 0.66 - 0.72$). Interestingly, the change in swimming effort while diving impacted energy expenditure of northern fur seals more rapidly than Antarctic fur seals. However, this was not the case while transiting at the surface (Figure 3.3).

3.3 $EE_{Dive} \sim (0.34 \pm 0.26) + (4.27\ 10^{-5} \pm 5.78\ 10^{-6}) \times Swim.Effort_{Dive}$
$+ [(0.17 \pm 0.45) + (3.64\ 10^{-5} \pm 2.03\ 10^{-5}) \times Swim.Effort_{Dive}$ for NFS only)] $R^2 = 0.72$, AIC = 53.6, slope $p < 5.10^{-8}$

3.4 $EE_{Transit} \sim (0.03 \pm 0.17) + (9.12\ 10^{-6} \pm 1.20\ 10^{-6}) \times Swim.Effort_{Transit}$
$+ (0.42 \pm 0.14$ for NFS only)
$R^2 = 0.67$, AIC = 33.3, slope $p < 3.10^{-8}$)

where EE_{Dive} and $EE_{Transit}$ are energy spent in MJ/kg, and $Swim.Effort_{Dive}$ and $Swim.Effort_{Transit}$ are the cumulative swimming effort in m/s^2 during dive or transiting.

Over the entire foraging trip, the sum of all flipper strokes showed limited relation to total energy expenditure at sea ($R^2 = 0.5$, Figure 3.4). The best models predicting total energy expenditures are summarized in Table 3.2 and Figure 3.4, and involve primarily swimming effort while diving and transiting. The most parsimonious model ($R^2 = 0.63$, AIC = 88.2) was:

3.5. $EE \sim (0.16 \pm 0.69) + (2.52\ 10^{-5} \pm 4.13\ 10^{-6}) \times Swim.Effort_{Total}$
$+ (1.33 \pm 0.54$ for NFS)

where EE is the total energy spent during foraging trip (in MJ/kg), Swim.EffortTotal is the cumulative swimming effort while diving and while transiting at the surface (sum of $Swim.Effort_{Dive}$ and $Swim.Effort_{Transit}$).

Table 3.2: Best models explaining at-sea energy expenditure in MJ/kg of northern (n=12) and/or Antarctic fur seals (n=13) as a function of flipper stroke count or of swimming effort during diving + transiting ($Stroke.Count_{Total}$ and $Swim.Effort_{Total}$), or while diving or transiting at the surface ($Total.Effort_{Dive}$, $Total.Effort_{Transit}$, $Swim.Effort_{Dive}$ and $Swim.Effort_{Transit}$ respectively). Only models with ΔAICc < 2 are presented and the model with only stroke count during diving + transiting.

Model	Parameters	Estimates	SE	*p*	R^2	ΔAICc	AICc weight
3.5	Intercept	0.16	0.69	0.820	0.63	0.00	0.185
	$Swim.Effort_{Total}$	$2.5\ 10^{-5}$	$4.1\ 10^{-6}$	$<10^{-5}$			
	Species (NFS)	1.33	0.54	0.022			
3.6	Intercept	0.15	0.67	0.824	0.67	0.48	0.146
	$Swim.Effort_{Total}$	$5.0\ 10^{-5}$	$1.7\ 10^{-5}$	0.007			
	$Stroke.Count_{Total}$	$-1.4\ 10^{-5}$	$8.9\ 10^{-6}$	0.138			
	Species (NFS)	1.97	0.67	0.008			
3.7	Intercept	-0.20	0.71	0.775	0.66	0.82	0.123
	$Stroke.Count_{Dive}$	$4.3\ 10^{-5}$	$1.5\ 10^{-5}$	0.008			
	$Swim.Effort_{Transit}$	$1.9\ 10^{-5}$	$5.7\ 10^{-6}$	0.003			
	Species (NFS)	0.96	0.51	0.075			
3.8	Intercept	0.46	0.65	0.487	0.61	1.52	0.087
	$Stroke.Count_{Dive}$	$4.2\ 10^{-5}$	$1.5\ 10^{-5}$	0.011			
	$Swim.Effort_{Transit}$	$1.7\ 10^{-5}$	$5.9\ 10^{-6}$	0.008			
3.9	Intercept	-0.02	0.71	0.920	0.65	1.78	0.076
	$Stroke.Count_{Transit}$	$7.7\ 10^{-6}$	$2.7\ 10^{-6}$	0.010			
	$Swim.Effort_{Dive}$	$6.0\ 10^{-5}$	$1.7\ 10^{-5}$	0.002			
	Species (NFS)	1.53	0.58	0.016			
3.10	Intercept	0.95	0.67		0.50	4.63	0.045
	$Stroke.Count_{Total}$	$1.2\ 10^{-5}$	2.510^{-6}				

Parameter estimates of other models are detailed in Table 3.2. It is interesting to note that only models involving swimming effort (*i.e.,*cumulative stroke amplitudes) showed a significant difference in the relationships between fur seal species, the ones involving flipper stroke count did not. Finally, rate of energy expenditure (in MJ/d) was not accurately predicted by flipper stroke counts or amplitudes, whether as rates per day or as cumulated over time (all $R^2 < 0.05$).

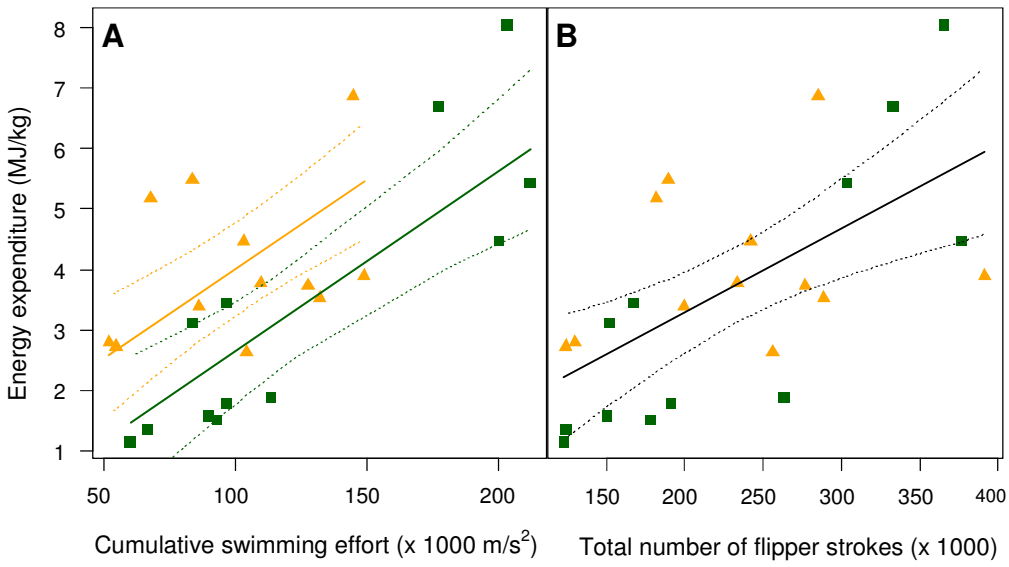

Figure 3.4: Relationship between energy expenditure (mass-corrected MJ/kg) and cumulative swimming effort (A: model 3.5 from Table 3.2, R^2 = 0.63) or total number of flipper stroke during time at sea (B: model 3.10 from Table 3.2, R^2 = 0.50) for female northern fur seals (n = 12, orange triangles) and Antarctic fur seals (n = 13, green squares). Plain lines are results of the general linear model and dotted lines are the 95% CI on the predicted values.

Cost of transport (COT) calculated using the slope of the relationship between diving energy expenditure and vertical distance traveled was 1.63 ± 0.18 J/kg/m ($p < 3.10^{-10}$, R^2 = 0.71) in northern and Antarctic fur seals (not significantly different between species, p > 0.10). I also calculated a cost of transportation of 1.88 ± 0.15 J/kg/m from the cost per stroke (*i.e.*,3.79 J/kg/stroke) and the number of strokes necessary to travel one meter for each seal individually (not different between species, p = 0.55).

3.5 Discussion

Flipper strokes or tail beats are generally believed to be good proxies for the cost of transportation and metabolic rates in marine mammals and fish (Williams et al., 2004; Gleiss et al., 2009; Wilson et al., 2013). In the case of fur seals, I found that flipper stroke count was, indeed, a good predictor of energy expenditure during diving, and to a lesser extent during transiting. However, flipper stroke count was a poor predictor overall of total energy

spent during a full foraging trip at sea for fur seals (R^2 = 0.50, Figure 3.4). In this case, cumulative amplitude of flipper strokes represented total energy expenditure better than flipper stroke counts.

3.5.1 Underwater locomotion

Detecting flipper stroke count and relative intensity was easy to resolve when animals were diving (Figure 3.1). Numbers of flipper strokes accurately predicted energy spent while diving in both species of fur seals (R^2 = 0.76, Figure 3.3), although energy spent while diving were not measured directly but predicted from total energy expenditure and time activity budget (Chapter 2). This is nevertheless consistent with diving Weddell seals which show a good correlation between flipper stroke count and energy expenditure measured from respirometry (R^2 = 0.87), post-dive at sea ice breathing holes (Williams et al., 2004). In addition, each Weddell seal hind flipper stroke had a predictable impact on oxygen consumption and cost 2.39 J/kg/stroke. However, their stroke patterns only took into account lateral movements from one side or from the other side. This means that total side-to-side stroking cost would be 4.78 J/kg/stroke. This falls within the range of values for other phocid seals, from 2.88 J/kg/stroke in harp seals to 5.74 J/kg/stroke for harbour seals (Davis et al., 1985; Fish et al., 1988). For fur seals, I found the cost per stroke was also within this rage at 3.79 ± 0.39 J/kg/stroke (with no significant difference between NFS and AFS) and similar to the 3-4 J/kg/stroke values found for northern elephant seals (Maresh et al., 2014). However, it was lower than the 7.33 J/kg/stroke found for another otariid, the California sea lion (range 1.93 - 23.16, from captive experiments, Dassis et al., 2012). These values show that energy expenditure per stroke differs by a factor of 2.5 among species, and by ~ 1.8 between otariids (*i.e.,*between the California sea lions and the study fur seals).

Buoyancy, dive angle, dive depth and mode of locomotion all affect the cost of transport in marine predators (Williams et al., 2000; Sato et al., 2003; Aoki et al., 2011; Richard et al., 2014; Jouma'a et al., 2015). Phocid seals mostly swim using their hind flippers in a pseudo-axial locomotion, while otariids use their fore flippers in an 'underwater flight' locomotion (Kuhn and Frey, 2012). The wide difference in these two modes likely results in different stroke power and efficiencies. In my case, northern fur seals and Antarctic fur seals

both showed similar flipper stroke rates and numbers of strokes to cover a given distance while diving, or while transiting at the surface, which supports the idea that similar stroking patterns have similar efficiencies.

Buoyancy in diving elephant seals has been shown to change stroking patterns and the numbers of strokes required to cover a given distance (Adachi et al., 2014). This in turn affects locomotor costs in different ways depending on seal density and whether the elephant seal descends or ascends with the cost of transport increasing when departing from neutral buoyancy (Miller et al., 2012). The northern and Antarctic fur seals in my study used their flippers at faster rates during descent than ascent (visually assessed but not reported here). This is consistent with another study of northern fur seals (Insley, 2008). As depth increased, less stroking or less energy was necessary to maintain a constant swimming speed. Locomotion costs are usually reduced with neutral buoyancy, which can be attained at different pressures or depths depending on body fat, body size, quantity of internal gas, or to a lesser extent seawater temperature or salinity. Otariids have a lower ratio of fat to lean mass than do phocid seals. Otariids also dive with fully inflated lungs and with air trapped in their fur, while phocid seals exhale before diving and are devoid of thick fur. In addition, otariids are shallower divers on average compared to phocid seals, and might not dive deep enough to attain neutral buoyancy as do elephant seals. Thus, differences in buoyancy could explain, at least partially, the difference in cost of stroking between taxa.

I estimated the mechanical power that fur seals generated while swimming by measuring the relative magnitude of dynamic acceleration output during a flipper stroke in m/s^2, which can vary depending on speed, drag, chasing behaviour, and other factors. It showed that the intensity of the average flipper stroke acceleration (flipper stroke amplitude or swimming effort) was greater for Antarctic fur seals while diving (0.75 ± 0.02 m/s^2) compared to northern fur seals (0.46 ± 0.01 m/s^2, Table 3.1). Since both species of fur seals had similar energy costs per stroke, it indicates that measured acceleration was intrinsically greater per joule spent for Antarctic fur seals to swim at depth than for northern fur seals. Another possible explanation for the difference is that underwater behaviours of Antarctic fur seals were such that they might have required a different filtering of the dynamic acceleration compared to northern fur seals.

3.5.2 Full foraging trip locomotion

Most studies trying to link energy expenditure to cost of locomotion through flipper stroke rates in the wild have done so for species that spend most of their time underwater (Williams et al., 2004; Maresh et al., 2014). However, fur seals spend ~70% of their at-sea time transiting at the surface and performing surface activities (grooming, slow movements), or resting (Chapter 2). Quantifying flipper stroke rates for fur seals at the surface was not as straightforward as counting them at depth due to the environmental acceleration 'noise' from wave movements at the surface that confounded interpretation of the dynamic acceleration signal. Another confounding factor is that fur seals tend to porpoise while transiting at the surface and switch between air and water, which have different densities that likely affect acceleration signals compared to underwater flipper stroke. It is, therefore, not surprising that flipper stroke count did not correlate as well with energy expenditure while transiting (estimated indirectly from a best fit model using Eq. 2.1 in Chapter 2) as it did while the seals were diving ($R^2 = 0.63$, Figure 3.3).

Fur seals transiting at the surface usually porpoise or travel at depths where wave drag is the lowest to reduce energy waste (3 body diameters below the surface, Hindle et al., 2010). These possibilities for reducing the cost of transportation are not available at depth, which means that energy spent per stroke likely differs between dive time and surface transiting. Unfortunately, the change of mode of locomotion and the residual parasitic noise of the surface interface prevented us from estimating a biologically accurate cost per stroke while transiting. However, it is clear from the slopes in **Figure 3.3** that it costs fur seals less to transit than it does to dive, which is opposite to what was found in another Antarctic fur seal study based on diving behaviour only (Arnould et al., 1996).

Diving and transiting only accounted for ~ 60% of total time at sea in fur seals. This means animals spent ~ 40% of their time performing other activities (surface activities, slow movements, grooming, sleeping). Whether animals do not stroke, or whether I could not detect it amongst environmental movements is unclear. In any case, most cost of transportation was spent during diving and transiting at sea. Resting and surface activities do not involve as much locomotion and are by definition less energetically expensive (Chapter 2). In the end, is it still possible to use flipper stroke metrics to estimate total energy

expenditure at sea despite the significant proportion of time not accounted for in my measures of flipper strokes and the uncertainties inherent to flipper stroke detection at the surface?

The best models to predict the total energy expended by the fur seals during their foraging trips all included swimming effort during diving and transiting (*i.e.,*relative intensity of acceleration during stoking), rather than flipper stroke count. Flipper stroke rate better reflected energy expenditure at the activity level while flipper stroke intensities performed better at the foraging trip level. Since the relationships between energy spent and flipper stroke differ between dive and surface transportation, the proportion of time that individuals allocate to these activities will result in different amounts of energy being spent over the full foraging trip. It, therefore, is logical that the acceleration intensities of flipper strokes (which provide an index of swimming effort during each type of activity) rather than stroke counts correlate better with energy expended over the entire foraging trip. Acceleration intensity incorporates an index of difference in effort between the costs of transport while diving and transiting that simple stroke counts cannot. It might also means that acceleration intensities of flipper strokes better accounts for surface activity, i.e. ~40% of total time not accounted for by flipper strokes. However, the overall accuracy of flipper stroke intensity as a predictor for total energy expenditure at sea remains limited ($R^2 = 0.63$).

Insley (2008) suggested that fur seals spend 70% of their time swimming (whether at depth or at the surface), and that multiplying the cost per stroke at depth by an average stroking frequency was a good approximation for energy spent at sea. However, this assumes that costs of transport at depth and at the surface are similar, which was not the case in the present study. For example, two fur seals could spend 70 % of their time swimming at sea, but allocate their swimming times differently (25 % dive time and 45 % transit time versus 45 % dive time and 25 % transit time). In my case, the northern and Antarctic fur seals spent 20 – 46 % of their time diving and 15 – 47 % of their time transiting. Time-activity budgets are, thus, important considerations when trying to estimate the cost of foraging given how different activities have different associated costs (Chapter 2).

3.5.3 Flipper stroke cost versus cost of transportation

The cost of transport (COT) in J/kg/m has been hypothesized to be consistent between marine mammals and to scale with body mass according to the equation COT = $7.79 \times \text{mass}^{-0.29}$ (Williams, 1999). I calculated the underwater COT to be ~ 1.6 - 1.9 J/kg/m in northern and Antarctic fur seals based on the slope of the relationship between diving energy expenditure and vertical distance traveled or the price of stroke and the number of strokes necessary to travel one meter. These values are somewhat lower than the theoretical value from Williams' equation (1999) of 2.7 J/kg/m for an average female fur seal mass. There is a ~30% discrepancy between the measured (1.9 J/kg/m) and calculated (2.7 J/kg/m) COT for my fur seals. Based on a cost per stroke ~ 3 - 4 J/kg/stroke (Maresh et al., 2014) and the 0.4 strokes on average required to cover 1 m (0.35-0.45 strokes over short foraging, Adachi et al., 2014), elephant seals also have a COT (~1.2 - 1.4 J/kg/m) 15 - 22% lower than the 1.55 J/kg/m theoretical value for a 250 kg female (1.55 J/kg/m from Williams (1999) equation).

It is interesting to note that the only otariid (California sea lion) included in the dataset used by Williams (1999) to derive the theoretical COT equation for all marine mammals also had a lower measured COT values compared to the predicted value (open circles in Figure 1 in Williams (1999)). The 2 extreme ranges of body mass estimates between pinnipeds (15 – 100 kg) and cetaceans (2000 – 10000 kg) might have driven the regression equation between the 2 clusters on their figure. Pinniped values on their own do not seem to follow a clear trend (Figure 1 in Williams (1999)). It could therefore be the case that the theoretical COT equation overestimates the COT of fur seals. There are also inherent errors in the detection of flipper strokes at sea from acceleration (although they are minimized during diving), and in calculated flipper stroke rate per distance that might have accounted for the difference between measured and calculated COT in fur seals.

3.5.4 Comparison of flipper stroke vs VeDBA as an index of total energy spent at sea

Swimming effort derived from the intensities of flipper strokes is one way to measure dynamic body acceleration associated with locomotion and estimate energy expenditure. ODBA or VeDBA are other acceleration-based metrics that have been used to estimate

energy expended by different species while foraging (Fahlman et al., 2008; Halsey et al., 2008; Gleiss et al., 2009; Halsey and White, 2010; Gomez-Laich et al., 2011; Halsey et al., 2011a). Overall, ODBA or VeDBA were found to be better proxies for energy expenditure than flipper stroke metrics during specific types of activities (analyses on same individuals, $R^2 > 0.90$ and Figure 2.3 of Chapter 2). Flipper strokes only reflect one specific type of movement, while active swimming and foraging usually involves many other body motions (undulations, etc.). In addition, flipper strokes are only detected over 2 body axes (up/down and forward/backward) and are not reflected on the third axis, while VeDBA is a measure of acceleration over the 3 body axes. Finally, using tri-axial acceleration takes into account the types of surface movements that flipper strokes could not (~ 40% of the activity budget). It is, thus, not surprising that VeDBA would correlate better with energy expenditure either at the activity specific level or at the full foraging trip timescale, as it considers more body movements than just flipper strokes. Consequently, VeDBA are better predictors of total energy spent at sea than are metrics of flipper strokes, especially at the activity-specific level.

3.5.5 Conclusion

Flipper stroke rate is an appropriate means to determine the energy spent by fur seals while swimming underwater (*i.e.,*while diving) as has been shown for other seals (Williams et al., 2004; Dassis et al., 2012; Maresh et al., 2014). However, in the case of otariids that spend a greater proportion of their time at the surface compared with phocids, flipper stroke count or flipper stroke intensities are not the best predictors of energy expenditure because of the time fur seals spend on the surface. Activity-specific ODBA/VeDBA is a more accurate means for predicting energy expenditure than are flipper stroke count or swimming effort (Chapter 2). While morphology and gaits have undoubtedly evolved to maximise locomotion efficiencies in the ocean, there are sufficient behavioral differences between species to confound application of a simple metric of movement that can be applied universally. Rather, foraging ecology studies need to consider the activity-specific metabolic rates and time-activity behavioural strategies that ultimately determine the foraging costs of individuals.

Chapter 4: Combined hard-parts and DNA analyses of scats, and stable isotope analysis of blood from lactating females reveal two distinct diets and foraging strategies for northern fur seals breeding in the Bering Sea

4.1 Summary

The key to understanding why the Pribilof population of northern fur seals (*Callorhinus ursinus*) has been declining may lie in what, where and how lactating females are eating in the Bering Sea. Unfortunately, it is unclear whether fur seal diet determined from hard-part remains in feces (e.g. fish bones and otoliths, and cephalopod beaks) collected on breeding beaches are representative of what the Pribilof population consumes each year. I collected 98 scats from a breeding beach (Reef rookery on St. Paul Island), and captured and tracked 20 lactating female fur seals. Foraging habitats and trophic levels of the tracked females were assessed using the stable isotope method on their blood. Prey were identified from scats using hard-part remains and DNA extracted from their soft matrix for comparison. DNA yielded a higher resolution of prey species and revealed a greater diversity of prey than previously recognized. Collectively, cluster analyses of prey present in individual scats indicated two basic prey associations indicative of two different foraging habitats corresponding to neritic and oceanic waters , *i.e.,*pollock, squid and mesopelagic fish (mostly deep water basin associated prey), and a second diet of pollock, salmon, hexagrammid, flatfish, and forage fish (continental shelf types of prey). These results are consistent with stable isotopes analyses in plasma that show two clusters of $\delta^{13}C$ and $\delta^{15}N$ values corresponding with whether the tracked fur seals fed over the shelf or off the shelf. In all likelihood, the scats collected on the Pribilof rookeries are representative of diets consumed in the preceding 12-24 hours and are biased toward shelf prey species given the location of the breeding islands on the shelf. These results show that combining clustering analysis of co-occurring prey species from results of hard-part- and DNA-based methods, C and N stable isotopes, and at-sea tracking of individuals can be used to adjust diet summaries and properly reflect the average diet of fur seals.

4.2 Introduction

Most of the world population of northern fur seals once bred on the Pribilof Islands in the Bering Sea, but this population has declined by ~6% per year for the last 30 years with no sign of slowing down (Towell et al., 2006). The decline coincided with a major environmental change that altered the distribution and relative abundances of different species of fish in the Bering Sea (Anderson et al., 1997; Anderson and Piatt, 1999). The decline also coincided with an increase in the dominance of walleye pollock and a decrease in squid in the fur seal diet (Sinclair et al., 2008). Such dietary changes can affect the foraging efficiency of lactating females and their capacity to successfully reproduce. Assessing diets is thus important for understanding the balance between energy input from food, and the energy spent foraging.

Diets of northern fur seals have been assessed in recent years by identifying the undigested hard-part remains of prey found in feces (scats) or to a lesser extent in spews (Perez and Bigg, 1981; Perez and Bigg, 1986; Antonelis et al., 1990). Taxon, size and relative number of prey ingested can be determined from hard-parts (Tollit et al., 2003), but the method is biased by differential digestion or retention rates of prey parts depending on species and sizes of prey consumed, and on species, sex, activity level, GI tract morphology and meal size of predator that lead to under- or over-estimation of prey occurrence (or size of prey consumed) in the diets (Bigg and Fawcett, 1985; Jobling and Breiby, 1986; Harvey and Antonelis, 1994; Tollit et al., 1997; Bowen, 2000; Arim and Naya, 2003; Gudmundson et al., 2006). In addition, assumptions underlying how the presence-absence based methods determines relative proportion of each species consumed are often not met (Olesiuk et al., 1990).

More recently, methodological advancements have increased interest in molecular-based tools that overcome some of the limitations of hard-part analyses (Deagle et al., 2005; Casper et al., 2007a; Deagle and Tollit, 2007; Deagle et al., 2009; Deagle et al., 2010; Cristescu, 2014; Thomas et al., 2014). Among them, the DNA meta-barcoding method allows species or groups of organisms to be identified within a sample. This molecular method relies on high-throughput DNA sequencing to identify prey species by detecting

DNA remains present in the soft organic matter of the feces. It is non-invasive, has the advantages of being quick, relatively inexpensive, and is more sensitive than the hard-part remains methods (Deagle et al., 2009). This new DNA approach is still being evaluated, however, and has its own inherent biases at the technical and interpretation levels (Casper et al., 2007a; Deagle et al., 2010; Thomas et al., 2014).

Scat samples have proven to be a useful means to estimate diet composition of pinnipeds. However, scats only represent what animals recently consumed (~ 48h, Orr and Harvey, 2001; Staniland, 2002; Deagle et al., 2005; Casper et al., 2007a). Stable isotope concentrations in blood, hair and bone synthesize dietary information over longer timescales; $\delta^{15}N$ provide insights into the trophic level at which the consumer has fed (Wada et al., 1991; Hobson and Welch, 1992) while $\delta^{13}C$ indicates the foraging habitat based on the isotopic composition of primary producers at the base of the food chain (France, 1995; Burton and Koch, 1999). In the marine environment, $\delta^{13}C$ values allow characterizing inshore versus offshore, or pelagic versus benthic consumers (Hobson et al., 1994; Cherel et al., 2007). Pairing high-resolution telemetric data that provide movement and diving information with their respective stable isotope analyses can provide a better understanding of foraging strategies and diets, and disentangle spatial, trophic and physiological differences between individuals (Newsome et al., 2010).

The Bering Sea where northern fur seals forage during the breeding season is composed of a shallow continental shelf separated from a deep oceanic basin by a shelf break. These differences in bathymetry and hydrographic structures define the prey associations within the ecosystems. Northern fur seals feed widely in the Bering Sea, but appear to have foraging areas that depend upon the location of the breeding beaches (Goebel, 2002; Robson et al., 2004; Kuhn et al., 2014). These foraging areas determine the northern fur seal's foraging behaviours, dive patterns and ultimately their diets (Sinclair et al., 1994; Antonelis et al., 1997; Gudmundson et al., 2003) given yearly environmental conditions (Gentry and Kooyman, 1986). It is thus important to assess diet composition and foraging behaviours of individual female fur seals for a given year to better understand foraging efficiency and reproduction success within specific environmental conditions.

My primary goal was to evaluate the limitations of previous diet determinations for northern fur seals on the Pribilof Islands, by combing DNA and hard-part analyses of scat samples, thereby creating enhanced fur seal diet data. I also sought to provide context for dietary analysis of the scats using the isotopic signatures of blood samples and the foraging habitats for 20 lactating females that tended to pups on the same rookery where the scats were collected. I thus sought to assess the reliability of current descriptions of fur seal diets and provide insights into the implications of having different diets and ways in which the diet estimates might be corrected to better reflect the average diet of northern fur seals breeding on the Pribilof Islands.

4.3 Material and methods

4.3.1 Data collection

All scats and blood samples were obtained from Reef Rookery on St. Paul Island (Bering Sea, 57° 6 'N - 170°17' W, Aug - Sep 2011) under the US NMFS permit #14329-01 and the UBC animal care permit #A10-0364. Isotopic data were collected on 20, mature, full-sized lactating northern fur seals with a confirmed suckling pup. Standard morphometric measurements were made to the nearest 0.5cm, and mass was recorded using scale at ± 0.2 kg. A blood sample was collected while the animals were anesthetized from the back flipper in Monovette syringes (Sarstedt) coated with Li-Heparin, and plasma was isolated from red blood cells by centrifugation at 1000 g for 10 min. Each female was equipped with a fastloc GPS datalogger (MK10, Wildlife Computers Inc.) glued to their fur roughly 8cm below their shoulder blades. The data loggers also recorded depth at 1 Hz, and were used to identify foraging locations and provide diving data to determine whether dives were benthic or pelagic (Tremblay and Cherel, 2000; Schreer et al., 2001). Upon recovery from anaesthesia, animals were allowed to return to the colony and to go on a single foraging trip before recapture upon their return on land. A second blood sample was taken following the same procedures and the GPS logger was retrieved by cutting the hair. Blood samples were frozen at -20 ºC until analyses in the lab.

4.3.2 Morphological identification from hard-parts in scats and prey size

I collected 98 scats on Reef rookery in September 2011, above the ~ 60 scats required to reach the maximum prey diversity (Zeppelin and Orr, 2010). Each scat was placed in a zip-lock plastic bag and was frozen at -20 ºC until processing at the UBC Marine Mammal Research Unit lab in Vancouver, Canada. Scats were then thawed and transferred into a nylon mesh paint strainer lining a 500 ml disposable container. 95 % Ethanol was added to the samples, and scat matrix was separated from the hard prey remains by manual homogenization. The hard-parts contained in the mesh bag were removed for analysis and cleaning procedures following a standard protocol (Trites and Calkins, 2008). Cleaned and dried hard-parts (*i.e.,*otoliths, bones, and lenses from teleost fishes; cartilage from cartilaginous fishes; and beaks, pens, and statoliths from cephalopods) were sorted out and identified to lowest possible taxon by Pacific IDentifications Inc. (Victoria, BC) using a reference collection of prey species skeletons. Types of hard-part present, the species from which they came, the estimated size of the prey by species, and the minimum number of individuals present (all species combined based on maximum paired numbers of eye lenses or other unique identifiable structures) were recorded. Unknown prey items were categorized as ‘‘unidentified’’ and were excluded from analyses. The relative diet composition was determined by first calculating the frequency of occurrence (FO) of a specific prey item as the percentage of scats that contained it among all the scats collected according to the following equation:

$$FO(\%) = \frac{\sum_i^n O_{pi}}{n} \times 100$$

where O_{pi} is the absence (0) or presence (1) of prey *p* in sample *i* from total number of scats *n.* Second, the proportion of a specific prey to the overall diet (adding up to 100%) was estimated using the split-sample frequency of occurrence SSFO (Olesiuk et al., 1990; Olesiuk, 1993).

4.3.3 Prey species identification from DNA sequences analyses

Ethanol preserved scat organic matter (matrix) was subsampled from thawed scats and used for genetic analyses. DNA extraction was performed following the protocol from

Thomas et al. (2014) on approximately 20 mg of scat sediment material from the same scats analysed for hard-part remains. Extraction was done using QIAamp DNA Stool Mini kit (Qiagen) and eluted in 100 µL elution buffer (10 mM Tris‑Cl, 0.5 mM EDTA; pH 9.0).

The scat DNA metabarcoding protocol used for this study followed the procedures outlined in Thomas et al. (in review). In brief, a ~260bp fragment of the 16S mitochondrial ribosomal gene was amplified by PCR from each scat sample using the Qiagen Multiplex PCR kit. This reaction contained two different primer sets, which were developed to amplify a species-diagnostic region of 16s for both Chordates and Cephalopods (Deagle at al. 2009). Sample identification was done using a two-tiered barcoding approach, employing 96 uniquely labeled forward primer sets and the ligation of barcoded sequencing adapters to sample amplicon pools. Sequencing was done on an Illumina MiSeq using the MiSeq Reagent Kit v3 (600 cycle) for PE 300 bp reads, and the samples were run alongside 288 harbour seal scat DNA samples from an unrelated study.

Demultiplexing of DNA sequences was done with the MiSeq platform itself (separating pools of 96 samples by adapter sequence) and in the software package QIIME (further separating samples by forward primer tags) (Caporaso et al., 2010). Taxonomic identification of prey species DNA was done with on a nucleotide BLAST search for each sequence against a reference database of potential prey, using a minimum similarity threshold (Thomas et al. *in review*). To ensure that no major prey groups were missing from the existing database, I also applied a clustering approach with scat sequences, picking a representative of each cluster and applying a GenBank query to add any new prey species to my database that were not there initially (Altschul et al., 1990; Edgar, 2010). For details see Thomas et al. *in review*. DNA detections of prey species in samples were treated as occurrences (presence/absence), similar to the treatment of prey hard-parts information.

4.3.4 Combined results and prey associations

I combined the results from the hard-part and the DNA analyses by merging occurrence of unique prey species detected by either technique per individual scat. When a species of salmon was detected with DNA analysis and presence of unidentified salmon was detected from hard-parts within the same scat, I considered hard-part remains were coming

from the specific species identified by DNA sequencing and did not duplicate occurrence of salmon. I did the same for cephalopod species, and obtained a combined presence-absence matrix of individual prey species per scat. Frequency of occurrence and split sampling frequency of occurence in the diet from DNA analyses of DNA and hard-parts combined were calculated as above.

Association between prey groups within individual scats were identified and illustrated using a cluster analyses (*hclust* in *stats* package, in R 3.1.3). I first calculated the gamma coefficient (Goodman & Kruskal 1954) for each pair of prey groups from a presence-absence matrix of prey within the different scats. The distances between 2 prey groups were estimated from "1 – gamma" and were used as the dissimilarity matrix for the cluster analysis (with the "complete" method).

4.3.5 Stable isotopes

Stable isotope analyses were performed at the LIENSs laboratory (La Rochelle University, France). Red blood cells (collected before the seal's foraging trip) and plasma samples (collected before and after the seal's foraging trip) were freeze-dried and powdered. Blood plasma can contain high and/or variable lipid content in animals (Cherel et al., 2005), so I performed a lipid extraction using cyclohexane following the method used for seabirds (Kojadinovic et al., 2008). Tissue subsamples were weighed (~0.4 mg) with a microbalance, packed in tin containers, and nitrogen and carbon isotope ratios were determined by a continuous flow mass spectrometer (Micromass Isoprime) coupled with an elemental analyser (Euro Vector EA 3024). Stable isotope concentrations were expressed in conventional notation ($\delta X = [R_{sample}/R_{standard}) - 1] \times 1000$), where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C:^{12}C$ or $^{15}N:^{14}N$. R standard is Vienna PeeDee Belemnite and atmospheric N2 for $\delta^{13}C$ and $\delta^{15}N$ respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors < 0.15 ‰ for $\delta^{13}C$ and < 0.20 ‰ for $\delta^{15}N$. The units are expressed in parts per mil (‰).

4.4 Results

4.4.1 Foraging location and behaviour

The female northern fur seals weighed on average 37.9 ± 1.34 kg prior to departure (range 30.8 - 55.6 kg, n = 20), and gained 1.13 ± 2.98 kg after their single foraging trips (a 3.5 ± 1.8 % gain in body mass). The average foraging trip was ~ 750 ± 50 km (range 391 - 1200 km) and lasted 7.96 ± 2.17 d (range 4.26 - 12.03 d). The females travelled widely, but 12 of the 20 stayed on the Bering Sea shelf (hereafter called on-shelf females), while the remaining 8 went off the shelf into more pelagic waters (hereafter called off-shelf females, Figure 4.1). Females foraging off the shelf spent on average 2.5 more days at sea and traveled 200 km more than on-shelf females (9.7 ± 1.8 d and 892 ± 144 km for off-shelf females versus 7.1 ± 2.4 d and 655 ± 218 km for on-shelf females).

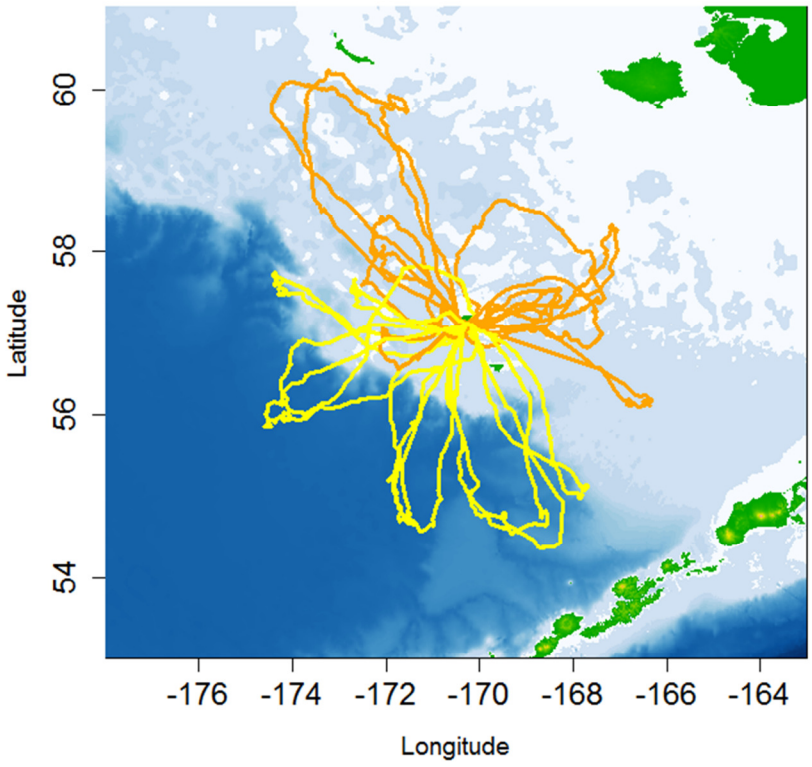

Figure 4.1: Foraging tracks of 20 lactating northern fur seal females breeding on Reef rookery on St. Paul Island, and foraging in the Bering Sea, AK. Tracks are derived from fastloc GPS locations. Orange and yellow tracks show the females that stayed foraging on the shelf (n = 12) and the females that went foraging off the shelf (n = 8) respectively.

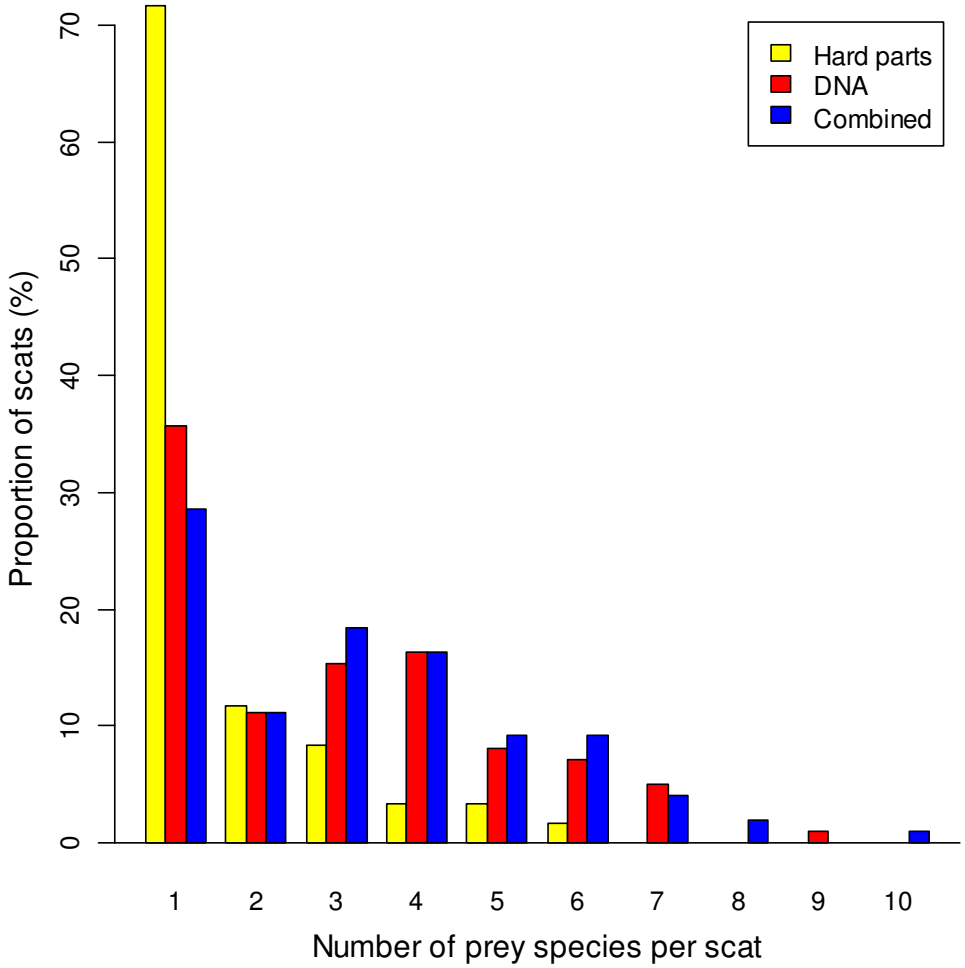

Figure 4.2: Number of prey species detected in scats depending on the analytical method used, DNA analyses in scat organic matter (in black, n = 98) or hard-part remains (in grey, n = 60). The difference in sample size is due to no identifiable hard-parts being recovered in 38 of the scats (collected on Reef rookery St. Paul Island, Bering Sea, Alaska in Aug-Sept 2011).

Females foraging on the shelf made a significant amount of benthic dives (15.2 ± 2.6 % of all dives) and occasionally foraged during the day, while females foraging off the shelf rarely performed benthic dives (2.2 ± 0.4 of all dives and 0% when off the shelf) and were specific nocturnal divers. Off-shelf females also performed significantly more foraging dives (2526 ± 155 dives) than the on-shelf females (1648 ± 2526 dives, $p < 0.001$), but the dives were on average shallower and lasted half the time (16 ± 2 m deep and 42 ± 6 s duration for off-shelf females and 28 ± 4 m deep and 84 ± 10 s duration for on-shelf females, $p < 0.05$).

4.4.2 Scats hard-part remains

At least 14 prey species from 11 taxonomic families were found in the scats collected on Reef rookery (including fish, cephalopods and worms). There were no identifiable hard-parts (or unidentifiable hard-parts) in 38 of the 98 scats collected, so the hard-part analyses were done only with 60 scats. On average 1.6 ± 0.2 species were detected per scat with the hard-part technique, and only one species was detected per scat in more than 70% of them (maximum 6 species detected in one scat).

Frequency of occurrence of different prey species (Figure 4.3) showed the most ubiquitous prey present in scats was walleye pollock (*Theragra chalcogramma,* in ~ 75% of scats), followed by salmon (in ~ 30% of scats), cephalopods (squids and octopus, in ~ 18% of scats) and Atka mackerel (in ~ 10% of the scats, *Pleurogrammus monopterygius*). The prey species were categorised in different taxonomic or ecological groups, according to their importance in the diet (Figure 4.3, Table 4.1). Frequency of occurrence of each of these groups were then converted into relative proportion of prey in the diet using the Split-Sample Frequency of Occurrence methods (Olesiuk, 1993). The main prey category in the diet of reef rookery fur seals was gadids (~69%), mostly composed of walleye pollock, followed by cephalopods (squids and octopus of unknown species, 12.6%), salmonids (6.4%) and hexagrammids (3.6%, mostly Atka mackerel). Flatfish, forage fish, mesopelagic fish, rockfish and others make the remaining 8.5% in the diet.

4.4.3 Scat DNA analyses

Twenty-six species of prey were detected in all the scats collected (n = 98) from DNA analyses in the scat organic matter. The DNA method detected more prey per scat and more prey species overall, and was able to tease apart species of the same family better than the hard-parts method (such as the 5 species of salmon; Figure 4.3). On average, 3.0 ± 0.2 species were detected per scat (max 9 species in a single scat), which is significantly greater than the 1.6 ± 0.2 species determined from the hard-parts technique ($p > 0.05$, Figure 4.2).

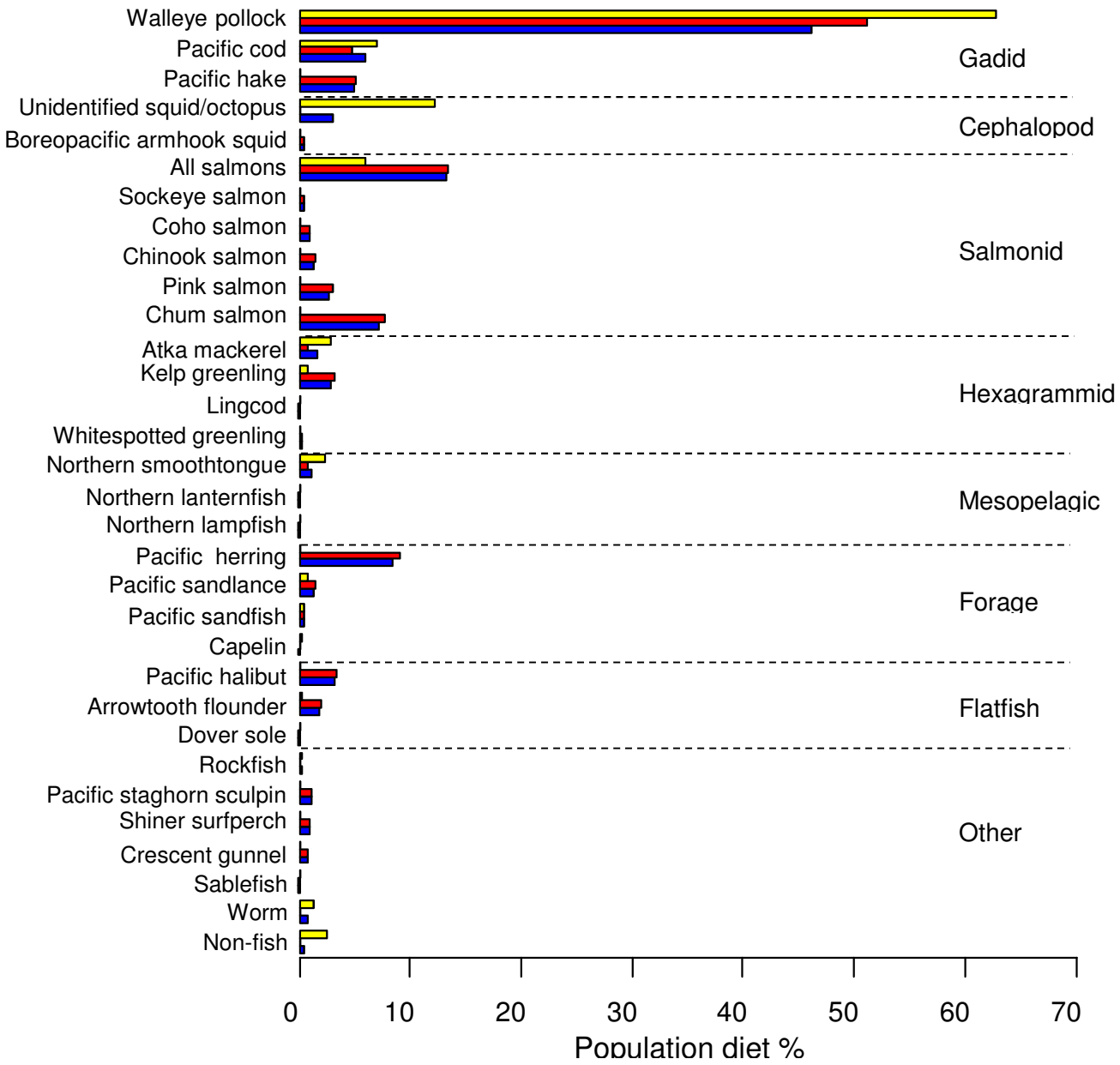

Figure 4.3: Proportion of prey species in the diet (split sample frequency of occurrence) of northern fur seals in scats collected on Reef Rookery, St. Paul Island, Bering Sea during the breeding season 2011 from hard-part remains analyses in yellow (n = 60), from DNA analysis in red (n = 98) and presence-absence results from both techniques combined in blue (n = 98, FO and SSFO values available in Table A.3 in the Appendices section).

Gadids (particularly walleye pollock) were the most ubiquitous prey found with this technique (~63% of the scats, Figure 4.3, Table 4.1). Overall, DNA analyses detected fewer cephalopods (0.5%) and more forage fish (10.6%), flatfish (5.2%) and salmon (~ 13%) than the hard-part analyses. Hexagrammids were detected within the same proportion between

methods. In the 38 scats in which no hard-parts were recovered, DNA analyses detected walleye pollock (n = 37), chum salmon (*Oncorhynchus keta*, n = 17), Pacific herring (*Clupea pallasii*, n = 16), Pacific hake (*Merluccius productus*, n = 13), Pacific cod (*Gadus microcephalus*, n = 10), Pacific halibut and kelp greenling (*Hippoglossus stenolepis* and *Hexagrammos decagrammus*, n = 6 each), among other less frequent prey species (n < 4).

4.4.4 Combined methods

There were 321 occurrences of prey in 98 scats with combined results from both methods, 225 of which were only detected with DNA analyses, 29 only with the hard-parts method, and 67 were simultaneously detected with both techniques. Given the overwhelming dominance of DNA identified species, the frequency of occurrence (FO) of prey were quite similar between the combined and the DNA only methods (Figure 4.3 and Table 4.1), with the exception of cephalopods. The same pattern was seen for the relative importance (SSFO) for all prey groups, except for gadids that were of slightly less importance in the population diet (~57 % combined compared to ~ 63 - 69% separately), and cephalopods that increased in importance to ~ 3.5% compared to DNA method only (which was still lower than estimated by the hard-part method).

Table 4.1: Frequency of occurrence (FO) and split sampling frequency of occurrence (SSFO) of prey in scats collected on Reef rookery, St. Paul Island during the breeding season 2011 measured from hard-part remains and from DNA analyses in scats.

Prey group	Hard-part remains			DNA analyses			Combined		
	FO (%)	SSFO (%)	Rank	FO (%)	SSFO (%)	Rank	FO (%)	SSFO (%)	Rank
Gadid	83.3	68.9	1	96.9	62.6	1	96.9	57.1	1
Cephalopod	20.0	12.6	2	2.0	0.5	8	14.3	3.5	7
Salmonid	15.0	6.4	3	39.8	12.8	2	42.9	13.2	2
Hexagrammid	13.3	3.6	5	19.4	4.2	5	23.5	4.9	5
Mesopelagic fish	5.0	2.6	6	4.1	1.1	7	5.1	1.4	8
Forage fish	5.0	1.5	7	34.7	10.6	3	35.7	10.4	3
Flatfish	1.7	0.3	8	20.4	5.2	4	19.4	5.2	4
Others	7.7	4.2	4	13.3	3.0	6	18.3	4.4	6

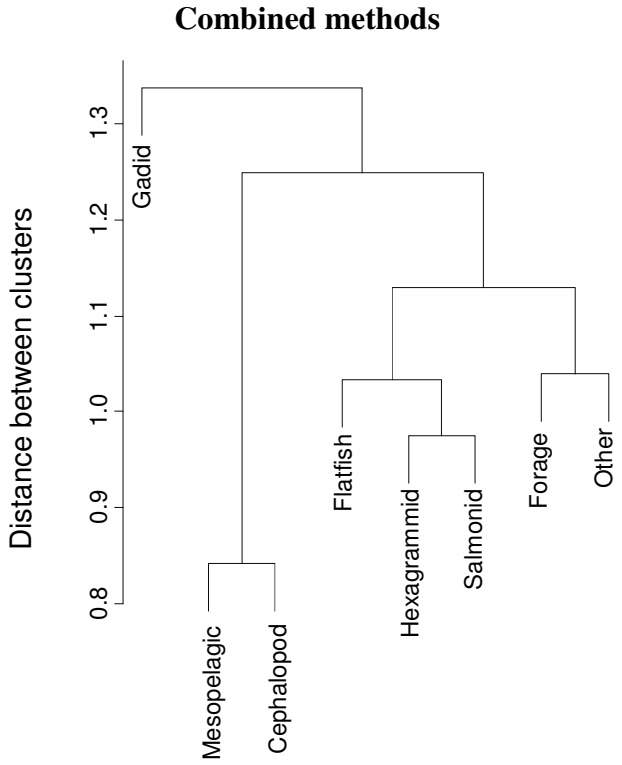

Figure 4.4: Hierarchical cluster dendrogram of prey groups found in 98 northern fur seals scats from Reef rookery on St. Paul Island, Bering Sea, AK, in Aug-Sept 2011 identified from both DNA analyses of organic remains and of morphological identification of hard-parts methods combined.

4.4.5 Prey associations

Prey in fur seal diet were clustered in 3 distinct groups (*i.e.,* consistently found together and not randomly distributed amongst the foraging range of the fur seals). Based on cluster analyses from the combined DNA and hard-parts results (Figure 4.4), gadids made up one group on their own. A second group was made of mesopelagic fish and cephalopods. Finally, a third group included a mixture of forage fish, salmonids, flatfish, hexagrammids and others, even though within-group associations varied with the method used. The same clusters were found using results from the DNA method only. However, numbers of prey found in each scat were not high enough to yield accurate cluster analyses from the hard-parts method only.

4.4.6 Stable isotopes

The stable isotope signature of lactating females breeding on St. Paul Island (Reef rookery) was -19.13 ± 0.48 for δ13C and 16.24 ± 1.37 for δ15N in plasma collected after their foraging trips. There were two distinct signatures, one centered around -18.77 ± 0.30 δ13C and 17.34 ± 0.64 δ15N, and the other centered around -19.56 ± 0.15 δ13C and 14.86 ± 0.50 δ15N (significantly different, both $p < 5.10\text{-}5$, Figure 4.5). These groups corresponded to females foraging on the shelf versus females foraging off the shelf (Table A.4 in Appendices section). The latter group is not significantly different from the isotopic signature found on fur seals breeding on and foraging off Bogoslof Island (*i.e.,*off the Bering Sea shelf ; ~ -19.5 ± 0.2 for δ13C and ~ 14,23 ± 0.3 for δ15N from Fig. 3 in Zeppelin and Orr 2010), despite the δ15N being slightly higher in my data (see red squares on Figure 4.5).

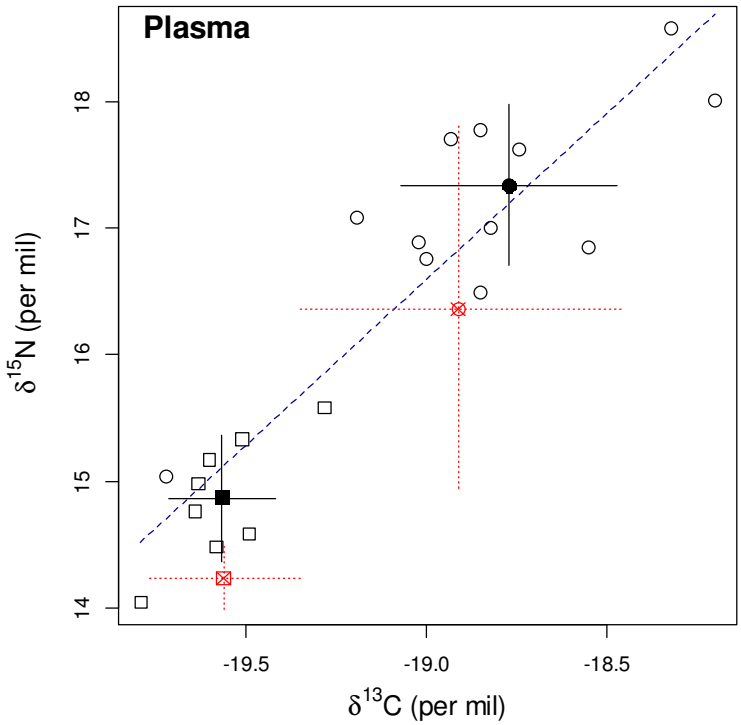

Figure 4.5: Stable carbon and nitrogen isotope values in the plasma of 20 adult northern fur seal females breeding on St. Paul Island, Bering Sea (open symbols) from blood samples taken after their foraging trip at sea. Open circles are values for females foraging on the shelf (n = 12) and the open squares for females foraging off the shelf (n = 8). Closed symbols are averages ± SD for on- and off-shelf groups. The red crossed circle represents stable isotopes values (± SD) for adult fur seals breeding on St. Paul Island and the crossed square isotopes values for adult fur seals breeding on Bogoslof Island from Fig. 3 in Zeppelin and Orr (2010).

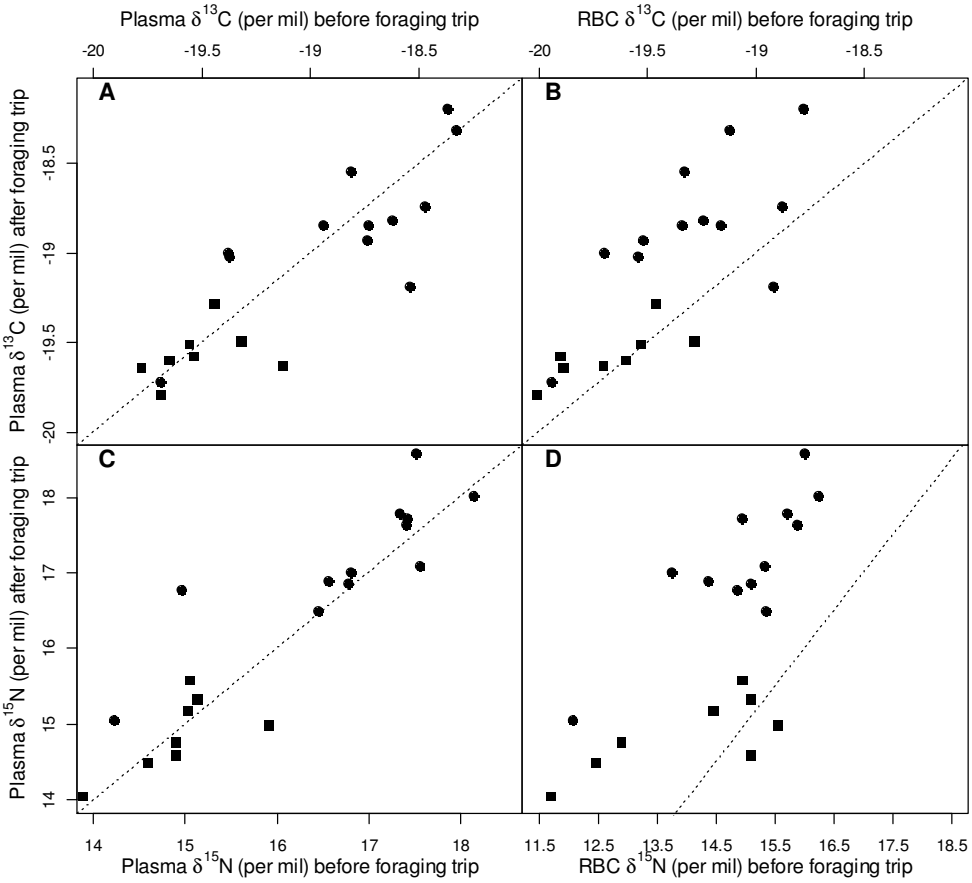

Figure 4.6: Stable carbon isotope values in the blood of 20 adult northern fur seal females breeding on St. Paul Island from samples collected before versus after their foraging trip. Graph A and C shows the relationship between carbon and nitrogen isotope levels in plasma after and before their foraging trip. Graph B and D shows the relationship between carbon and nitrogen isotope levels in red blood cells collected before the foraging trip and carbon isotope levels in plasma collected after the foraging trip. Circles are values for females foraging on the shelf (n = 12) and the squares for females foraging off the shelf (n = 8). Dotted lines show 1:1 lines.

Isotopic values from blood collected before the seals' foraging trip had average δ13C in plasma of -19.05 ± 0.49 (-18.75 ± 0.36 for on-shelf group and -19.51 ± 0.21 for the off-shelf group) and average $\delta^{15}N$ of 16.03 ± 1.31 (17.00 ± 0.84 for on-shelf group and 14.92 ± 0.56 for the off-shelf group). These values were both significantly greater than isotopic values measured on RBC collected before the foraging trip, *i.e.*,-19.44 ± 0.36 for $\delta^{13}C$ (-19.23 ± 0.29 for on-shelf females and -19.67 ± 0.25 for off-shelf females) and 15.02 ± 1.58 for $\delta^{15}N$ (15.24 ± 0.73 for on-shelf females and 14.03 ± 1.45 for off-shelf females). However,

none of the isotopic values in plasma collected before and after the seals' foraging trip differed significantly from each other ($p > 0.34$). Plasma $\delta^{13}C$ and $\delta^{15}N$ before and after the foraging trip showed a clear separation between on- and off-shelf groups (Figure 4.6, graphs A & C), with the exception of a couple of females (# 12, # 14 and # 9) whose signatures shifted between the two groups.

4.5 Discussion

4.5.1 DNA versus hard-parts techniques

DNA analyses added considerable value to determining the diet of northern fur seals by providing a more refined global picture of what they eat. In particular, my results show that northern fur seals consume a much more diverse diet than estimated from the traditional hard-part remains approach. My results also show that DNA meta-barcoding analysis was better than hard-part analysis at detecting the presence of prey in individual scats—detecting almost twice the number of taxonomic groups than did hard-parts (26 species detected in 100% of the scats for DNA analyses vs 14 species in 60% of scats for the hard-part method). As a result, the minimum sample size needed to detect of the maximum prey diversity is lower using the DNA method than the hard-part method.

DNA analyses were able to detect prey to a finer taxonomic level than hard-parts analysis, and performed particularly well for prey species that were morphologically identified with structures other than otoliths. For example, molecular analyses assigned occurrences of salmonids and cephalopods to the species level, while hard-parts could only identify them at the family level. Similar results have been shown for Steller sea lions (Tollit et al., 2009). Interestingly however, hard-part analysis did detect two species (rockfish and capelin) that the DNA method failed to pick up (although there was only 1 occurrence of each). These rare species were either not present in the soft matrix or may have been filtered out in the analytical process that removed DNA sequences that were proportionally less than 1%.

Despite biases in both techniques, results on the global diet composition of harbour seals and Steller sea lions have shown that they provide similar results at the population level

(only species of minor importance differed between methods, (Austen Thomas thesis (being submitted), Tollit et al., 2009). In the case of northern fur seals, walleye pollock and gadids were the most ubiquitous prey group in their diet (Figure 4.3 and Table A.3) irrespective of the method used. This is consistent with previous findings from hard-parts in scats and spews (Sinclair et al., 1994; Gudmundson et al., 2003; Waite et al., 2012). However, there were some differences in their ability to detect some taxonomic groups. Most notably, hard-parts overestimated cephalopods and underestimated mesopelagic, flatfish, and salmons compared to DNA analyses.

Hard-parts detected the cephalopod group ~25 times more frequently than did the DNA sequences (SSFO ~12.6% for hard-parts and ~ 0.5% for DNA, Table 4.1). Squid beaks are hard chitinous-fibrous structures resistant to digestion and are known to accumulate by hooking themselves onto the lining of the digestive system before being excreted (Bigg and Fawcett, 1985; Harvey and Antonelis, 1994). This 'pulse-like' and unpredictable excretions of beaks might create an artificially inflated detection of cephalopods (Tollit et al., 1997; Staniland, 2002; Casper et al., 2007a). In contrast, the DNA meta-barcoding method may underestimate the occurrence of squids because the soft parts of squids and octopuses have a high water content and consequently a low total proportion of DNA in the body to be detected in the organic matter of scats compared to other prey species (A. Thomas PhD thesis, being submitted). The overestimation from hard-part and the underestimation from DNA might thus explain the 25-fold difference in detection between the two techniques.

DNA analysis found more salmon, forage fish and flatfish in the scats than did hard-parts analysis. The relative absence of hard-part structures of salmons might mean that seals consumed young salmon whose hard-parts were highly digested, as was found in a similar study performed on harbour seals (A. Thomas PhD thesis, being submitted), or that seals might have not ingested the heads of larger salmon (*i.e.,*a 'belly-biting' strategy, Hauser et al., 2008). This is consistent with the fact that the only bones I recovered were vertebrae and gill rakers whose sizes suggest the ingested salmon were 20 to 45 cm long (although this is based on only 10 occurrences). Thus the discrepancy in FO between hard-parts and molecular methods either reflects differential digestibility of salmon hard-parts or different feeding strategies or both.

Flatfish and forage fish also seemed to be detected much more frequently by the DNA analyses compared to the hard-part analysis. Pacific halibut were detected 15 times out of 25 occurrences of flatfish, but hard-part remains were not present. The same pattern was seen for the 25 occurrences of Pacific herring out of 33 for forage fish. The low recovery rate of herring otolith (Tollit et al., 1997) could partly explain why hard-part analysis failed to detect herring, but this would not be the case for halibut. DNA sequences of flatfish and herring generally occurred in low quantities in the fur seal scats, suggesting they were relatively insignificant prey species. Species frequently consumed in low quantities will tend to be given greater importance when their occurrence is calculated using SSFO. This bias can be corrected using the proportion of sequence occurrences within individual scats averaged over all scats. However, interpreting the percent occurrence of sequences is not straightforward because it is species-specific and proportion-dependant (Deagle et al., 2013; Thomas et al., 2014). In addition, DNA meta-barcoding is known to have a proportion-dependent bias in the read of sequence abundance whereby species present in low proportion tend to be overestimated while species in high proportion are comparatively underestimated (although this proportion dependence decreases the more complex the diet) (Kembel et al., 2012; Thomas et al., In prep.). As a consequence, I relied on the presence and absence of prey in individual scats to calculate SSFO, but provide the calculated percent of sequence occurrence in Appendices section for comparison (Table A.3).

Combining results from the DNA and hard-parts techniques can increase the accuracy of diet interpretation than either method alone, and has the potential to increase diet richness by suppressing specific biases (Casper et al., 2007b; Tollit et al., 2009). Only 21% of the prey I found were simultaneously detected with both techniques in the same scats (67 occurrences out of the 321 in total). Out of the 254 occurrences detected with a single method, ~ 88% of the prey were identified by the DNA-based method, and only 12% by the hard-part method. The numbers of scats containing multiple prey items also increased from ~ 28% using hard-parts alone—to ~71% with combined methods (~ 64% with DNA method, Figure 4.3). In my case, the DNA results drove the combined results, which was not necessarily the case in other studies (Casper et al., 2007b; Tollit et al., 2009). This means that biases of the DNA methods will likely have a greater effect on the interpretation of final results than will the biases inherent to the hard-parts method.

The digestion process likely explains why the DNA and hard-parts methods did not detect similar prey within single scat samples. Hard-parts pass though the GI tract slower than soft parts, and are more likely to be excreted in pulses compared to the continuous passage of soft tissues (Gudmundson et al., 2003; Casper et al., 2007a; Tollit et al., 2009). Morphological identification of prey taxa requires that hard-parts retain their morphological integrity, which was not the case as ~ 40% of my samples had no identifiable hard-parts. Similarly, the quality and integrity of DNA impacts detection rates, as would the numbers of sequences in the prey tissue.

Combining the outputs of the DNA and hard-part analyses may yield better estimates for some species such as cephalopods, reduce the overall importance of other dominant species in the diet such as gadids, and probably over-estimate the proportion of forage and flatfish in the diet as discussed above. In my case, the proportion of gadids in the diet decreased from ~69% using the hard-part method to ~ 57% using the combined methods. This decrease occurred because the DNA method detected increased numbers of prey species while the cumulated occurrence of pollock remained stable (high detection in both method), such that the overall relative proportion of pollock in the diet decreased. Squid, on the other hand, became 7 times more important compared to using just DNA alone—or conversely, was reduced in importance by a factor of 3.6 when the DNA offset the presence of squid beaks. Collectively, combining the DNA and hard-part diet descriptions shows northern fur seals are generalist predators that consume a diet more diverse than detected from hard-parts remains alone. It is still dominated by pollock and salmonids, but squids appear to be less important than the presence of beaks alone might suggest, while forage fish and flatfish may be overestimated in the combined results.

Despite the clear benefits of DNA-based methods in scats to determine diet composition of predators, they cannot provide the size or age class of prey ingested. This can only be obtained from the lengths of sagittal otoliths, squid beaks or other hard-parts remains in scats. Reconstructing the size of ingested prey based on relationships with otolith and beak lengths (Harvey et al., 2000; Tollit et al., 2004) is important given that the energy content of fish and squids differ depending on age and size (Paul and Paul, 1999; Logerwell and Christiansen, 2000; Iverson et al., 2002). Following the flow of energy from prey to

predators require this information from the hard-part method. Integrating morphological and molecular-based data thus improves the quantitative and qualitative information about diets, and contributes to a better understanding of the trophic relations and foraging efficiencies of northern fur seals.

4.5.2 Stable isotopes and prey associations reveal two foraging strategies

The DNA meta-barcoding and morphological identification are scats-based methods that provide useful information about diet composition. However, they are only representative of what animals consumed over a short 10 – 48 h period before they returned to land (Orr and Harvey, 2001; Staniland, 2002; Deagle et al., 2005; Casper et al., 2007a). Longer timescales are sometimes equally or more relevant in ecological studies for understanding foraging behaviours and efficiencies, as well as the relationships between prey fields and predators, and the link to fitness.

Plasma isotopic turnover is considered to be ~ 2 weeks (Kurle, 2002; Orr et al., 2008), so I assumed it reflects the foraging strategy during the foraging trip I monitored. The stable isotope results showed that female fur seals foraged in two different habitats ($\delta^{13}C$) and on prey at different trophic levels ($\delta^{15}N$, Figure 4.5) When combined with foraging locations (Figure 4.1), these groups corresponded to 1) females foraging off the shelf on pelagic prey at lower trophic levels, and 2) females foraging in a more nearshore/benthic system on higher trophic level prey. The females foraging on the shelf (~100 m depth) had access to the benthos and its associated prey, which was not possible for fur seals feeding in the basin (>1000 m). Females foraging over the shelf dove to deeper depths (sometimes to the bottom) for longer times overall compared to the strictly pelagic, shallow and short dives of the off-shelf females. Such differences in on-shelf and off-shelf foraging behaviours have been previously noted for females breeding on Reef rookery (Gentry, 1998; Nordstrom et al., 2013).

The 'on-shelf' isotopic signatures did not differ significantly from previous measurements (~ -18.9 ± 0.5 for $\delta^{13}C$ and ~ 16.4 ± 1.4 for $\delta^{15}N$ from Zeppelin and Orr (2010) added in red on Figure 4.5 and the 17.3 ± 0.1 $\delta^{15}N$ measured for females from St.

Paul and St. George in July August (Kurle and Worthy, 2001). Unfortunately, the foraging locations associated with these additional measures of isotopic signatures were not recorded.

It is noteworthy that female fur seals foraging off the shelf had $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures that were similar to females foraging off of Bogoslof Island (53.9N, 168.0W) north of the Aleutian Islands within the Bering Sea deep Basin (~ -19.6 ± 0.2 for $\delta^{13}C$ and ~ 14.2 ± 0.3 for $\delta^{15}N$ from Zeppelin and Orr (2010) shown with a red square Figure 4.5). This indicates that the off-shelf Pribilof fur seals have similar diet and foraging habitats than fur seals breeding on Bogoslof Island. The exception was female #6 which stayed foraging on the shelf but showed an isotopic signature corresponding to off-shelf diet (see Table A.4 in Appendices section). Her foraging trip lasted only 5.5 days however. This means that my isotopic values likely take into account diet from previous foraging trips. In addition, she was the only 'on-shelf' female that went foraging SW towards the shelf. Even though she did not seem to go foraging in the basin, she might have stayed around the shelf break and consumed basin prey advected on the shelf break.

Diet composition estimated from scats collected on Bogoslof island indicate that fur seals breeding there consume mid-water prey in oceanic domains consisting mostly of mesopelagic fish and gonatid squid (both 73.2% FO in Zeppelin & Orr 2010, >75 % FO Trites A.W., Pers. Comm.) and, to lesser extent, myctophids (17.1% FO, Zeppelin and Orr, 2010) and salmon (~ 15 % FO, Trites A.W., Pers. Comm.). Fewer than 10 % of the scats in both studies contained walleye pollock. In all likelihood, females from the Pribilofs that travelled off shelf likely consumed a similar diet to those breeding on Bogoslof Island. Such a possibility is consistent with the cluster analyses of prey associations (Figure 4.4) showing one cluster of mesopelagic and cephalopods species associated with pelagic mid-water oceanic ecosystems, and a second cluster of flatfish, hexagrammids, forage fish and salmon that are associated with shelf systems.

It is noteworthy that 100% of the scats that contained mesopelagic species also contained cephalopods (although cephalopods were not exclusively associated with mesopelagic), but the scats with the cluster mesopelagic/cephalopod represented only ~ 5 % of the total number of scats. If we consider this cluster representative of the diet of the off-shelf females, then 40 % of my tagged animals foraged off-shelf while only 5 % of the scats

collected represented their diet. This means that this foraging strategy is under-represented in the scats collected on St. Paul Island, such that the dietary results would have to be multiplied by a factor of 8 to reach the same ratio and represent its overall importance. This is not surprising knowing that scats are indicative of food ingested within the last 10 - 48 h in fur seals (Bigg, 1981; Casper et al., 2007a), and that females foraging off the shelf travel for ~150 km (~ 24 h and up) to return to land. The probability they defecate their meals eaten off-shelf before reaching the shore is consequently greater than for females foraging in waters surrounding the rookery.

The slightly higher δ15N for off-shelf females from St. Paul compared to the Bogoslof females (Figure 4.5) likely reflects greater amounts of walleye pollock in the St. Paul diets. My cluster analysis shows an association of gadids with the other 2 clusters (Figure 4.4). This indicates that even if the pollock is less strongly associated with the mesopelagic + cephalopod cluster (longer distance), it is still ubiquitously present in the scats containing these prey. Juvenile pollock are widely distributed in basin and shelf regions of the Bering Sea (Benoit-Bird et al. 2013), and are likely consumed off the shelf in the deep oceanic domain to a certain extent. Dive profiles of the females I tracked indicate that they also foraged in these relatively shallow waters while transiting, and thus likely consumed gadids and other shelf-associated prey during their transit over the Bering Sea shelf to and from their rookery. This could explain the slight but not significant difference in δ15N signature between off shelf and Bogoslof females.

Nitrogen isotopic signature $\delta^{15}N$ of females foraging off the shelf would increase compared to the Bogoslof females only if they consumed prey with isotopic signatures above the isotopic signatures of squid and mesopelagic species (~10 - 13 ‰, Kurle and Worthy, 2001; Kline, 2010; Barger and Kitaysky, 2012). Pollock isotopic signatures increase with age and size as they consume higher trophic level species (Gorbatenko et al., 2008). Age > 2 pollocks have a $\delta^{15}N$ isotopic signature of 15 - 16 ‰ (Gorbatenko et al., 2008; Barger and Kitaysky, 2012), while younger pollock have isotopic signatures ~11 - 12 ‰. Consequently, given the ~ 4.5 ‰ enrichment between prey and predators for fur seals (Kurle, 2002), consuming juvenile pollock would have not increased overall $\delta^{15}N$ of the off-shelf females from the Pribilof Islands to the point that it is statistically different from the exclusive basin-

foragers that feed around Bogoslof Island, but marginal consumption of older pollock (or other shelf associated prey with greater $\delta^{15}N$) might have.

Carbon and nitrogen isotopic levels in plasma before and after the foraging trip (Figure 4.6 graphs A & C) show that overall female fur seals maintain their foraging strategy, *i.e.,*habitat and trophic levels over successive foraging trips. This is consistent with females tending to maintain their foraging habitat over successive trips (Call et al., 2008). However, isotopic levels in red blood cells collected before the foraging trip at sea (*i.e.,*between 20th of August and the 10th of September) were lower overall than plasma levels, consistent with the results of controlled studies comparing plasma and serum levels (Kurle, 2002; Orr et al., 2008). Given a 2-month or greater turnover rate of a red blood cell (Kurle, 2002; Zhao et al., 2006), the change in isotopic levels might also partially reflect the diet and feeding habitats during the spring migration through the Pacific Ocean to the Bering Sea (lower trophic level and/or in more offshore/pelagic/low latitude locations than during the foraging trip I studied.).

4.5.3 Conclusions

DNA analyses of scats indicate a more diverse diet of fur seals than hard-part methods alone do, and thus allow more accurate analyses of prey association. In addition, C and N stable isotopes measurements complement the dietary information gleaned from scats. They show distinct differences in the trophic levels of prey consumed that are related to off-shelf and on-shelf habitats. Combining this information with the clustering analysis of prey species co-occurring in scats suggest that females foraging off-shelf likely consumed mostly cephalopods and mesopelagic fish (with some pollock), while females foraging on the shelf likely consumed mostly walleye pollock and salmon. Teasing apart individual diets based on multiple techniques has important consequences for studies seeking to describe diets, energetic costs of foraging and ultimately foraging efficiency. It also provides a means to adjust summaries of diets derived from scats collected on rookeries to properly reflect the average diet of fur seals breeding on the Pribilof Islands.

Chapter 5: Foraging efficiency is related to the reproductive fitness of lactating Antarctic fur seal through increased prey catch success and reduced time at sea

5.1 Summary

The efficiency with which individuals extract energy from their environment defines their survival and reproductive success, and thus their selective contribution to the population. Individuals that forage more efficiently (*i.e.,*energy gained exceeds energy expended) are likely to be more successful at raising viable offspring than less efficient individuals. I tested this by equipping 20 lactating Antarctic fur seals (*Arctocephalus gazella*) breeding on the Kerguelen Island in the Southern Ocean with tags that recorded GPS locations, depth and tri-axial acceleration to determine at-sea behaviours and detailed time-activity budgets during their foraging trips. I also simultaneously measured energy spent at sea using the doubly labeled water method, and estimated the energy acquired while foraging from 1) type and energy content of prey species present in scat remains, and 2) numbers of prey capture attempts determined from head acceleration. Finally, I followed the growth of 36 pups from birth until weaning (of which 20 were the offspring of my 20 tracked mothers), and used the relative differences in body mass of pups at weaning as an index of first year survival and thus the reproductive success of their mothers. My results show that females with greater foraging efficiencies produced relatively bigger pups at weaning. These mothers achieved greater foraging efficiency by extracting more energy per minute of diving rather than by reducing energy expenditure. This strategy also resulted in the females spending less time diving and less time overall at sea, which allowed them to deliver higher quality milk to their pups, or allowed their pups to suckle more frequently, or both. The linkage I demonstrate between reproductive success and the quality of individuals as foragers supports the optimal foraging theory, and provides a quantitative framework to investigate how changes in the availability and accessibility of prey affect the time-activity budgets and foraging efficiencies of mothers—and ultimately the growth and survival of their pups.

5.2 Introduction

Optimal foraging theory postulates that natural selection favours animals that forage more efficiently, where foraging efficiency is defined as the ratio of energy gained to energy expended to acquire food (MacArthur and Pianka, 1966; Pyke, 1984; Stephens and Krebs, 1986). The energy gained in excess of energy expended can be allocated to reproduction, survival and growth (Boggs, 1992). Individuals that maximise their energy return per unit of energy (and time) spent have more energy (and time) to allocate to reproduction over their lifetime and thus a greater fitness than less efficient conspecifics. Foraging efficiency thus ultimately shapes the dynamics of populations.

Empirically testing optimal foraging theory requires knowing the amount of energy spent foraging, the nutritional quality and quantity of resource ingested, and a concomitant measure of reproductive success of individuals. Studies that have controlled energy gain and energy expended, as well as controlled studies of species with 'rapid' reproductive rates have yielded findings consistent with the optimal foraging theory (Ritchie, 1990; Lemon, 1991). However, validating the theory in the wild is more complicated because of the difficulty of simultaneously measuring individual energy intake and output, as well as an individual's own reproductive success. This is particularly true for marine mammals that are long-lived and elusive, and live in an environment where direct observation of foraging is impossible.

Some studies have investigated life history traits including reproductive rates in marine predators (Chastel et al., 1993; Boyd et al., 1995a), but have generally not linked them to foraging efficiency. Others have looked at foraging efficiency indices, but often assume that these indices are linked to fitness without explicitly linking the two parameters (Luque et al., 2007). There is therefore a need to link reproductive success with measures of foraging efficiency, which would allow predictions to be made about how the individual fitness and population trends of top predators are affected by changes in prey availability and foraging behaviours.

The energetic cost of foraging in free-ranging pinnipeds can be assessed using indirect calorimetry techniques such heart rates or doubly labeled water (Lifson and McClintock, 1966; Butler et al., 1992; Butler, 1993; Speakman, 1997; Froget et al., 2004). In

contrast, the energy gained while foraging has been traditionally measured by identifying prey species in regurgitates, scats, or stomach contents (Arim and Naya, 2003; Gudmundson et al., 2003; Karnovsky et al., 2012) and estimating numbers consumed from changes in body water pool (Costa, 1993), or with stomach temperature sensors that measure the changes in temperature between the predator's body and the cold prey ingested (Grémillet and Plös, 1994; Kuhn and Costa, 2006), both of which present challenges in wild otariids. Consequently, studies have tended to either report foraging effort but not gain (Costa et al., 1989; Shaffer et al., 2003), foraging gain but not effort (Lea et al., 2006; Staniland et al., 2007), or have used behavioural indices rather than quantitative measurements of foraging efficiency (Bailleul et al., 2005; Weimerskirch et al., 2005; Lea et al., 2006). More recently, however, tri-axial accelerometers have been validated and used to measure numbers of prey capture attempts in free-ranging marine predators (Skinner et al., 2009; Suzuki et al., 2009; Viviant et al., 2010; Watanabe and Takahashi, 2013; Ydesen et al., 2014). This technological innovation makes it possible to quantitatively estimate foraging efficiency of individual marine predators by combining cost of foraging through doubly-labeled water, with gain of foraging from diet composition analyses and measure of prey capture attempts using accelerometers.

Antarctic fur seals give birth to a single pup once a year. Mothers then nurse their pups for 4 months during which time they alternate periods of foraging at sea to replenish reserves and fasting periods on land while nursing their pups. Allocation of energy to their pup will dictate their growth rate and mass at weaning. This is directly linked to survival of the pup during their first year at sea, the critical period in the life cycle of fur seals (Doidge and Croxall, 1989; Baker and Fowler, 1992; Boltnev et al., 1998; McMahon et al., 2000; Hall et al., 2001; Beauplet et al., 2005). Consequently, growth rates and mass at weaning of pups can be used as indices of annual reproductive success of female fur seals. As central place foragers, mothers are also time-limited during their foraging trip by the fasting capacity of their pups and must trade-off the time they take to replenish their reserves with the nutritional needs of their pups. Thus, given the time constraints mothers face while feeding, the allocation of their time to different activities at sea will affect both energy expenditure and return. It is thus important to study foraging efficiency linked to reproduction success within the context of individual time-activity budgets.

Antarctic fur seals employ a range of foraging strategies depending on environmental conditions and the distribution of prey patches (Lea et al., 2002b). The disproportional effects of climate change have made environmental conditions and the availability of prey less predictable in high-latitude marine ecosystems (Serreze et al., 2000; Walther et al., 2002). Top predators such as marine mammals living in high-latitude areas are expected to be affected more by these changes, but it is difficult to predict their response with any confidence. One means of predicting how marine mammals will respond to climate change is to quantify foraging efficiency within the context of optimal foraging theory and investigate how foraging efficiency varies depending on behavioural choices and strategies of individuals at sea, and how it impacts fitness via reproductive success. I sought to test optimal foraging theory on a wild population of pinnipeds (Antarctic fur seals) by linking foraging strategies to efficiencies and proxies of fitness. I determined 1) whether foraging efficiency of individual fur seals could be quantitatively estimated, 2) how their foraging behaviours shaped their foraging efficiencies, and 3) whether foraging efficiency affected reproductive success as indicated by the body size of pups at weaning.

5.3 Material and methods

5.3.1 Data collection

Data were collected on 20 lactating Antarctic fur seal females at Pointe Suzanne, Kerguelen Island (Southern Ocean, 49°26'S - 70°26'E) during the breeding season (Jan-Feb 2012) under the ethical regulations approval of the French Polar Institute (IPEV) and the UBC Animal Care Committee. Doubly-labeled water data were collected on healthy-looking females with a confirmed suckling pup. They were captured using a hoop net, carried over a short distance to a restraint board where they were anesthetized with isoflurane gas. Standard morphometric measurements were made to the nearest 0.5 cm, and mass was recorded using a scale at ± 0.2 kg. Measurements of daily energy expenditure (kJ/day) were performed using the Doubly-Labeled Water (DLW) method (Lifson and McClintock, 1966; Butler et al., 2004). This method has been previously validated by comparison to indirect calorimetry in a range of small mammals (Speakman and Krol, 2005), as well as on seals (Sparling et al., 2008). A blood sample was collected from the back flipper in Monovette syringes (Sarstedt)

coated with Li-Heparin and plasma was isolated from red blood cells by centrifugation at 1000g for 10 min before injection of the doubly-labeled water intravenously. More details on the doubly-labeled water material and method used in this study can be found in Chapter 2.

Females were also equipped with data loggers glued to the dorsal mid-line fur using a 2-part Devcon 5min epoxy glue. Daily Diary tags (DD, Wildlife Computers) recording tri-axial acceleration and tri-axial magnetic field at 16 Hz, and depth, light level, and water temperature at 1 Hz were glued as close as possible to the projected center of mass on the back of the animal (roughly between the scapula). Fastloc GPS MK10 loggers (Wildlife Computers) were glued lower down the back from the DD tags and recorded GPS coordinates along the track of the animal at sea, as well as depth and water temperature at 1 Hz. Finally, GCDC X6 or X8 accelerometers were glued on the head of the animals that recorded tri-axial acceleration at 16 or 20 Hz. Once the devices were securely attached and a second blood sample was taken at the end of the equilibration period (~ 2 h), the females were released on full recovery from the anaesthesia and allowed to rejoin the colony. Individuals were recaptured after a single foraging trip and anaesthetized as previously described. A final blood sample was taken to determine isotope levels of ^{3}H and ^{18}O at the end of the foraging trip, and all the data loggers were removed by cutting the fur beneath the devices. Blood samples were frozen at -20 ºC until analyses in the lab. A second set of morphometric measurements were also taken at this time.

5.3.2 Energy expenditure

All methods for analyses and calculations of the energy expenditure of female fur seals using the doubly-labeled water are detailed in Chapter 2. In short, the isotope ratios ^{18}O: ^{16}O and ^{2}H: ^{1}H were analysed using gas source isotope ratio mass spectrometry (Optima, Micromass IRMS and Isochrom μG, Manchester, UK). Isotope enrichments were converted to CO_2 production for each individual using a two-pool model and initial isotope dilution spaces were calculated using the plateau method (Halliday and Miller, 1977). I used the equation from Speakman et al. (1993) to calculate metabolic rates from DLW concentrations and a respiratory quotient of 0.80. Three of the 20 females had isotopic levels too close to background levels for accurate measurements and were discarded.

Individuals spent time on land after the post-equilibration sample and upon return to the colony before recapture and the final blood sample was collected. Energy spent during this 'non-foraging' time was part of the DLW measurement, and given I were interested in estimating only energy expenditure at sea, energy expenditure at sea was calculated by subtracting on-land expenditure from the total estimate using previously determined values for lactating Antarctic fur seals (4.56 W/kg in Costa and Trillmich, 1988) while on land. Energy spent while diving or transiting were calculated using activity-specific metabolic rates determined in Chapter 2.

5.3.3 Foraging behaviours

I used depth data recorded by the DD tags to determine diving behaviours, or depth data recorded by the fastloc MK10 during the rare times that the DD tags malfunctioned. Any drift in the pressure sensors or error spikes were corrected prior to analyses. Diving behaviours were reconstructed using a custom-made R program previously developed for Antarctic fur seals. Dives were defined as periods of time that animals spent under water below a minimum depth of 3 m and for a minimum of 4 s until they went back to the surface and I derived dive duration and maximum dive depth for each of them.

Distances traveled at the surface of the ocean (or horizontal distances) were calculated by measuring the linear distance between 2 successive GPS locations taking into account the curvature of the Earth using the Haversine formula (Sinnott, 1984). GPS locations have a high spatial and temporal resolution (they were set to record a location every 5 min), so GPS tracks did not required interpolation (Tremblay et al., 2006). Part of the distance traveled under water while diving was inherently taken into account in the measured horizontal distance traveled. Consequently, I only estimated vertical distance traveled while diving by doubling the maximum dive depth of each dive, which should provide an acceptable estimate because fur seals are known to dive at relatively shallow depths (~35m average).

Time spent foraging or diving was calculated from the time when the animal was below the water surface and performing confirmed dives plus the post-dive interval as calculated from the Bout-Ending Criterion using the R package DiveMove (Luque and

Guinet, 2007). The animals were considered to be transiting (*i.e.,* traveling fast between 2 locations) whenever they were neither diving, nor sleeping and when the calculated speed at the surface (*i.e.,* time needed to travel a distance between 2 GPS points) was >1 ms^{-1}. All methods to determine time-activity budgets in fur seals (and time-activity budget results) are detailed in Chapter 2.

Average dive parameters, such as for dive depths and dive durations, were nested within animals and were calculated using linear mixed effect models with no fixed effects (only the intercept was calculated) and with individual as a random effect to take into account that each animal performed a different number of dives.

5.3.4 Prey capture attempts

Prey capture attempts (PrCA) were measured using acceleration data recorded on the head of the animals at 16 Hz (Skinner et al., 2009; Suzuki et al., 2009; Viviant et al., 2010; Watanabe and Takahashi, 2013; Ydesen et al., 2014). Only acceleration while the animal was diving below 3 m was kept for analyses. The head acceleration was recorded from a GCDC accelerometer, and dive depth was recorded by the DD tags attached to the back of the animals. Upon careful investigation of the signals, I noticed clock drifts between the 2 loggers for most of the animals. The first step in my analyses was thus to synchronise the 2 loggers using a custom-made code in Matlab so that the head acceleration matched the dive depth and back acceleration. The first and last dives of each foraging trip were singled out for both the head and the back loggers. Whenever a clock drift was noticed between the 2 acceleration channels, I estimated the time difference, and added data points at random throughout the data on the channel that was shorter following a uniform distribution to compensate for this time difference. Extra data points were added as the average acceleration from 2 successive data points to not change the shape of the signal. The resulting synchronized channels were thus within 2 s of each other at the end of a foraging trip.

Once synchronization was satisfied, I only used the heave and surge channels to detect PrCAs (movement up and forward) (Viviant et al., 2010). I filtered the raw acceleration for these 2 channels using a 3rd order high-pass filter at 3 Hz (Viviant et al., 2010; Iwata et al., 2012) to filter out the static acceleration due to the position of the animals.

This only left out the signal from rapid head movements. The surge (x) and heave (z) dynamic accelerations were then summed and a running variance was applied over a 2-sec window. A cluster analyses on the resulting variance of dynamic acceleration was then performed using the k-mean function in R, which provided each animal with an individual threshold above which the signal was considered to correspond to a PrCA. Events detected within less than 1 sec of each other were considered coming from the same PrCA event (as assessed from feeding trials with live fish on harbour seals—Austen Thomas, pers. comm.) and from video recordings of Steller sea lions (Viviant et al., 2010). PrCAs represented only an index of attempts to capture prey, since it was impossible to determine whether animals were successful at capturing the targeted prey.

The PrCA detection method with head accelerometers has been validated on otariids in captive settings (Viviant et al., 2010) and has been used on phocid seals in the wild (Liebsch et al., 2007; Gallon et al., 2013; Naito et al., 2013; Guinet et al., 2014; Volpov et al., 2015). It has also been used on diving birds (Kokubun et al., 2011; Watanabe and Takahashi, 2013). However, I tested the accuracy of using the acceleration signal from the back of the animals by performing the same analyses on the data collected from the DD tag glued between the shoulder blades and by comparing it to the results obtained from the head signals. I found that back acceleration could estimate PrCA as well as acceleration on the head of the seals with this method (Figure 5.1, linear regression: $PrCA_{Back} = 34.25 + 1.00 \times PrCA_{Head}$; $p < 10^{-15}$, $R^2 = 0.90$). Similar results have been found for head and back accelerometers deployed on southern elephant seals (C. Guinet, pers. comm.). Consequently, I calculated PrCA using back acceleration corrected for the ~ 34 PrCA overestimation per night whenever the head accelerometer failed to record data over the full foraging trip.

Differences between prey capture attempts per days or per dives were estimated using linear mixed effect models with no fixed effect and with individual as a random effect to account for each animal performing a different number of dives or days at sea.

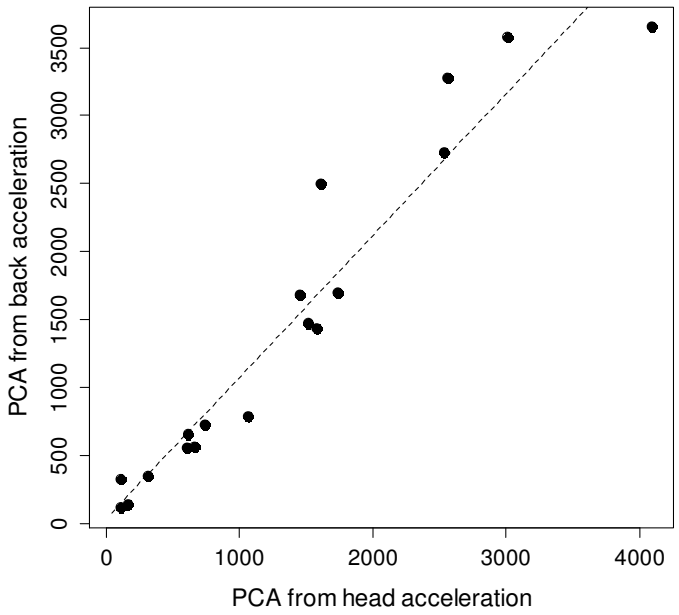

Figure 5.1. Prey capture attempts (PrCA) detected from back acceleration compared to PrCAs detected from head acceleration signals. Each dot represents one animal. The dotted line shows the results of regression model $PrCA_{Back} = 34.25 + 1.00 \times PrCA_{Head}$ ($R^2 = 0.90$, p slope $< 10^{-15}$).

5.3.5 Diet estimates

I determined diet composition of Antarctic fur seals from 20 scats collected at Pointe Suzanne rookery on Kerguelen Island in March 2012. Samples were kept frozen at -20ºC until ready to be processed in the lab as detailed in Chapter 4. Hard part remains were identified to the smallest taxon possible at the Centre d'Etudes Biologiques de Chize (France) following recommendations from Lea et al. (2002c). Frequency of occurrence (FO) and relative proportion of each prey item in the diet (SSFO) were calculated the same way as for NFS (Chapter 4) and were compared to previously determined diet composition on Antarctic fur seals (Lea et al. 2002b). Upon identifying the main prey items, the size and energy content of the fish and squids found in the scats were taken from published sources (Cherel et al., 2002; Lea et al., 2002a; Lea et al., 2002c; Tierney et al., 2002; Fernández et al., 2009). The size and energy content of squids were averaged per year and then over the 3 years from Lea et al. (2002b) to obtain a squid estimate for my study as most of the squid beaks I found were unidentifiable.

I obtained energy density of the diet (ED_{Diet}) by averaging the energy density of different prey (ED_i) weighted by their proportion within the diet (P_i) over the number of prey in the diet N using:

Eq. 5.1 $$ED_{Diet} = \frac{\sum(ED_i \times P_i)}{N}$$

Whenever information was missing for prey of low frequency of occurrence in the diet, I replaced it with the energy density of the closest related prey item or by the average of the energy content for the specific prey group. Once the mass (BM in g) and the energy density (ED in kJ/g) of each prey item (i) were estimated, I calculated the average energy content of a specific fish (EC in kJ) using:

Eq. 5.2 $$EC_i(kJ) = BM_i(g) \times ED_i(kJ/g)$$

The average energy content (in kJ) of a random non-specific prey (p) consumed by fur seals given a specific diet was calculated by weighting the energy content of a specific prey item by its relative proportion in the diet (P):

Eq. 5.3 $$EC_p(kJ) = \sum_i (EC_i(kJ) \times P_i)$$

Means ± SD of energy content of each prey (EC_i in kJ) were calculated by generating 1000 values of mass and 1000 values of energy density (ED_i) using normal distributions of their respective means ± SD from Table A.5. I calculated the error around P_i by bootstrapping scats (*i.e.,*random sampling with replacement of individuals scats), and recalculating FO and SSFO for each new generated dataset (n = 1000). I then obtained the 95% CI and the SD from these values. Means ± SD of energy densities (ED_{Diet}), and energy content of an average prey (EC_p) in the 2 diets were calculated by generating values of EC_i and ED_i for each prey type (i) in proportion to their respective importance in the diet (P_i) out of 1000 values from normal distributions using their respective mean ± SD. For prey species with no ED_i or EC_i values, I used the average ED or EC from the prey group as their values weighted by their own proportion within the diet. As the prey group 'Other' did not have values for mass or energy density, I considered it as an average of the rest of the diet weighted by its relative importance in the diet.

5.3.6 Foraging efficiency

The foraging efficiency (*FE*) of each seal (*i*) was calculated as the ratio between the energy expenditure at sea obtained from the DLW measures (EE_i) per animal *i* and energy gained while foraging at sea. Energy gained was estimated as the specific energy content of a non-specific prey (EC_p) in their diet multiplied by the number of time seals *i* attempted to capture prey ($PrCA_i$).

Eq. 5.4 $$FE_i = \frac{EC_p \times PCA_i}{EE_i}$$

Seals with DLW results that were too close to background and seals that did not have acceleration data for the complete foraging trip were omitted from calculations. I am aware that PrCAs represent attempts and not confirmed prey captures, but I assumed that unsuccessful PrCA were minor compared to successful ones (93% of attempts were successful in Australian fur seals, Volpov et al., 2015), and that proportion of unsuccessful attempts were consistent between seals.

As the 3 parameters used to calculate the foraging efficiency of each individual animal (FE_i) contain inherent errors, I calculated the resulting uncertainty around FE_i using the following 3 steps: **1)** I calculated error in EE_i by generating 1000 values following a normal distribution of 1.8 ±7.2% of the measured values of DLW. This error was estimated by Dalton et al. (2014b) when DLW was compared to respirometry on northern fur seals (using same equation and in the fall months). **2)** I calculated error in EC_p by generating 1000 values using a normal distribution following the means ± SD for mass and energy density for each prey in the diet mentioned above (see Diet estimates section). **3)** I calculated error in $PrCA_i$ by adding a detection error and subtracting a false positive error generated using uniform distribution between the ranges mentioned above to the measured $PrCA_i$ value (1000 values generated). Detection rate of PrCA (true positive rate) is known to range from 68 to 97% (underestimation of true PrCA) and the false positive rate from 6 to 48 % (overestimation of true PrCA) in Steller sea lions and Australian fur seals (Viviant et al., 2010; Volpov et al., 2015).

Mean ± SD of FE_i was calculated over the 1000 generated $PrCA_i$, EE_i and EC_p using Eq. 2.1. I calculated uncertainty over the average FE per group of foraging strategy (on-shelf

versus off shelf) using the bootstrap method over 1000 simulations, where the random sampling with replacement were taken within the 1000 values of FE_i generated per animal within the group.

A sensitivity analysis was performed to estimate the contribution of each input variables uncertainty to the overall variance in the resulting foraging efficiency. This was done by computing the standardized regression coefficients (SRC), its bias and its 95% confidence intervals for each of the input variable using the *src* function in R ('*sensitivity*' library, R3.0.3) over 1000 simulated values.

5.3.7 Pup growth

Thirty-six pups were randomly chosen in the Pointe Suzanne colony and were followed from birth until they could no longer be found on the colony. Mothers of 20 of the 36 pups initially followed were selected to be tracked. Standard morphometric measurements were recorded at birth and every 7-10 days or longer as the pups started to wander further from the colony. Length and girth were measured to the nearest 0.5 cm, and mass was recorded using scale at ± 0.1 kg.

Growth from birth to weaning of each individual pup was modeled with the von Bertalanffy equation (von Bertalanffy, 1938) using the nls function (nlme package in R):

Eq. 5 $$BM = A \times (1 - e^{(-K \times age - t_0)})$$

where BM is body mass in kg, A is the asymptotic mass of pup at weaning, K is the curvature parameter (day^{-1}), age is the pup age (day) and T_0 is the age (day) at which the pups have a mass equal 0 kg. I also modeled the average male growth and the average female growth separately because male pups have a higher growth rate than female pups in fur seals (Kerley, 1985; Trites, 1993; Davis et al., 1996; Chambellant et al., 2003; Osman et al., 2010).

5.3.8 Linking foraging efficiency of mothers and growth of pups

I calculated the difference between individual foraging efficiencies of each female and the average foraging efficiency of all the females as a metrics of relative quality of the mothers as foragers. I simultaneously calculated the individual estimated mass at weaning

(127d) from individual pup growth curves and calculated the difference with the average mass at weaning calculated from the average sex-specific growth curve as described above as a metrics of relative size at weaning of pups. I tested the relationship between these two metrics using a type II linear regression that took into account the fact that there were errors associated with both the response and the explanatory variables (*lmodel2* package in R) using the ranged major axis (RMA) method. I also tested the relative size of pups at weaning against other foraging metrics of mothers, such as time spent at sea or diving or rate of energy gain while diving using the same methods.

5.4 Results

5.4.1 Foraging behaviours

Antarctic fur seal females all foraged east to south-east of Kerguelen Island on the Kerguelen plateau (plateau with depths > 500 m). They weighed 31.1 ± 0.9 kg prior to departure (range: 24.0 - 34.0) and gained 0.6 ± 0.6 kg during their trip (2.2 ± 1.8 % of their body mass). They traveled 635 ± 77 km (271 - 1295) with foraging trips lasting for 7.6 ± 3.8 d (2.5 - 15.5 d). During these trips, they performed an average of 3949 ± 597 dives to a mean depth of 19.9 ± 2.7 m (75.5 % of which were less than 15 m deep, and exclusively nocturnal) that lasted 42.6 ± 4.5 s on average. They spent 29.0 ± 0.7 % (51.3 ± 5.9 h) of their time diving, 26.4 ± 1.6% (49.8 ± 7.9 h) transiting, 36.3 ± 2.0 % (60.9 ± 7.6 h) performing surface activities, and 8.2 ± 1.7% (12.9 ± 3.0 h) resting.

5.4.2 Energetic cost of foraging

Rates of energy expenditure per day at sea averaged 17.7 ± 1.1 MJ/d (0.59 ± 0.04 MJ/d/kg for all females, n = 17). This translated into animals spending an average of 66.0 ± 7.5 MJ (2.2 ± 0.3 MJ/kg) while diving and 38.4 ± 6.4 MJ (1.3 ± 0.2 MJ/kg) while transiting from activity-specific metabolic rate equations in Chapter 2.

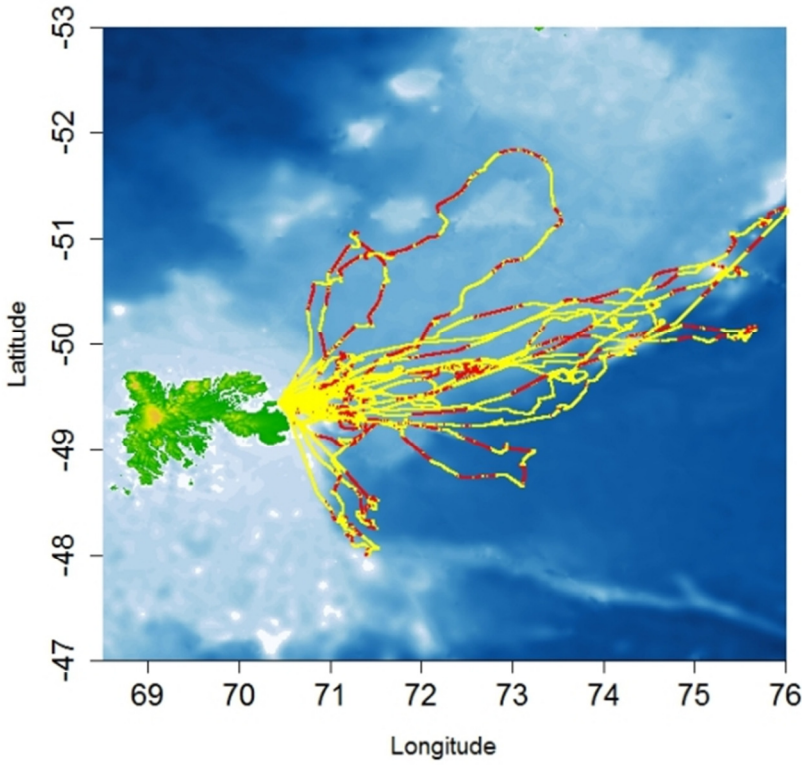

Figure 5.2: Example of a dive profile of a female Antarctic fur seal during a foraging trip (left panel) and over 5 min (right panel). Orange dots show where prey capture attempts occurred during the dives.

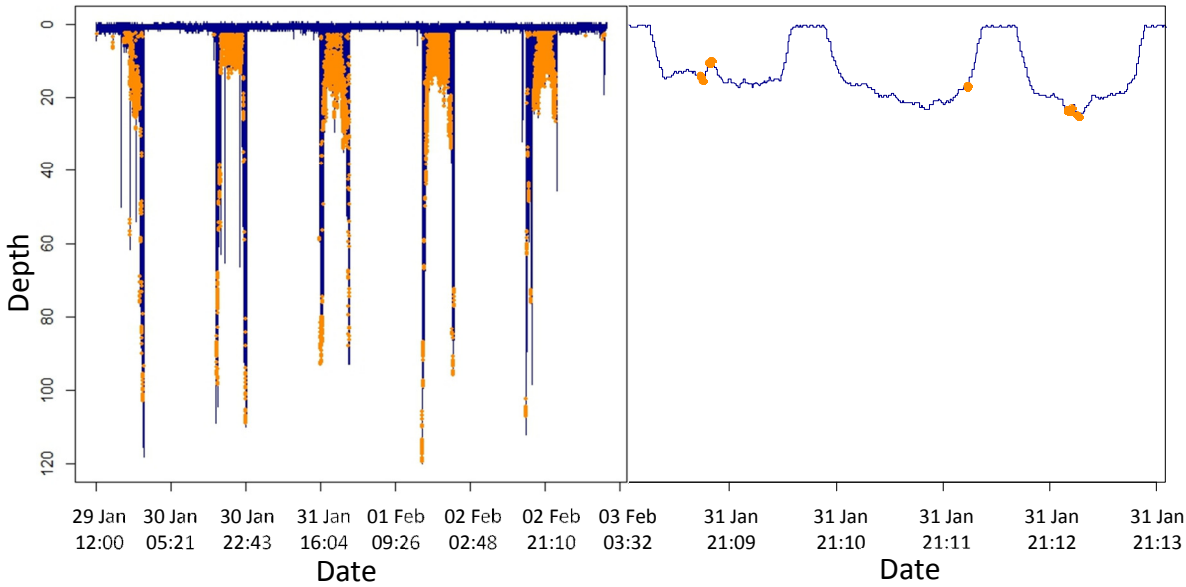

Figure 5.3: Foraging locations of the 20 Antarctic fur seal females tracked on the Kerguelen plateau. Red dots show where the animals attempted to capture prey within the range of their foraging location (with yellow showing no prey capture attempts). Trips of females with no acceleration are shown in yellow only.

5.4.3 Prey capture attempts

Females attempted to capture prey 0.87 ± 0.11 times per dive while foraging (Figure 5.3). When only selecting dives in which at least one PrCA occurred, their capture rate increased to 2.04 ± 0.11 prey per capturing dive. This translated in females capturing on average 336 ± 38 prey per night of foraging and 2328 ± 387 prey over their entire foraging trip (range 704 – 6613 prey). When corrected for detection rate of PrCA (true positive rate) ranging from 68 to 97 % and a false positive rate of PrCA from 6 to 48 % (Viviant et al., 2010; Volpov et al., 2015), the total PrCA over the foraging trip was slightly lower at 2139 ± 424 (704 – 6612).

Table 5.1: Relative proportion (%), average prey mass (in g), prey energy density (ED in kJ/g), energy content (in kJ) of prey groups in diets of female Antarctic fur seals breeding to Pointe Suzanne on Kerguelen Island. Groups 'Other' were assigned average diet values weighted by its percentage in the total diet for a calculation of ED_{Diet} and EC_p. Bold values are for the total Prey group.

	Prey group	Perc. in diet (%)	Mass (g)	ED (kJ/g)	EC (kJ)
Cephalopod	Cephalopod	**12.11 ± 3.38**	**82.67 ± 32.05**	**4.05 ± 0.10**	**347.11 ± 4.14**
Myctophid		**75.50 ± 7.01**	**12.19 ± 0.11**	**8.56 ± 0.25**	**112.9 ± 0.94**
	E. antarctica	3.50 ± 1.50	3.20 ± 1.80	13.30 ± 2.60	40.97 ± 0.82
	E. subaspera	10.78 ± 1.66	11.80 ± 4.30	7.40 ± 1.00	88.45 ± 1.09
	G. fraseri	2.08 ± 1.11	5.17 ± 0.22	10.20 ± 3.50	52.63 ± 0.57
	G. nicholsi	9.11 ± 1.77	17.33 ± 1.95	9.80 ± 1.00	168.92 ± 0.84
	G. piabilis	14.11 ± 2.06	24.93 ± 0.87	9.50 ± 1.70	235.25 ± 1.36
	G. sp.	9.53 ± 1.88	15.81 ± 0.62	9.83 ± 0.90	155.48 ± 0.50
	K. anderssoni	0.83 ± 0.55	0.47 ± 0.12	8.10 ± 0.30	3.82 ± 0.03
	P. bolini	3.75 ± 0.85	0.87 ± 0.03	5.93 ± 0.38	5.15 ± 0.01
	P. choriodon	1.83 ± 2.27	0.87 ± 0.03	6.08 ± 0.55	5.28 ± 0.01
	P. tenisoni	12.11 ± 1.85	0.77 ± 0.20	6.23 ± 0.12	4.75 ± 0.04
	Myctophidae sp.	7.86 ± 1.52	NA	NA	NA
Notothenid	*Notothenid*	**4.44 ± 2.59**	**58.40 ± 0.00**	**5.03 ± 0.17**	**293.99 ± 0.31**
Other		**7.94 ± 2.54**	NA	NA	NA
	S. hamiltoni	1.25 ± 0.95	NA	NA	NA
	crustacean	3.33 ± 2.5	NA	NA	NA
	mollusc	2.36 ± 1.16	NA	NA	NA
	penguin	1.0 0.69	NA	NA	NA

5.4.4 Diet and prey energy contents

Diets of female Antarctic fur seals (Table 5.1) contained mostly myctophids (~75 %) and cephalopods (~12 %). Myctophids are small mesopelagic fish of mass 1 - 25g with a high energy density (range ~ 6 – 13 kJ/g). The largest prey item of the seals were cephalopods (~83 g) which are also the least energetically dense of their prey (~ 4 kJ/g). Overall, the energy content of their prey ranged from 5 to 350 kJ (Table 5.1). Given the contribution of each prey item to the total diet composition, the female fur seals ingested an average of 7.75 ± 2.47 kJ per gram of prey (ED_{Diet}) with an energy content of 152.46 ± 1.08 kJ per average prey (EC_P).

5.4.5 Foraging efficiency and pup growth

Only 14 females out of the 20 tracked had simultaneous data for energy expenditure and for prey capture attempts available to calculate foraging efficiency (Table 5.2). The calculated rates of energy gains for these 14 animals were 177.7 ± 21.4 kJ/dive, which was 130.6 ± 16.3 kJ/min spent diving and 37.6 ± 4.6 kJ per min spent at sea. The average foraging efficiency for Antarctic fur seals was 3.44 ± 0.45 (range 1.24 - 6.86, 95% CI: 2.54 - 4.38).

Sensitivity analyses showed that the largest contributor of the uncertainty around FE is related to diet estimates, and within the diet component, the estimation of mass of the fish ingested. Uncertainty around PrCA estimates comes second, and estimates of energy expenditure contributes the least to overall FE uncertainty (Table 5.3).

Deviation from average foraging efficiency of individual females ranged from -1.85 to 3.56. Neither the mass, nor the change in body mass of the females before and after foraging trips or the body condition (estimated as mass/length) were linked to the foraging efficiencies of the females (all $p > 0.62$). Foraging trip duration or time spent performing different types of activities at sea were also not related to foraging efficiencies (all $p > 0.21$). Foraging efficiency was positively related to rate of energy gained per min spent diving ($p = 0.034$) but not to rate of energy expenditure ($p = 0.231$).

Out of the 36 pups monitored, the 13 female pups weighed 4.6 ± 0.5 kg and the 23 male pups were 4.9 ± 0.5 kg at birth (Table 5.2, $p = 0.02$). Three pups disappeared rapidly

and I could not fit any growth curve on their data points, and 3 of them had no data close to weaning which means the model could not reach an asymptote. Growth model for male and female pups (Figure 5.4) were:

$$BM_{Male} = 12.04 \times (1 - e^{(-0.038 \times age + 14.07)})$$

$$BM_{Female} = 10.26 \times (1 - e^{(-0.020 \times age + 27.65)})$$

Calculated average masses at weaning (127-day old) from these equations were 11.73 kg for male pups and 9.74 kg for females. Deviation from average sex-specific mass at weaning of individual pup mass ranged from +3.46 kg to -4.56 kg (see Table 5.2).

Table 5.2: Measured and corrected energy expenditure (EE in MJ), measured and corrected number or prey capture attempts (PrCA) during a foraging trip at sea for female Antarctic fur seals (n=14). The corrected values of EE and PrCA were used with the estimated energy content per average prey (EC prey in kJ) to calculate the energy animals gained while foraging at sea (in MJ) and their foraging efficiency (*i.e.*,the ratio of energy gain/EE). The calculated mass at weaning (from individual Von Bertalanffy growth models) of pups from the tracked mothers are indicated with their sex in brackets.

Mother ID	Meas.EE (MJ)	Corr.EE (MJ)	Meas. PrCA	Corr. PrCA	Energy gain (MJ)	Foraging efficiency	Pup mass at 127d (sex)
21	229.31	225.20	7229	6613	1008.23 ± 168.09	4.50 ± 0.83	12.53 (F)
22	120.91	118.72	1976	1819	277.36 ± 45.11	2.35 ± 0.42	7.28 (F)
23	46.50	45.70	1656	1519	231.63 ± 39.70	5.10 ± 0.96	14.27 (M)
26	246.67	242.49	4417	4082	622.28 ± 104.31	2.58 ± 0.47	10.69 (M)
27	60.64	59.59	2093	1921	292.86 ± 49.79	4.94 ± 0.92	11.29 (M)
28	50.06	49.17	768	704	107.32 ± 17.87	2.19 ± 0.40	13.66 (M)
29	35.88	35.25	1719	1576	240.33 ± 40.19	6.86 ± 1.27	12.29 (F)
31	46.09	45.26	1066	981	149.53 ± 24.92	3.32 ± 0.61	8.34 (F)
32	59.00	57.90	1498	1364	207.97 ± 35.31	3.61 ± 0.67	11.08 (F)
33	112.36	110.24	1251	1148	174.95 ± 28.94	1.60 ± 0.29	8.76 (F)
34	89.51	87.86	1410	1295	197.46 ± 33.31	2.26 ± 0.42	11.76 (M)
36	130.43	128.11	3844	3557	542.17 ± 92.39	4.26 ± 0.80	7.17 (F)
37	193.83	190.14	2072	1909	291.04 ± 48.96	1.54 ± 0.29	7.18 (M)
40	185.52	182.25	1600	1469	224.00 ± 38.24	1.24 ± 0.23	8.02 (M)

The deviation of individual mothers foraging efficiency from average foraging efficiency was positively correlated to the deviation of individual pups mass to average mass at weaning (p = 0.0078, R^2= 0.41, Figure 5.5). The relationship in which the foraging efficiency of mothers was corrected for their size (mass-specific foraging efficiency) was also positive and significant (p = 0.02), but did not explain as much of the variation in the data (R^2 = 0.29). Relative body condition of the pups (as expressed by the deviations compared to the sex specific average mass at weaning), was however negatively correlated to the number of hours females spent diving at sea (p = 0.0067, R^2 = 0.36) and positively related to rate of energy gain per min of diving in kJ/min (p = 0.0050, R^2 = 0.49, Figure 5.6). The relationship was also significant with foraging trip duration, but was not as tight (p = 0.0166, R^2 = 0.28).

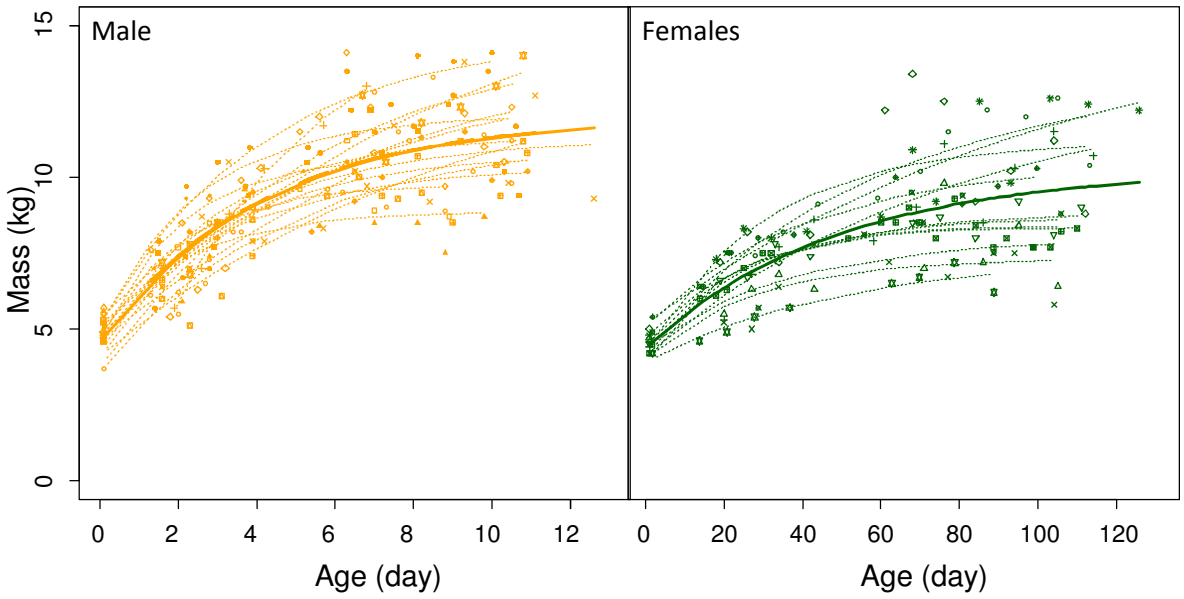

Figure 5.4: Growth of 36 individual Antarctic fur seal pups (n = 23 for males and n = 13 for females) from birth to weaning on Pointe Suzanne colony, Kerguelen Island in the breeding season 2012. Twenty of these pups belonged to mothers I tracked at sea. Dashed lines represent Von Bertalanffy growth curves fitted over individual pups during the nursing season and the solid lines are the average growth curve for all the pup of each sex. Plotting symbols are unique to individual pups).

Table 5.3: Standardized regression coefficients (SRC), minimum and maximum 95% confidence interval, bias and standard error (SE) of the sensitivity analysis on the calculated foraging efficiency from energy expenditure at sea (EE in MJ), prey capture attempts (PrCA), mass (g), energy density (ED in kJ/g) and relative proportion in the diet (Prop.) of myctophids (Myct.) and cephalopods (Ceph.). I omitted prey groups with SRC below 0.1 in the table.

Parameters	SRC	Min 95%CI	Max 95%CI	Bias	SE
EE	-0.576	-0.586	-0.564	0.000	0.006
PrCA	0.687	0.675	0.697	0.001	0.006
Myct. Mass	0.332	0.320	0.341	0.001	0.005
Myct. ED	0.103	0.094	0.111	0.001	0.004
Myct. Prop.	0.050	0.041	0.058	0.000	0.004
Ceph. Mass	0.221	0.211	0.229	0.000	0.005
Ceph. ED	0.145	0.135	0.154	-0.001	0.005
Ceph. Prop.	0.166	0.157	0.174	0.000	0.004

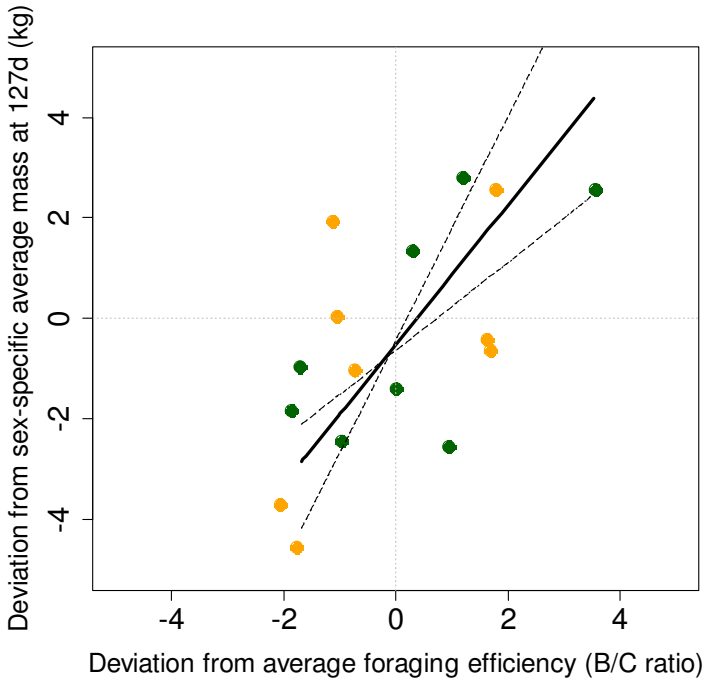

Figure 5.5: Deviation of individual Antarctic fur seal pup mass at weaning from average pup mass at weaning as a function of the deviation of foraging efficiency of individual pup's mothers from the average mothers foraging efficiency over one foraging trip during the 2012 breeding season on Kerguelen Island. Orange dots are male pups and green dots are female pups. Solid lines show the type II linear regression output (Y = 1.38 X - 0.51, p = 0.0078, R^2 = 0.41, n = 15. Spearman rank correlation rho = 0.62, p = 0.032.)

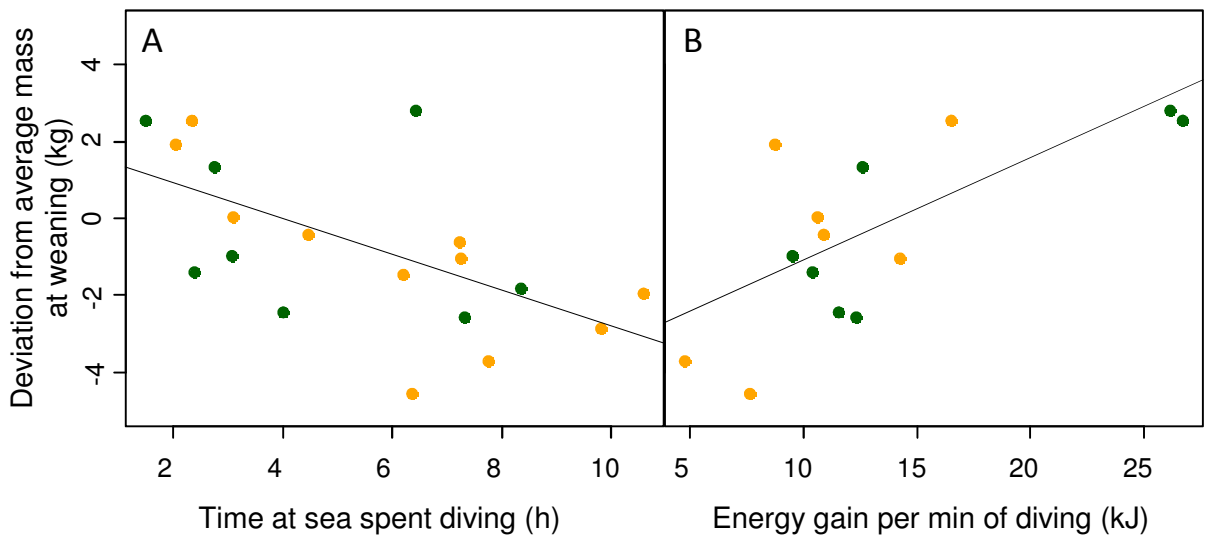

Figure 5.6: Relationship between relative mass of pups at weaning (calculated as deviation from mass-specific average pup mass at weaning) and time mothers spent diving during their foraging trip at sea in h (graph A, p = 0.0067, R^2 = 0.36), and energy gain per min spent diving (Graph B, p = 0.0050, R^2 = 0.49). Time at sea was also linked to pup mass at weaning (p = 0.0166, R^2 = 0.28).

5.5 Discussion

I calculated foraging efficiencies of individual females from quantitative measures of at-sea energy expenditure and energy gained while foraging, and linked this to time-activity budgets and pup growth as an index of reproductive success. Foraging efficiencies differed between individuals irrespective of their time-activity budgets. Most notably, individuals generally attained high foraging efficiencies by increasing their rate of prey capture attempts rather than by decreasing the energy they expended at sea. Pups of females that were relatively more efficient at foraging were bigger than average at weaning, which implies that pup growth rates reflect the quality of their mothers as foragers. This direct link between individual efficiencies at foraging and reproduction success via maternal investment provides empirical support for the Optimal Foraging Theory.

5.5.1 Estimation of foraging efficiency (FE)

Antarctic fur seal females gained more energy on average than they spent during their foraging trips at sea (all ratios > 1) with an average FE of 3.4. This value was much lower than the gain/cost ratio of 23 calculated for northern fur seals (Costa, 1993) or 20 for semi-captive Steller sea lions foraging on simulated high-density patches (Goundie et al., 2015). The differences reflect a much greater rate of energy gain of 406 kJ/min of diving for northern fur seals or ~ 438 kJ/min for Steller sea lions compared to my estimate ~131 ± 16 kJ/min for Antarctic fur seals. My results are more consistent with foraging efficiencies calculated for northern elephant seals (FE of 4), California sea lions (FE of 4 and energy gain of 112 kJ/min) and the same semi-captive Steller sea lions feeding on a simulated low prey-density patch ~ 206 kJ/min (Costa, 1993; Goundie et al., 2015).

This 6-fold difference between different calculated foraging efficiencies shows that either changes or errors in estimating costs or gains of foraging can greatly affect the final results. Costa (1993) estimated foraging benefit from water influx using H and O stable isotopes, which can overestimate prey ingestion (Nagy and Costa, 1980), and did not provide information on what type of prey was ingested (they estimated a diet of squids) or their size. Steller sea lions in the Goundie et al. (2015) study were also trained to dive at specific depths and wait to obtain prey via a feeding tube. Energetic costs and gains were controlled and were thus accurately measured, but energy spent by these animals was most probably significantly less compared to wild counterparts that must search for their food. It is thus important to identify and estimate sources of uncertainties around the results of foraging efficiency values.

Foraging efficiency was estimated from foraging costs (using the DLW method) and from foraging success (energy gain) on free-ranging animals by combining the number of prey capture attempts at sea with an estimation of diet composition, mass, and energy density of prey from scats and from previously published data. Each of these parameters have inherent errors. For example, the DLW method is known to be accurate at the population level, but to either over- or under-estimate metabolic rate at the individual level (Sparling et al., 2008; Dalton et al., 2014b). As I calculated FE individually for each female, the low precision could have affected my final results.

Estimation of diet composition from scat hard-parts is also biased by differential digestion and retention rates depending on prey consumed and on meal sizes, and by the fact that it represents only the last 48 h before the seals come back to land (where the scat is collected). It is also limited by the assumptions underlying the presence-absence methods of calculating relative proportion of prey in the diet (SSFO) (Bigg and Fawcett, 1985; Jobling and Breiby, 1986; Olesiuk et al., 1990; Harvey and Antonelis, 1994; Tollit et al., 1997; Bowen, 2000; Arim and Naya, 2003; Gudmundson et al., 2006). The degree of digestion of different hard parts also incorporate errors in the estimation of prey mass from size of fish otoliths, squid beaks or other hard parts (Tollit et al., 1997; Bowen, 2000). It is known that fish energy density varies by age, season and year (Anthony et al., 2000; Vollenweider et al., 2011) but I used a fixed value in my estimates.

Finally, detection of prey capture attempts from acceleration has been used for several species of top marine predators (Skinner et al., 2009; Suzuki et al., 2009; Viviant et al., 2010; Watanabe and Takahashi, 2013; Ydesen et al., 2014). However, validation studies on captive or free-ranging otariids using cameras simultaneously to accelerometers showed that the accuracy of head acceleration to detect PrCA depends on animal behaviours, type of foraging (benthic versus pelagic) and on type/size of prey ingested (Viviant et al., 2010; Volpov et al., 2015).

I accounted for these aforementioned errors as much as possible by using correction factors when available or by including uncertainties in the final calculations (see Material and Method section). The sensitivity analyses performed over the final estimates of foraging efficiency revealed that errors associated with prey capture attempts affected the final result the most. This is not surprising given that different validation studies did not consistently agree on their detection and false positive rates (Viviant et al., 2010; Volpov et al., 2015), and provided overall wide ranges that were incorporated into my calculations. Errors associated with mass of the prey affects FE more than energy density or relative proportion of prey in the diet, at least given the errors I estimated from the bootstrap method. Ultimately, all parameters related to foraging success tended to overestimate foraging efficiency, but this was partially compensated by the error associated with the doubly-labeled water method, which affects the final estimate in the opposite direction. Thus, it is not

surprising that errors in foraging success affected the final foraging efficiency more than errors in cost given the larger number of parameters needed to calculate it. Consequently, I advise giving greater care to estimating parameters related to energy gain given the overall higher risk of error around foraging success compared to foraging expenditure.

5.5.2 Foraging efficiency and pup growth

Despite all the sources of uncertainties listed above, foraging efficiencies of Antarctic fur seal females were positively related to the relative body size of their pups at weaning (Figure 5.5). Thus, foraging efficiency reflected maternal investment in the pup, or the extra energy available to allocate to reproduction (even though all energy available might not all be allocated to reproduction, Fedak et al., 1996). It is also important to remember that I measured foraging efficiency over a single foraging trip and that I compared it to overall growth of pups over the entire nursing season until weaning. The fact that the relationship between quality of mothers as foragers and the pup size at weaning is still significant therefore suggests 1) that it is extremely robust, and 2) that individual females were consistently good or poor foragers throughout the breeding season.

The mass of pups at weaning has been shown for a number of species to correlate to its chances of surviving the first year at sea (Doidge and Croxall, 1989; Baker and Fowler, 1992; Boltnev et al., 1998; McMahon et al., 2000; Hall et al., 2001; Beauplet et al., 2005), and thus by extension to fitness of mothers. Consequently, the robustness of the relationship between mother's foraging efficiency and its pup growth provides grounds for the optimal foraging theory. Fitness of an animal in its evolutionary sense should be assessed over its lifetime, but I only looked at the link between foraging efficiency and an index of reproductive success over one single reproduction cycle. I am aware that one reproduction cycle might not reflect lifetime fitness as individuals make trade-offs between reproduction and survival over their lifetime (Boyd et al., 1995a), but parents are usually consistent in their quality as foragers over years with few individuals producing a large portion of the next generations in top marine predators (Pomeroy et al., 1999; Beauplet et al., 2006; Lescroël et al., 2010). Consequently, if I apply these findings to this study, fur seal females that were

better foragers during the breeding season would consistently produce bigger pups more capable of surviving their first year at sea.

5.5.3 Effect of time-activity budget

It is difficult to assess which behaviours are 'optimal' because the mechanisms by which an animal can 'optimize' them are unclear. It is also unlikely that animals consciously behave to optimise energy gain per unit of energy expended at all time. In any case, flexibility in strategies reflects individual variability and the wide ranges of their adaptive behaviours to environmental conditions, food availability and accessibility. Fur seal females typically display this wide variation in foraging behaviours and time-activity budget at sea (Guinet et al., 2001; Lea et al., 2002b). In my study, foraging trip duration ranged from 2.5 to 15.5 days, distance traveled 225 to 1295 km, and time spent diving or transiting from 22 to 34 % or 15 to 43 % of their foraging trip. These are within the ranges of previously reported values (Gentry and Kooyman, 1986; Lea et al., 2002b; Bailleul et al., 2005), but translate into a 7 - 8-fold difference between the minima of 15-16 h to the maxima of 105 - 125 h allocated to different activities between individuals.

Given the difference in metabolic rates associated with different types of activities (Chapter 2), time activity budgets would be expected to affect the foraging efficiency. However, I found no statistical relationships between foraging efficiency and time at sea or with any metrics of time-activity budgets, which indicates that quality of females depended more on individual capacities rather than on time spent performing different activities at sea. The more efficient females in my study attained greater foraging efficiencies by having a greater rate of energy gain per min of dive time rather than by reducing their energy expenditure (which translated into rate of energy gained per min also being positively related to rate of pup growth). Females that were better at extracting food from their environment during dive time irrespective of energy costs produced bigger pups at weaning. This provides a direct quantitative linkage between the quality of females as foragers (*i.e.,*at catching prey per unit of time spent diving), and their quality as breeders.

Although time activity budgets did not directly affect foraging efficiency, it did impact pup growth rates. Most notably, females that spent less time diving during their

foraging trips and less time foraging produced relatively bigger pups at weaning. Foraging trip duration is a common measure of foraging effort in fur seals (Costa et al. 1991, Francis et al. 1998, McCafferty et al. 1998, Georges & Guinet 2000). In my study as in others (Lunn et al., 1993), foraging trip duration was negatively related to relative pup mass at weaning, although the relationship I found was not as strong as with foraging efficiency, time spent diving, and rate of energy gain while diving (which were overall all better indexes of pup growth rates). It is interesting to note that trip duration (or time spent diving at sea) and foraging efficiency (or rate of energy gained while diving) were both linked to pup growth—but that trip duration or time diving were not related to foraging efficiency. This suggests that the two currencies that shape maternal investment in offspring and thus pup growth (*i.e.,*time and energy currencies) might operate independently in some individuals. It also suggests that time and energy are important currencies for maternal investment in terms of diving (time spent diving and rate of energy gained while diving) and overall trip duration (foraging efficiency and time at sea).

It is difficult to tease apart whether females spending less time at sea produce bigger pups because they feed their pups more frequently, or because they are more efficient foragers and return to land with greater energy overhead to allocate to feeding their pups, or both. In my case, foraging efficiency and feeding frequency (determined from trip duration) were both related to the size of pups at weaning, but foraging efficiency was a more accurate predictor. Marine mammals with a high maternal investment such as otariids are thought to optimize the frequency of feeding their offspring rather than their foraging efficiency to increase their success as reproducers (Costa, 1993; Boyd, 1999), but both could be confounding factors that relate to the quality of individuals in terms of efficiency at acquiring prey.

The time that mothers allocate to different activities while foraging varies with resource availability (Gentry and Kooyman, 1986; Trillmich and Ono, 1991). Antarctic fur seals, like all otariids, have an expensive reproductive system (Costa, 1991). Northern fur seal mothers consume 80% more food than non-lactating females (Perez and Mooney, 1986), and lactating Steller sea lions consume 70% more (Winship et al., 2002). The high energy requirements of lactation can likely only be sustained in highly productive areas with

concentrated and predictable high-energy content prey (Costa, 1993; Boyd et al., 1995a). This also means that lactating fur seals operate closer to their metabolic ceiling and might be physiologically and behaviourally limited in their capacities to adapt to drastic changes in environmental conditions (Costa et al., 1989; Costa, 2007). This is consistent with the females in my study attaining higher foraging efficiencies by increasing their rate of energy gain rather than by decreasing their energy expenditure.

5.5.4 Effect of phenotypic traits

Phenotypic traits that facilitate foraging efficiency should increase fitness of the animals if the efficiency with which mothers capture prey is the ultimate determinant of weaning mass and pup survival. Bigger females or females with better body conditions are thought to be better foragers, as they can dive aerobically for longer (have a higher ADL, Kooyman, 1989) and might be better able to buffer the cost of lactation through higher energy stores (Iverson et al., 1993). Foraging efficiency has been routinely estimated by measuring foraging success through changes in body mass during foraging trip (Gentry and Kooyman, 1986; Lea et al., 2006; Luque et al., 2007). However, the foraging efficiency values I found were not related to body mass, changes in body mass, or changes in body condition indices during their foraging trips. It is well known that female mass fluctuates during nursing bouts (Gentry and Kooyman, 1986; Arnould, 1997), but I could neither control for, nor estimate, how long the females had been on land with their pups prior to capture. Consequently, my measures of female body masses were not standardized, which probably skewed my results and explains why foraging efficiency was not related to mass metrics. Mass of female fur seals is also related to age (which was unknown in my study) and thus experience. Foraging efficiency is thought by some to increase with time as young and small females gain body mass and experience (Lunn et al., 1994).

The fact that mass-related metrics did not relate to foraging efficiency could also indicate different strategies in energy allocation between different essential physiological functions for females. Fur seals are income breeders, which means that they do not accumulate and store all the energy they need to provide their pups prior to the breeding season, but rather rely on energy obtained during frequent foraging trips within the nursing

season (Boyd, 2000). In this case, animals have to determine energetic priorities between conflicting functions such as growth, maintenance, and reproduction during the breeding season itself. The uncoupling I observed between changes in body mass and foraging efficiency might indicate that some females compromised the growth of their pups to the benefit of their own physiological functions, or that some females might actually supplement the energy they acquire from foraging trips with limited body reserves, while others do not. This is for example the case of Blue petrels (*Halobaena caerulea*) which alternate long trips to replenish their reserves with shorter trips close to the nest to feed their chick during which they lose mass (Weimerskirch et al. 2003).

The lack of a relationship between the mass of females and their foraging efficiency is consistent with previous studies of Antarctic fur seals performed during years with favorable environmental conditions (Boyd et al., 1991; Lea et al., 2006). It indicates that 2011 was not a particularly challenging year for lactating fur seals. However, while maternal size did not contribute to differences in foraging efficiency between individuals in years of high food availability, it did positively influence pup growth rates during years of bad environmental conditions (McCafferty et al., 1998; Lea et al., 2006). This means that the physical advantages of larger females—that are probably older and more experienced—makes a difference during years when environmental conditions are poor (Lunn et al., 1994; Lea et al., 2006) because accessibility of prey is likely to be more challenging and females are more likely to be foraging closer to their metabolic limits (Boyd, 1999; Costa, 2007). A similar conclusion has been drawn for Adélie penguins (Lescroël et al., 2010) for which better foragers only held a reproductive advantage during challenging years. On the other hand, foraging costs become greater for individuals of larger size during years with normal conditions (Massardier-Galatà et al., In review). Consequently, the evolutionary pressure dictated by optimal foraging theory might select specific heritable phenotypic traits such as size, but the fact that these phenotypic traits might only become an advantage during years of challenging conditions could explain why there is so much variability in the population.

5.5.5 Conclusions

My results show that quantitative measures of maternal foraging efficiencies and offspring growth rates in free-ranging marine mammals provided empirical support for the optimal foraging theory. Direct energetic links between maternal investment and maternal foraging behaviours and efficiencies can help infer the fitness of individuals and the dynamics of populations. My findings further provide a quantitative energy-based framework to investigate and model the impacts of hypothetical and forecasted environmental and prey-related changes on the behaviours, and energetic costs and benefits of foraging by individual animals.

Chapter 6: Lactating females in a declining population of northern fur seals compromise either on foraging efficiency or pup feeding rates during the breeding season

6.1 Summary

Understanding the efficiency (energy gain/cost ratio) of foraging can shed light on how animals cope with environmental changes and how such changes affect population trajectories. I determined the foraging efficiency (energy gained to energy spent ratio) of foraging trips made by lactating females from a declining population of northern fur seals (*Callorhinus ursinus*) breeding on St. Paul Island in the Bering Sea to gain insights into why they are declining. I captured and equipped 20 females with tags that recorded GPS locations, depth and triaxial acceleration to determine at-sea foraging behaviours and detailed time-activity budgets. Energy expenditure for each foraging trip (the cost) was measured using the doubly-labeled water method—while the energy gained while foraging (the benefit) was measured by 1) determining the types and energy densities of prey consumed (based on scat remains and blood C and N stable isotopes), and by 2) estimating numbers of prey capture attempts from head acceleration data. I also collected milk samples from 10 of the tracked fur seals and randomly selected other pups three times during the breeding season to determine growth trajectories. The 20 tracked fur seals employed two foraging strategies. Eight of the females fed mostly on small high energy-density prey (5.75 ± 1.44 kJ/g or 194.64 ± 8.49 kJ/prey) in deep waters off the Bering Sea shelf—while the 12 others stayed on the relatively shallow Bering Sea shelf feeding mostly on larger fish of lower quality (3.89 ± 0.74 kJ/g or 324.47 ± 10.40 kJ/prey). Females foraging off the shelf made 3 times more prey capture attempts on average than females foraging on the shelf, which meant that off-shelf females had consistently greater foraging efficiency compared to on-shelf females (*i.e.,*benefit/cost = 1.44 ± 0.71 on shelf vs. 3.02 ± 0.60 off shelf). The females that fed in the Bering Sea basin obtained 1.61 – 5.27 more energy than they expended, but some of the

females that foraged over the shelf failed to meet their costs of obtaining prey. However, the on-shelf females that had the lower efficiencies also made comparatively shorter trips, which likely resulted in their pups being fed ~20% more frequently. Foraging strategies with lower efficiencies or with lower nursing rates meant that either lactating females reduced the available energy they transferred to their pups or they reduced the time they allocated to feeding them. Both options resulted in less overall energy being transferred to their offspring over a breeding season and would have resulted in pups attaining a lower mass at weaning and incurring higher mortality during their first year at sea. This need for lactating females to have to compromise on one or the other of these parameters provides an important clue into the decline of this population.

6.2 Introduction

A central concept in life-history theory is that organisms must optimally allocate resources between the competing demands of reproduction, body maintenance, and growth in order to maximize survival and reproductive success. Changes in environmental conditions that result in sub-optimal energy intake will likely result in animals modifying how they allocate energy. In long-lived animals, self-maintenance has priority over reproduction because fitness, and lifetime reproductive success depend on longevity Bouten et al. (1994). Hence, reductions in energy intake or foraging efficiency are expected to affect breeding performances before it affects the adult survival. However, the extent to which reproduction is impaired by food availability depends in part on the flexibility and capacity of animals to acquire energy (foraging efficiency) and allocate it (physiological plasticity). Consequently, how well an animal adjusts to localized environmental changes and the availability and distribution of prey will determine its body condition, fitness and capacity to survive and successfully reproduce.

Northern fur seals breeding in the central Bering Sea have been declining by 6% per year for the last 10-15 years (Towell et al., 2006), as have other top predators in this area (Wanless et al., 2005). Female fur seals sustain high energy output while nursing their pups for 4 months by making frequent foraging trips. The breeding season is a crucial period in the life history of otariids when foraging success of mothers determines the quantity of

energy available to transfer to their pups and ensure their survival (Reid and Forcada, 2005). Marine predators such as otariids utilise areas of high productivity that are linked to higher and more predictable prey concentrations (Costa, 1993).

In the Bering Sea, major environmental changes starting in the mid-1970s altered the distribution and relative abundances of different species of fish (Anderson et al., 1997; Anderson and Piatt, 1999). The main prey available to top marine predators in the Bering Sea switched from mainly high energy fish to mainly low energy-density prey (Trites et al., 2007; Sinclair et al., 2008). Free-ranging predators usually buffer changes in the availability of prey by changing their foraging areas. However, northern fur seals are limited in where they can search by the fasting constraints of their young. They are also limited by time to optimise their foraging and provide enough energy to their pups before they abruptly wean. As a consequence, localized oceanographic variations within the foraging range of northern fur seals during the breeding season likely affect foraging success of fur seals and the rearing of their pups.

When faced with environmental changes, animals have to employ strategies that balance the energetic costs and time spent foraging, against the potential energy gained from prey. Foraging efficiency is the difference between the energy gained through prey intake and the energy spent to extract the prey from the environment. Estimating foraging efficiency requires that foraging costs and energy obtained be measured at the same time. Unfortunately, foraging efficiency has not been traditionally measured, but has rather been only inferred by comparing the change in mass before and after a foraging trip (Gentry and Kooyman, 1986; Lea et al., 2006; Luque et al., 2007), which is insufficient (Insley, 2008).

The foraging efficiency of lactating fur seals may have declined and reduced the fitness (i.e. reproductive success) of the breeding females in the central Bering Sea compared to pre-1970s. If so, it may explain the declining population trend of northern fur seals. There is therefore a need to determine, at the finest scale possible, the foraging and feeding behaviours of individual fur seals to accurately link specific environmental parameters, fitness, and demographic parameters. It is rare that both sides of the 'efficiency equation' have been studied on same individuals (Costa, 1993). Estimation of field metabolic rate (FMR) with the doubly-labelled water (DLW) method was validated for pinnipeds

(Speakman, 1997; Butler et al., 2004; Sparling et al., 2008) but only seldom used on northern fur seals since the 1980s on very few animals (Costa and Gentry, 1986; Costa, 1987). Feeding success, or the energy gained while foraging, is more difficult to measure. Proxies for feeding success such as changes in mass and body composition, changes in buoyancy during drift dives, changes in stomach temperatures, transit rate, dive shape and bout structures have all been tried and validated to some extent on marine predators under certain conditions (Hindell et al., 2010), but none of these techniques provide a quantitative measure of energy gain. The development of high sampling rate of multiple channels and the use of tri-axial accelerometers can provide indices of prey capture attempts which when paired with an estimate of diet composition can provide a quantitative estimate of energy gained during a feeding trip. Together with measures of foraging effort, foraging efficiency of individuals can be calculated.

Comparing foraging efficiencies relative to foraging strategies can further shed light on the trade-offs animals make between spending and gaining energy. It is these trade-offs that likely impact the energy reserves that mothers have to feed their pups, which in turn influences their chances of surviving their first year at sea (Doidge and Croxall, 1989; Baker and Fowler, 1992; Boltnev et al., 1998; McMahon et al., 2000; Hall et al., 2001; Beauplet et al., 2005). In this context, the objectives of my study were to 1) determine the foraging strategies of lactating northern fur seals, including locations, diving patterns and targeted prey, 2) measure foraging efficiency (foraging gain/cost ratio) and determine how it relates to foraging strategy, and 3) assess how different foraging strategies and efficiencies might be related to reproductive success and the declining trend of the fur seal population breeding in the central Bering Sea.

6.3 Material and methods

6.3.1 Data collection

Data were collected from 20 healthy lactating northern fur seals at Reef rookery on St. Paul Island (Bering Sea, 57° 6 ‘N - 170°17’ W) during the breeding season (Aug-Sep

2011) under US NMFS permit # 14329-01 and UBC animal care permit # A10-0364. Data collection procedures were similar to those reported for Antarctic fur seals in Chapter 5.

6.3.2 Energy expenditure, foraging behaviours and prey capture attempts

Analyses and calculations of the energy expenditure, foraging behaviours and prey capture attempts were done as per Chapter 5. In brief, measurements of daily energy expenditure (DEE, kJ/day) were performed using the DLW method (Lifson and McClintock, 1966; Butler et al., 2004). Energy spent during the 'non-foraging' time was corrected by subtracting on-land energy expenditure from the total estimate using previously determined values specifically for lactating northern fur seals (4.67 W/kg, Chapter 5 in Gentry and Kooyman, 1986). The females were also equipped with Daily Diary tags (DD, Wildlife Computers) recording tri-axial acceleration and tri-axial magnetic field at 16 Hz, and depth, light level, and water temperature at 1 Hz and Fastloc GPS MK10 loggers (Wildlife Computers) recorded GPS coordinates along the track of the animal at sea, as well as depth and water temperature at 1 Hz. Finally, GCDC X6 or X8 accelerometers glued on the head of the animals recorded tri-axial acceleration at 16 or 20 Hz. Prey capture attempts (PrCA) were measured while the animal was diving below 3 m using acceleration data recorded on the head of the animals (Skinner et al., 2009; Suzuki et al., 2009; Viviant et al., 2010; Watanabe and Takahashi, 2013; Ydesen et al., 2014).

Statistical differences between groups (fur seals that stayed and fed over the continental shelf vs. those that travelled off the shelf) were tested with two-sample *t*-tests ($\alpha = 0.05$) or Mann-Whitney tests depending on normality. Averages for dive parameters, such as for dive depths and dive durations, were nested within animals and were calculated using linear mixed effect models with no fixed effects (only the intercept was calculated) and with individual as a random effect to account for each animal performing a different number of dives. Differences between prey capture attempts per night or per dives between on-shelf and off-shelf groups were estimated using linear mixed effect models with group (on-shelf or off-shelf) as the fixed effect, and individual as a random effect to account for intrinsic behavioural characteristics of each animal and for their difference in trip duration.

6.3.3 Diet estimates

The female northern fur seals breeding on Reef Rookery had two diets that differed depending on whether they feed on-shelf or off-shelf (see Chapter 4). I applied these two diets to the respective foraging strategies of the individuals tracked, and used hard part remains recovered in fecal samples collected at Reef rookery in 2011 to determine size of prey consumed and estimate energy density of the two diet types. I also relied on hard parts recovered from scats collected at Bogoslof Island in 2009 as a proxy for diets of fur seals that feed off-shelf (see Trites et al. 2015). This method is less accurate than DNA-based methods, but is the only method that provides indication of prey size. As I only have DNA-based results for the scats collected on St. Paul Island, working with hard part remains only allows results to be standardized between the estimated on-shelf and off-shelf diets (consistency of methods and associated biases). Consequently, females foraging on the shelf were considered to feed on a diet with a composition estimated from the scats I collected on Reef rookery in 2011 while the females foraging off the shelf were assumed to feed on a diet similar to the one estimated on Bogoslof island in 2009 (Chapter 4, Trites et al., 2015).

I first estimated the energy densities of the different diets using the relative proportion of prey items in each diet and the energy densities of the different species from the literature (Perez, 1994; Van Pelt et al., 1997; Paul and Paul, 1999; Logerwell and Christiansen; Iverson et al., 2002; Gende et al., 2004; Andrews et al., 2009; Whitman, 2010; Vollenweider et al., 2011). Energy density of walleye pollock differs by age class (Paul and Paul, 1999), so I obtained the overall energy density of pollock (85% of age-0 at 3.36 kJ/g and 15% of age-1+ at 4.73 kJ/g, Whitman, 2010) by accounting for the proportion of each age class in the diet (from their size, see below). Salmonids were not identified at the species level from hard part remains, so I averaged the energy density of several species found in Alaskan water (Hendry and Berg, 1999; Anthony et al., 2000; Rosen and Trites, 2000; Gende et al., 2004) weighted by the proportion of different species identified though the DNA meta-barcoding method (Chapter 4). Energy density of squids in the Eastern Bering Sea vary by region (Whitman, 2010). Squids caught in the shelf slope area have a higher average total energy density than both squids in the middle and the outer shelf areas. However, specific values were not available by region, so I considered squids to have the same average energy

density wherever the fur seals fed. I estimated the variation in these parameters by reporting ranges of prey body mass and ranges of published energy density values (min and max values calculated as mean ± SD).

Whenever information was missing for prey with low frequencies of occurrence in the diet, I replaced it by energy density of the closest related prey item or by the average of the energy content for the specific prey group. I obtained energy density in diet (ED_{Diet}) by averaging the energy density of different prey (ED_i) weighted by their proportion within the diet (P_i) over the number of prey in the diet N:

Eq. 6.1
$$ED_{Diet} = \frac{\sum(ED_i \times P_i)}{N}$$

The second step in estimating the energy densities of the two diets was to estimate the gross energy intake in kJ for each prey ingested. I did this by estimating size of prey ingested using hard part remains in the collected scats. I relied on all identifiable bones to estimate number of prey items in each scat, but only used unbroken otoliths in good or fair condition to estimate fish length (Tollit et al., 2004). Lengths of otoliths were measured using the method described in Harvey et al. (2000), and correction factors were applied to these measured lengths to account for digestion whenever a species-specific correction factors were available (Tollit et al., 2004) (*i.e.,*1.1691 for Atka mackerel and 1.1593 for walleye pollock). Measured otoliths of the same size (± 0.1 mm) were paired and assumed to come from the same fish (Hunt Jr et al., 1980; Dragoo, 1991).

Squid beaks were measured using guidelines from Wolff (1984). Northern fur seals are known to mostly consume squids from the gonatid family (*Gonatopsis borealis and Berryteuthis magister*) in the Bering Sea, more so than other squids from the *Gonatus* genus (Gudmundson et al., 2006), but I did not identify squid beaks to the species level from hard part remains. I therefore referred to squids as gonatid squids and used the general size equation available for this family (Clarke, 1962; 1986). Squid beaks did not require a correction factor because there are much more resistant to digestion than bones (Tollit et al., 1997).

Fish otolith lengths (OL) or squid lower beak rostrum lengths (LRL) were converted to fish/squid length (FL) then body mass (BM) using the species-specific equations listed in

the Appendices section. For species of fish found in the scats that were identified by other hard parts than otoliths (vertebrae and gill rakers, etc.), the range of sizes was assessed by comparing the size of hard parts with those of reference skeleton from Pacific ID Inc.). These range of sizes are summarized in Table 1 and Figure 6 from Trites and Calkins (2008). I estimated average size ± SE of these species fish by simulating random selection of fish sizes from the range of sizes in each category using a uniform distribution (1000 simulations). For example, the hard part remains of salmon showed 55 % of them were between 16 and 24 cm, and 45 % were between 35 and 59 cm. I thus estimated that the average salmon would be 31.75 ± 0.14 cm (and thus determined an average mass of 797.78 ± 8.92 g from the length to mass conversion equation, see Appendices section) from the 1000 simulations. The same analysis was done for arrowtooth flounder, sand lance and rockfish.

Once the mass (*BM* in g) and the energy density (*ED* in kJ/g) of each prey item (*i*) were estimated, I calculated the average energy content of a specific fish (*EC* in kJ) as follows:

$$EC_i(kJ) = BM_i(g) \times ED_i(kJ/g)$$

The average energy content (in kJ) of a random non-specific prey (*p*) consumed by fur seals given a specific diet was calculated by weighting the energy content of a specific prey item by its relative proportion in the diet (*P*).

$$EC_p(kJ) = \sum_i (EC_i(kJ) \times P_i)$$

Means ± SD of energy content of each prey (EC_i in kJ) were calculated by generating 1000 values of mass and 1000 values of energy density (ED_i) using normal distributions of their respective means ± SD. Means ± SD of energy densities (ED_{Diet}), and energy content of an average prey (EC_p) in the two diets were calculated by generating values of EC_i and ED_i for each prey type (*i*) in proportion to their respective importance in the diet (P_i) out of 1000 values from normal distributions using their respective mean ± SD. For prey species with no ED_i or EC_i values, I used the average *ED* or *EC* from the prey group (e.g., gadid, cephalopod, etc.) as their values weighted by their own proportion within the diet. As the prey group 'Other' did not have values for mass or energy density, I considered it as an average of the rest of the diet weighted by its relative importance in the diet.

6.3.4 *Foraging efficiency*

The foraging efficiency (*FE*) of each seal (*i*) was calculated as in Chapter 6. In brief, *FE* is the ratio between the energy expenditure at sea obtained from the DLW measures (EE_i) per animal *i* and energy gained while foraging at sea. Energy gained was estimated as the specific energy content of a non-specific prey (EC_p) in their diet multiplied by the number of time seals *i* attempted to capture prey ($PrCA_i$):

Eq. 6.2 $$FE_i = \frac{EC_p \times PrCA_i}{EE_i}$$

I calculated uncertainty around FE_i using Monte Carlo simulations that reflected errors in the 3 equation parameters as described in Chapter 5.

I also used simple liner regression models to test whether mass, body condition (*i.e.,*mass/length ratio) or change in mass during the foraging trips were linked to foraging metrics such as time spent at sea, diving rate or rate of energy gain.

6.3.5 *Milk energy content*

Milk samples were opportunistically collected while females were under anaesthesia. I obtained milk in quantity sufficient for proximate composition analyses (> 3 ml) in only 10 of my 20 females (5 before their foraging trip and 5 after). After collection, milk samples were stored in the freezer at -20ºC until analyses. Proximate composition analyses were performed by SGS Canada Inc. Moisture, ash, protein and fat content of milk samples were measured using the AOAC 935.29, 942.05, 990.03, and 989.05 methods respectively. Energy density of milk samples were calculated using the Atwater method. Relationship between time at sea and milk fat content prior or after foraging trip and trip duration was estimated using simple linear regressions.

6.3.6 *Pup growth*

I captured the pups associated with the tracked females before the mothers left the rookery to forage, and took standard morphometric measurements of length and girth to the nearest 0.5 cm and ± 0.1 kg. Unfortunately, field conditions made it impossible to follow the growth of individual pups associated with each tracked mother. Consequently, I resorted to

capturing random pups on the colony as an index of pup growth over the breeding season. Eighty pups of both sexes were selected at random and morphometric measurements were taken 3 times over the course of the breeding season: between the 18th and the 21st of August 2011, between the 7th and the 10th of September 2011, and between the 20th and the 21st of September 2011.

Male and female pups were analysed separately as there were significant differences in mass between them (tested with a *t*-test), which is known in otariids (Mattlin, 1981; Kerley, 1985; Trites, 1993; Davis et al., 1996; Chambellant et al., 2003; Osman et al., 2010). A linear model was fit to my 2011 data for each sex individually, as well as to data from the 1980s on Bering Island ((Boltnev et al., 1998)), and from 1996 on St. Paul Island ((Donohue et al., 2000)). Differences in slopes between these models were estimated using a test for equality of regression coefficients (Paternoster et al., 1998). I estimated the significance of relationships between female mass, mass changes, and foraging efficiencies, and the relationships between pup parameters and mother parameters using linear regressions models.

6.4 Results

6.4.1 Foraging behaviours

Females breeding on Reef rookery, St. Paul Island, are known to disperse in all directions around St. Paul Island to forage (Gentry, 1998; Robson et al., 2004; Nordstrom et al., 2013). Eight females from the 20 tagged went foraging off the shelf in the deep basin of the Bering sea (up to 3000 m deep), hereafter called off-shelf females, and 12 stayed foraging on the shallow Bering Sea shelf (0 – 200 m deep), hereafter called on-shelf females (Figure 6.1). The females weighed on average 37.9 ± 1.34 kg prior to departure (range 30.8 - 55.6 kg, n = 20). Overall, 12 females gained mass (0.7 - 5.2 kg gained), and 8 of them lost mass during their foraging trip (0.2 - 4.2 kg lost). This corresponds to 3.5 ± 1.8 % of initial body mass (range from 9.9% lost to 16.1% gained, 3.2 ± 2.5 % for on-shelf females and 3.9 ± 2.7% for off-shelf females). Foraging trips lasted 7.96 ± 2.17 d (range 4.26 - 12.03 d) and average horizontal (surface) distance traveled was ~ 750 ± 50 km (range 391 - 1200 km).

Females foraging off the shelf spent on average 2.5 more days at sea during their foraging and traveled 200 km more than on-shelf females (off-shelf females: 9.7 ± 1.8 d and 892 ± 144 km; on-shelf females: 7.1 ± 2.4 d and 655 ± 218 km, $p < 0.009$, Figure 6.1, Table 6.1).

Females foraging on the shelf regularly performed benthic dives (15.2 ± 2.6 % of all dives) and occasionally foraged during the day, while females foraging off the shelf rarely performed benthic dives (2.2 ± 0.4 % of all dives and 0 % when off the shelf) and were nocturnal divers (Figure 5.3). Off-shelf females also performed significantly more foraging dives (3631 ± 313 dives) than the on-shelf females (1831 ± 374 dives, $p < 0.001$), but were shallower and of shorter duration (~ 17 ± 2 m deep and 37 ± 6 s duration for off-shelf females and ~ 27 ± 3 m deep and 80 ± 8 s duration for on-shelf females, $p < 0.05$). In addition, ~ 73% of off-shelf female dives were shallower than 15 m, while only ~ 55 % were for on-shelf females. This translated into on-shelf seals spending significantly more time diving (~ 33.1 ± 3.1 % of their time at depth + recovery period) and less time transiting (28.3 ± 2.3 % of their time with a moving speed $\geq$ 1m/sec) over the full foraging trip time scale than off-shelf females (24.7 ± 0.8 % of time diving and 32.0 ± 2.2 % of time transiting, both $p < 0.05$). In other words, females foraging off shelf travelled ~ 30 h more than on-shelf females, for the same number of hours spent diving (Figure 6.1, Table 6.1). Overall, body condition of females (mass/length) prior to foraging trip duration was negatively related to time at sea (slope $p = 0.004$, $R^2 = 0.38$, Figure 6.2).

6.4.2 Energetic cost of foraging

Rate of energy expenditure per day at sea was not significantly greater for females foraging on the shelf than foraging off the shelf whether mass-corrected or not (on-shelf: 22.1 ± 1.8 MJ/d or 0.56 ± 0.05 MJ/d/kg; off-shelf: 18.9 ± 2.4 MJ/d or 0.54 ± 0.07 MJ/d/kg, $p > 0.07$, Table 6.1, Table 6.1). When measured during a trip at sea in MJ or MJ/kg, females foraging off the shelf tended to spend more energy per trip (4.9 ± 0.8 MJ/kg) than females foraging on the shelf (3.7 ± 0.4 MJ/kg, although not statistically significant $p > 0.09$). However, females foraging off the shelf spent significantly more energy transiting to and from feeding grounds (1.6 ± 0.2 MJ/kg) than females foraging on the shelf (1.0 ± 0.2 MJ/kg,)

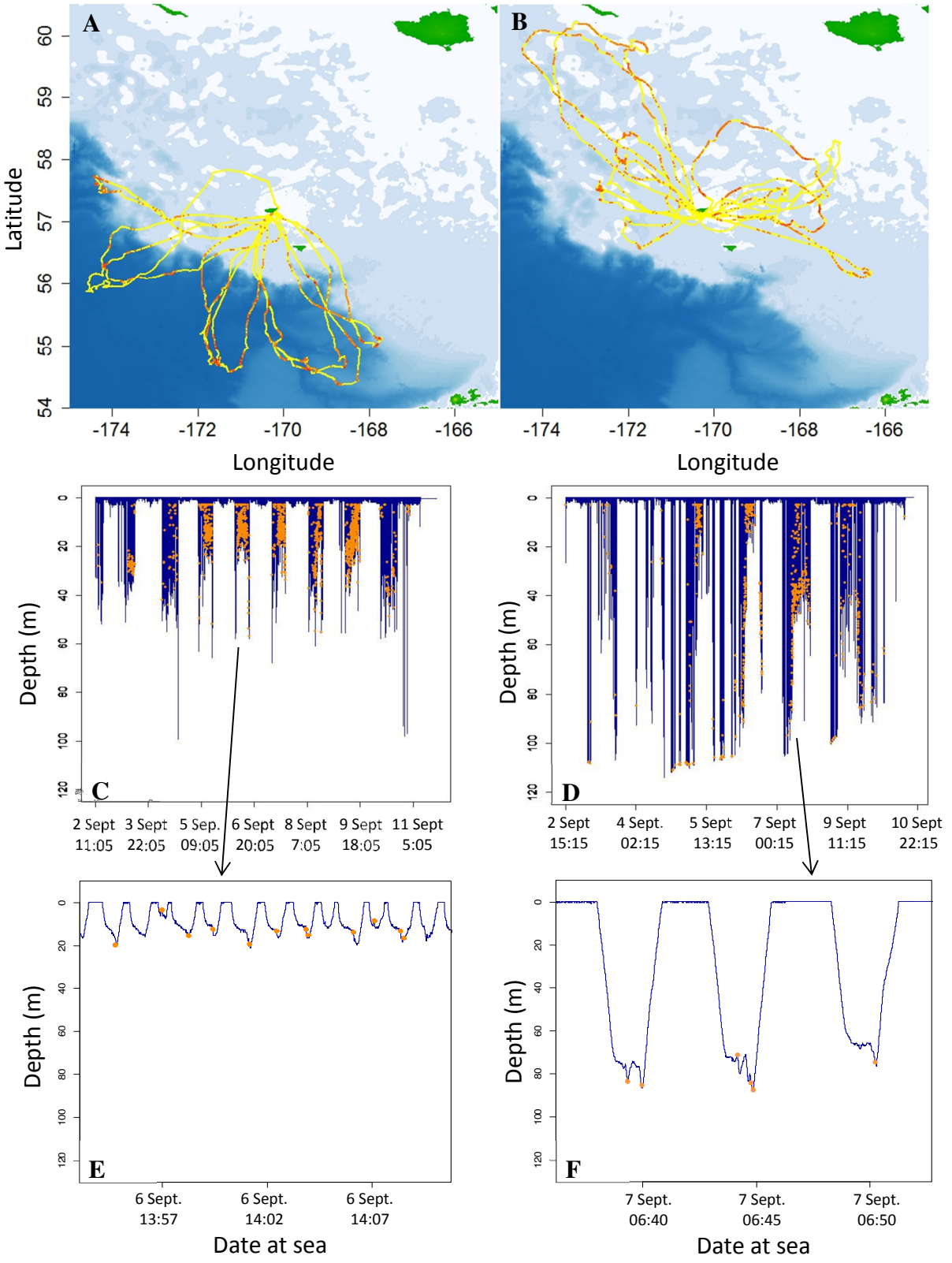

Figure 6.1: Foraging location, dive profiles over a full foraging trip, and over 5-min of diving of lactating northern fur seals from Reef rookery on St. Paul Island foraging off the shelf (n = 8, A, C, E) or on the shelf (n = 12, B, D, F) in the Bering Sea. Orange and red dots show where and when the animals attempted to capture prey within the range of their foraging location

(with yellow being no prey capture attempt, A and B), or during their dives (C, D, E, F). Females foraging off the shelf attempted to capture prey in limited and localised areas (A) while attempts to capture prey on the shelf occurred over a greater geographic area over longer periods each day (B). Females foraging on the shelf dove on average deeper and attempted to capture prey less frequently over similar periods (E, F, and partly during daytime) compared to females foraging off the shelf (C, E).

Table 6.1: Foraging and metabolic parameters of female northern fur seals (NFS) foraging on (n = 12) or off (n = 8) the Bering Sea shelf for one trip at sea. Values are mean ± SE, and letters in superscript indicate significant differences between the groups ($p > 0.05$). Values of similar parameters for Antarctic fur seal females (AFS) are added for comparison.

Parameters	On-Shelf NFS	Off-Shelf NFS	*AFS*
Mass (kg)	39.4 ± 2.0^{a}	35.7 ± 1.2^{a}	*31.1 ± 0.9^{b}*
Mass change (kg)	0.9 ± 0.9	1.4 ± 0.9	*0.6 ± 0.6*
Mass change (%)	3.2 ± 2.5	3.9 ± 2.7	*2.2 ± 1.8*
Trip duration (d)	7.1 ± 2.4^{a}	9.7 ± 1.8^{b}	*7.6 ± 3.8^{a}*
Distance traveled (km)	655 ± 63^{a}	892 ± 51^{b}	*635 ±77^{a}*
Dive number	1831 ± 374^{b}	3631 ± 313^{a}	*3949 ± 597^{a}*
Dive depth (m)	26.8 ± 3.3^{a}	16.9 ± 2.0^{b}	*19.9 ± 2.7^{a}*
Dive duration (s)	79.8 ± 8.5^{b}	37.3 ± 6.4^{a}	*42.6 ± 4.5^{a}*
Benthic dives (%)	15.2 ± 2.6^{b}	2.2 ± 0.4^{a}	*0 ± 0^{a}*
Time diving (%)	33.1 ± 3.1^{a}	24.7 ± 0.8^{b}	*29.0 ± 0.7^{a}*
Time transiting (%)	28.3 ± 2.3	32.0 ± 2.2	*26.4 ± 1.6*
Time diving (h)	55.8 ± 7.9	55.1 ± 3.5	*51.3 ± 5.9*
Time transiting (h)	49.0 ± 7.2^{a}	72.2 ± 7.8^{b}	*49.8 ± 7.9^{a}*
At-sea metabolic rate (MJ/d/kg)	0.56 ± 0.05	0.54 ± 0.07	*0.59 ± 0.04*
Total EE (MJ/kg)	3.7 ± 0.4	4.9 ± 0.8	*4.1 ± 0.6*
EE diving (MJ/kg)	2.0 ± 0.3	2.0 ± 0.2	*2.2 ± 0.3*
EE transiting (MJ/kg)	1.0 ± 0.2^{a}	1.6 ± 0.2^{b}	*1.3 ± 0.2^{ab}*
PrCA per dive	0.46 ± 0.09^{a}	0.76 ± 0.09^{b}	*0.87 ± 0.1^{b}*
PrCA per capturing dive	1.77 ± 0.23	1.75 ± 0.17	*2.04 ± 0.11*
PrCA per day	100 ± 26^{a}	275 ± 39^{b}	*336 ± 38^{b}*
PrCA per trip	789 ± 163^{a}	2404 ± 338^{b}	*2328 ± 387^{b}*
ED_{Diet} (kJ/g)	3.89 ± 0.74	5.75 ± 1.44	*7.75 ± 2.47*
EC_{Prey} (kJ)	324.47 ± 10.40	194.64 ± 8.49	*152.46 ± 1.08*
EGain per dive (kJ)	176.5 ± 48.9	188.3 ± 34.4	*177.7 ± 21.4*
EGain per time diving (kJ/min)	82.1 ± 16.3^{a}	145.9 ± 24.4^{b}	*130.6 ± 16.3^{b}*
EGain per time at sea (kJ/min)	24.9 ± 6.1^{a}	35.21 ± 5.4^{b}	*37.6 ± 4.6^{b}*
Foraging efficiency	1.44 ± 0.71^{a}	3.02 ± 0.60^{b}	*3.44 ± 0.45^{b}*

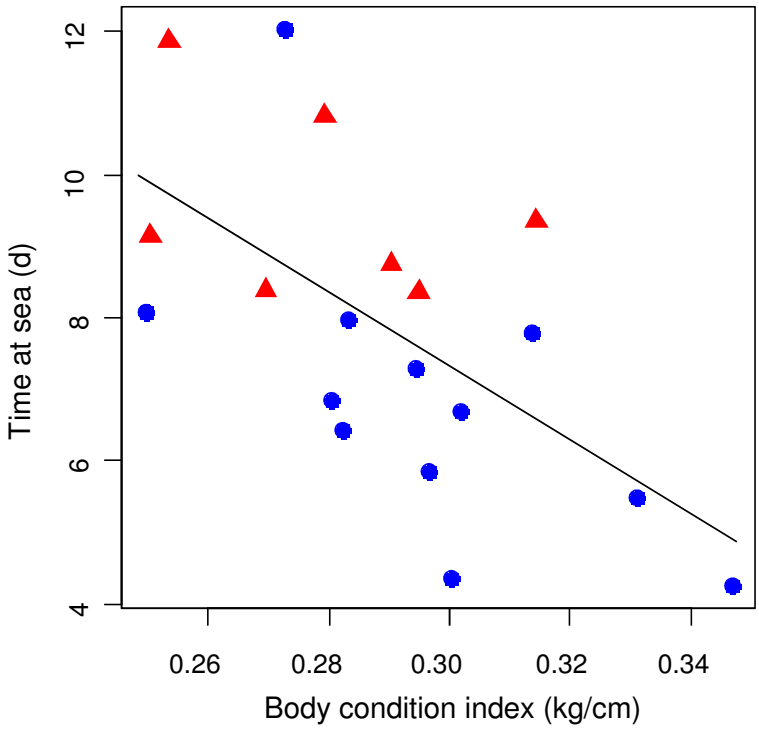

Figure 6.2: Time spent at sea by females during a foraging trip as a function of their body condition (mass/length in kg/cm) prior to the trip at sea (in days, n = 19). Red triangles are for females foraging off the shelf, blue circles are for females foraging on the shelf and the line is for the linear regression between the 2 parameters (slope $p = 0.004$, $R^2 = 0.38$).

6.4.3 Prey capture attempts

Females foraging off the shelf attempted to capture prey 0.76 ± 0.09 times per dive, which is greater than for females foraging on the shelf (0.46 ± 0.09, p = 0.004). However, when looking only at dives in which at least one PrCA occurred, both groups attempted to capture prey ~ 1.76 times per dive (1.77 ± 0.23 for females foraging on the shelf, and 1.75 ± 0.17 for females foraging off the shelf, $p = 0.73$). Females foraging on the shelf attempted to capture 100 ± 26 individual prey per day of foraging on average, which is equivalent to 789 ± 163 individuals per trip. This is ~3 times less than what females foraging off the shelf attempted to capture per day of foraging (275 ± 39 individual prey, $p = 0.24$) or per trip (2404 ± 338 individuals, $p = 0.003$, Figure 6.1graphs C, D, E & F). Most of the attempted prey captures occurred during nighttime (92.9 ± 2.9 % for on-shelf females and 99.0 ± 0.4 % for off-shelf females, $p = 0.05$). Visually, prey capture attempts for females foraging off the

shelf were localised to small and specific areas (orange and red dots, Figure 6.1 graph A), while females that foraged on-shelf had greater geographic and temporal spread in feeding areas (Figure 6.1 graph B).

6.4.4 Diet and prey energy contents

Relative proportion of species within the diets of females foraging on or off the shelf differed (Table 6.2). Females foraging on the shelf mostly consumed gadids (~70%), cephalopod (~12%) and salmon (~6%), while diets of females foraging on the shelf (based on scats collected at Bogoslof Island from Chapter 4 and Trites et al., 2015) consisted mostly of mesopelagic fish (~49%), cephalopods (~43%) and salmon (~4%).

Analyses of prey size from otoliths, beaks and other bone structures in the scats showed that adult female fur seals prey mostly on small fish (3 – 20 g). For example, size class of ingested pollock (Figure 6.3) were mostly of age 0 and 1-year-old. The only exception was salmonids which were ~ 31 cm long and weighed ~ 800 g. Energy density of each major fish species as taken from the literature ranged from ~ 3.5 kJ/g for flatfish and gadids to ~ 9 kJ/g for northern lampfish (Table A.5). Given size of ingested fish, this translates into energy content of prey groups ranging from 20 to 75 kJ, except for larger salmon that reached ~ 4500kJ (Table 6.2). Mass, energy density and energy content of individual prey species are detailed in Table A.5 in the Appendices section.

The total energy density of diet ED_{Diet} for females foraging on the shelf was ~3.89 ± 0.74 kJ/g. Salmonids and gadids contributed the most to the energy content per prey ingested EC_P, and averaged 324.47 ± 10.40 kJ per prey for females foraging on the shelf. The energy density of the diet ED_{Diet} for off-shelf females was greater than that of the on-shelf females at 5.75 ± 1.44 kJ/g. However, due to the smaller size of prey ingested, the energy content per prey ingested EC_P was only 194.64 ± 8.49 kJ (Table 6.2).

Table 6.2: Relative percent (%), average prey mass (g), prey energy density (ED in kJ/g), energy content (EC in kJ) of prey groups in diets of northern fur seal females breeding on St. Paul, and of females breeding on Bogoslof Island rookeries. Groups 'Other' were assigned average diet values. Percent in diet (SSFO%) were obtained from morphological identification of hard part remains in my study and from collection of samples of Bogoslof Island rookeries in 2009, and mass was calculated from the size of hard part remains.

	Prey group	SSFO (%)	Mass (g)	ED (kJ/g)	EC (kJ)
ON-SHELF NFS	Gadid	69.75	15.49 ± 0.13	3.51 ± 0.35	54.69 ± 0.14
	Cephalopod	12.28	3.74 ± 1.16	4.76 ± 0.11	17.79 ± 0.04
	Salmon	6.03	797.78 ± 35.65	5.53 ± 0.30	4425.00 ± 9.80
	Hexagrammid	3.64	18.67 ± 2.48	3.90 ± 0.23	75.19 ± 0.31
	Mesopelagic	2.42	3.87 ± 0.25	5.67 ± 0.25	21.91 ± 0.05
	Forage	1.53	10.69 ± 0.19	4.54 ± 0.66	49.61 ± 1.34
	Flatfish	0.28	3.78 ± 0.01	5.14 ± 0.65	19.45 ± 0.08
	Other	4.08	NA	NA	NA
OFF-SHELF NFS	Gadid	0.86	16.48 ± 0.11	3.57 ± 0.30	58.59 ± 0.20
	Cephalopod	42.70	3.74 ± 1.16	4.76 ± 0.11	17.79 ± 0.04
	Salmon	3.87	797.78 ± 282.00	5.53 ± 0.30	4425.00 ± 9.80
	Hexagrammid	0.60	18.69 ± 2.37	4.02 ± 0.08	75.19 ± 0.29
	Mesopelagic	48.97	3.77 ± 0.52	5.85 ± 0.88	21.68 ± 0.01
	Forage	1.55	16.47 ± 0.51	5.47 ± 0.57	92.28 ± 3.14
	Other	1.46	NA	NA	NA

6.4.5 Foraging efficiency

The calculated rates of energy gains were 176.5 ± 48.9 kJ/dive of females foraging on the shelf and 188.3 ± 34.4 kJ/dive for those foraging off the shelf (p = 0.78). This translates in 82.1 ± 16.3 kJ/min for on-shelf diving and 145.9 ± 24.4 kJ/min off-shelf diving. In terms of the entire foraging trip, females foraging on the shelf gained 24.9 ± 6.1 kJ per min spent at sea, which was lower than what females foraging off the shelf gained (35.21 ± 5.4 kJ per min spent at sea). Based on this, the average foraging efficiency of all individuals for which I had simultaneous measures of energy expenditure and prey capture attempts (Table 6.3) was 2.13 ± 0.44 and ranged from 0.42 - 5.68. Foraging efficiency was 1.44 ± 0.71 (range 0.83 - 3.05, 95% CI: 0.86 - 2.42) for females foraging on the shelf and 3.02 ± 0.60 (range 1.61 – 5.27, 95% CI: 2.17 - 4.02) for females foraging off the shelf.

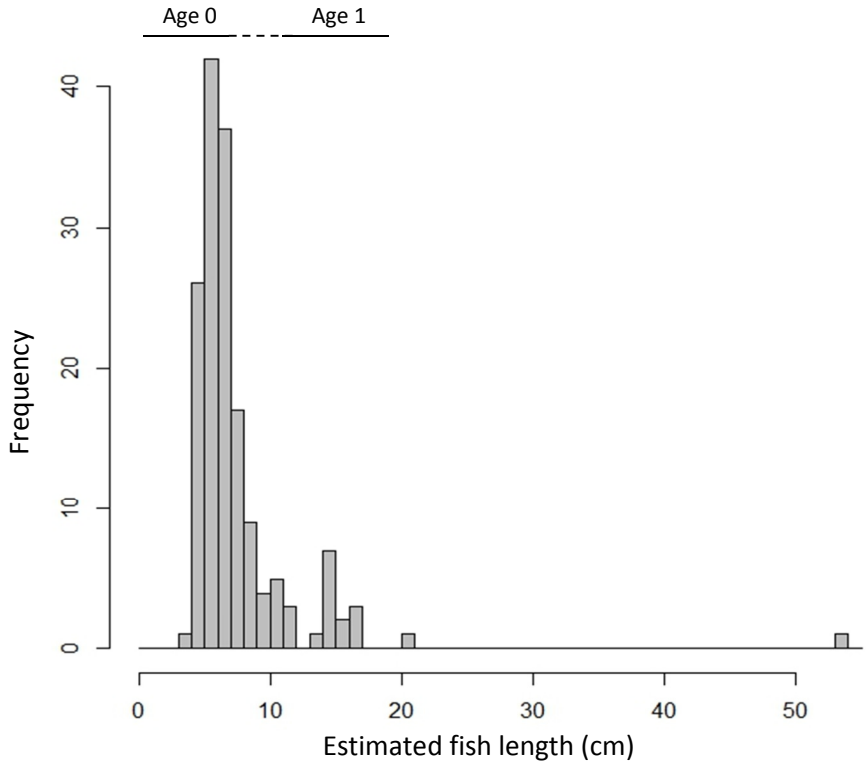

Figure 6.3: Frequency of estimated walleye pollock length (in cm) consumed by female fur seals in the Bering Sea estimated from otolith size (n = 173) found in 98 scats collected on Reef Rookery in August 2011.

It was impossible to know how long the females had been on land prior to capture, or how much weight they had lost between the time they came back to land and the time of recapture, as I did not measure the time they spent with their pups. Neither the mass of the females before (p = 0.87) and after (p = 0.19) their foraging trips, nor the change in body mass over the course of the foraging trip (p = 0.26) were related to the foraging efficiencies of the females.

6.4.6 Milk energy content

Energy density of milk collected from 10 lactating northern fur seal females averaged 2.06 ± 0.08 kJ/g and consisted of 47.98 ± 1.98 % fat and 11.48 ± 0.49 % protein (Table 6.4). Energy content of the milk was slightly but not significantly greater for females that foraged off-shelf (2.13 ± 0.09 kJ/g energy density, 50.50 ± 2.12 % fat and 12.32 ± 0.66% protein) compared to females foraging on the shelf (2.00 ± 0.11 kJ/g energy density, 46.30 ± 2.93 % fat and 10.92 ± 0.63 %, protein) (energy density: p = 0.41, fat: p = 0.28 and protein: p

= 0.16). On the other hand, the milk of females foraging on the shelf contained greater carbohydrate and water content (4.81± 2.77 % carbohydrates and 37.62 ± 3.67 % water) compared to off-shelf females (1.60 ± 0.33% carbohydrates and 35.00 ± 2.65 % water), but differences were not statistically significant (carbohydrates: p = 0.29; water: p = 0.58). Half of the milk samples were taken before the foraging trip and half were taken after the foraging trip, but there was no difference in milk composition between sampling times.

Milk fat (%) in samples collected after females foraging trips (n = 5) were positively related to foraging trip duration (p = 0.007, R^2 = 0.93), while milk fat in samples collected prior to foraging trips (n = 5) were negatively linked to foraging trip duration (although not significantly, p = 0.104, R^2 = 0.63, Figure 6.4 A and B).

Table 6.3: Measured and corrected energy expenditure (EE in MJ), measured and corrected number or prey capture attempts (PrCA) during a foraging trip for female northern fur seal foraging on (n = 9) or off (n = 7) the Bering Sea shelf. The corrected values of EE and PrCA were used with the estimated energy content per average prey (EC prey in kJ) to calculate the energy animals gained while foraging at sea (in MJ) and their foraging efficiency (i.e. the ratio of energy gain to energy expended). See section 'Foraging efficiency' in Material and Methods for how EE and PrCA were corrected.

Group	Seal ID	Meas.EE trip (MJ)	Corr.EE trip (MJ)	Meas. PrCA	Corr. PrCA	EC prey (kJ)	Energy gain (MJ)	Foraging efficiency
ON-SHELF NFS	1	367.43	360.55	1008	921	324.47 ± 10.40	298.78 ± 52.55	0.83 ± 0.16
	5	177.37	174.16	346	319		103.37 ± 17.56	0.60 ± 0.11
	6	115.74	113.58	321	295		95.56 ± 16.49	0.85 ± 0.16
	8	115.07	113.01	152	140		45.26 ± 7.81	0.40 ± 0.08
	12	205.27	201.40	718	660		214.05 ± 36.42	1.07 ± 0.20
	13	152.06	149.36	1681	1538		499.01 ± 86.48	3.36 ± 0.64
	14	440.71	432.94	635	580		188.22 ± 32.68	0.44 ± 0.08
	17	146.65	143.96	549	503		163.27 ± 27.64	1.14 ± 0.21
	19	122.60	120.56	1693	1567		508.46 ± 88.63	4.24 ± 0.81
	Mean	204.77 ± 39.40	201.06 ± 38.68	789 ± 189	725 ± 174			
OFF-SHELF NFS	2	249.57	244.92	2727	2505	194.64 ± 8.49	487.56 ± 84.07	2.00 ± 0.38
	3	156.54	153.81	1474	1351		262.94 ± 46.22	1.72 ± 0.33
	4	428.07	420.02	3576	3252		633.01 ± 111.82	1.52 ± 0.29
	10	73.97	72.67	1996	1839		357.92 ± 61.99	4.95 ± 0.93
	11	120.03	117.89	1518	1397		271.90 ± 47.35	2.32 ± 0.44
	15	125.03	122.81	3654	3378		657.34 ± 112.82	5.38 ± 1.01
	20	136.22	133.86	2381	2194		427.34 ± 73.81	3.21 ± 0.61
	Mean	184.20 ± 45.40	180.85 ± 44.53	2475 ± 339	2274 ± 310			

Table 6.4: Proximate composition of milk samples collected on 10 lactating female northern fur seals (NFS) during the breeding season in August 2011 on Reef rookery, St. Paul Island, Bering Sea, Alaska. Six samples were collected from females foraging on the Bering Sea shelf, and 4 from females foraging off the shelf within the deep basin. Samples were either collected before (pre) or after (post) their foraging trip at sea.

Group	Seal ID	Time	Moisture (%)	Ash (%)	Carb. (%)	Protein (%)	Fat (%)	Energy (kJ/g)
ON-SHELF NFS	1	pre	39.8	0.5	5.4	10.8	44.5	1.945
	14	pre	51.1	0.7	0.2	10.6	37.4	1.59
	19	pre	30.2	0.5	3.1	11.6	54.6	2.302
	6	post	44.5	0.6	0.5	11.2	43.2	1.823
	7	post	30.6	0.3	18.1	8.3	42.6	2.047
	17	post	29.5	0.4	1.6	13	55.5	2.333
OFF-SHELF NFS	2	pre	37.1	0.6	0.8	12.5	48.9	2.066
	3	pre	39.4	0.5	2.4	11.1	46.6	1.98
	4	post	27.3	0.6	1.5	14.1	56.5	2.39
	15	post	36.2	0.5	1.7	11.6	50	2.103

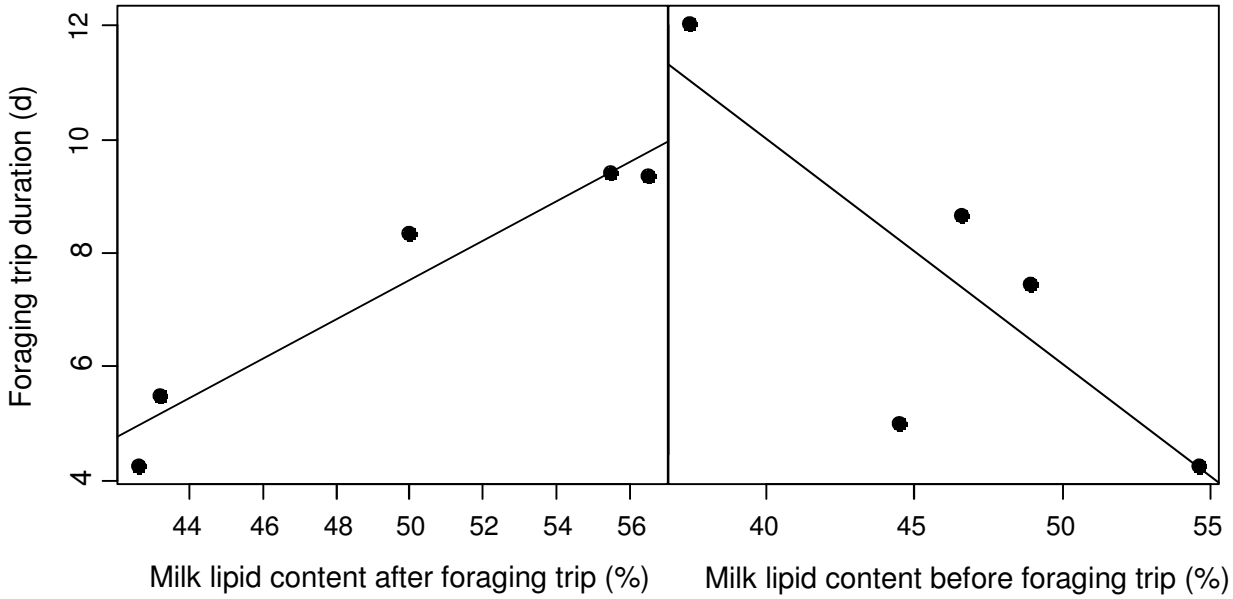

Figure 6.4: Foraging trip duration of females as a function of the milk lipid content after the trip (A, n = 5) or prior to it (B, n = 5). Regression lines between the 2 parameters are added on both graphs (A: slope $p = 0.007$, $R^2 = 0.93$, B: slope $p = 0.104$, $R^2 = 0.64$).

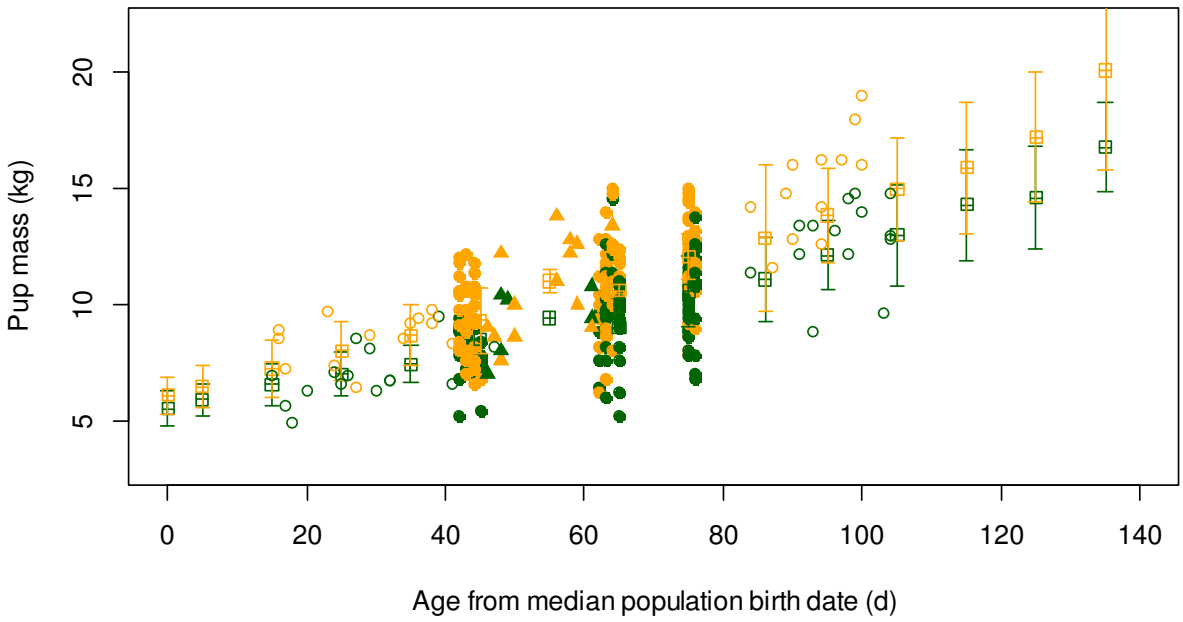

Figure 6.5: Mass of male (in orange) and female (in green) northern fur seal pups over the course of the nursing period, from age 0 to weaning (in days). Closed circles show data collected on random pups during the nursing season 2011 on St. Paul Island. Triangles show the mass of pup associated with the females tracked at sea during the same field season. Open circles show the mass-at-age data collected on St. Paul Island in 1996 (Donohue et al., 2000) and open squares show the mean mass ± SD of pups weighed on Bering Island, Russia in the 1980s from Boltnev et al. (1998).

6.4.7 Pup growth

Female pups weighed 7.93 ± 1.00 kg at age 42 - 45 days, 9.51 ± 1.82 kg at 62 - 65 d, and 10.24 ± 1.6 1kg at ages 75 - 76 d (Figure 6.5). In contrast, male pups were about 15% bigger, weighing 9.45 ± 1.53 kg at age 42 - 45 days, 10.88 ± 1.98 at 62 - 65 d, and 11.95 ± 1.79 kg at 75 - 76 d (Figure 6.5). Ages were approximated based on a median date of pupping of the 6th of July (Trites, 1992). My measures of pup body mass are consistent with weights of pups from Bering Island, Russia in the 1980s (for example, 10.56 ± 1.53 kg for female pups and 12.04 ± 0.97 kg for males at age 70 – 80 d from Boltnev et al. (1998); Figure 6.5).

A single measure (prior to foraging trip) of mass of pups associated with mothers were not linked to foraging efficiency of mothers (p = 0.98). I could not determine if captured pups had been feeding or fasting, which created variation in the data that can heavily skew the pup mass data on single measurements. Linear models fitted to data collected in 2011 were: BM (kg) = 0.072 × Age (d) + 4.88 for female pups and BM (kg) =

0.078 × Age (d) + 6.08 for male pups. Linear models fit to data from the 1980s (Boltnev et al., 1998) were: BM (kg) = 0.072 × Age (d) + 4.88 for females and BM (kg) = 0.077 × Age (d) + 5.03 for males. Linear models fit to data from 1996 (Donohue et al., 2000) were: BM (kg) = 0.082 × Age (d) + 4.67 for females and BM (kg) = 0.102 × Age (d) + 5.62 for males. Analyses of variances on the slopes of these models showed that pups in 2011 had a slower growth than pups in the 1980s or in 1996 ($p < 10^{-5}$ in all cases).

6.5 Discussion

Food is not evenly distributed in space and time in the environment, so acquiring food in the wild requires animals to make behavioral 'decisions' as to where, when, and for how long to search for food. These strategies will affect the amount of energy predators spend searching for food and obviously the amount of energy they manage to extract from the environment. Energy is the fundamental currency underlying behavioral, physiological, reproductive and developmental processes and is crucial to an animal's growth, survival and reproductive fitness. Research often addresses only one side of the cost/benefit ratio equation—either studying energy input or energy output in isolation. In my study, I looked simultaneously at energy in and energy out during a foraging trip, depending on foraging behaviors or strategies at sea.

6.5.1 Foraging efficiency varies with foraging strategy

Out of the 20 females I tracked from Reef Rookery, 40% went to forage in the deep basin and 60% stayed to forage on the Bering Sea shelf. I selected breeding females for my study from Reef rookery because these individuals were known to use a wide range of foraging locations (Robson, 2001). These two strategies have also been observed in female fur seals from Russian and Alaskan breeding islands (Gentry, 1998). However, quantitative estimates of energetic costs associated with the two strategies had not been previously measured.

Females foraging off the shelf traveled greater distances, spent ~2.5 more days at sea, and spent ~10% less time at sea actually diving to capture prey compared to females foraging

on the shelf. However, their dives were overall shallower and of shorter duration. Foraging behaviours of marine mammals indicate prey type, prey distribution and availability in the marine environment (Boyd, 1996; Forcada and Staniland, 2009). The main prey of the off-shelf females were mesopelagic fish such as northern smoothtongue or myctophids, small energy-dense schooling fish that display a diel migration to the surface so they were feeding only at night (Chapter 4). In contrast, females foraging over the shelf dove deeper and for longer times than those that went off-shelf. Female fur seals were capable of diving benthically to the relatively shallow bottom of the Bering Sea shelf (~150 m). On average they spent 15 % of their time diving to the bottom (and up to 30 %) including diving during daytime, and fed mostly on gadids or other shelf-associated prey. Females foraging on the shelf tended to obtain less energy per g of prey ingested as they fed on a diet with an energy density 44% lower than females foraging off the shelf (~3.9 vs ~5.8 kJ/g). However, they fed on prey of bigger size than females foraging off the shelf, which means that the average prey item ingested (~325 kJ) provided them with ~60 % more energy than the average prey consumed by females foraging off the shelf (~195 kJ).

Females foraging in the deep basin attempted to capture 3 times more prey than females on the shelf per day at sea. Both strategies captured ~ 1.76 prey per dive when at least one capture occurred, which is in the range of the ~ 1.88 (Viviant, M. pers. comm.) and ~ 2 prey capture attempts (Chapter 5) measured in Antarctic fur seals. However, the fact that females foraging on the shelf have significantly lower prey capture rates over all the dives (0.46 vs 0.76) indicates that they have a greater rate of unsuccessful dives compared to females foraging off the shelf. Given the greater energy intake per prey ingested for the on-shelf group, energy gained per dive (including unsuccessful dives) was similar between strategies (~ 180 kJ/dive). However, as females foraging in the basin performed shallower dives that were shorter than females on the shelf, they could perform more dives within a specific timespan and thus gained almost twice as much energy per minute spent diving (146 vs 82 kJ/min diving). Since females foraging off the shelf spent on average ~ 10 % less time diving that females staying on the shelf, the difference in rate of energy gain was reduced over the entire foraging trip (35 vs 25 kJ/min at sea) but was still greater for females feeding in the deep basin.

Females foraging in the deep basin might have had a greater rate of energy gain, but they also expended more energy during their foraging trip than females staying on the shelf. The increase in energy expenditure while at sea was not due to a greater metabolic rate, but rather to them spending more time and energy transiting to and from their foraging grounds, which were further away from the colony. This compromise on energy expenditure did not completely offset the relative advantage in rate of energy gain that the strategy of feeding in the deep basin offers. Consequently, females foraging off the shelf remained more efficient at foraging (3.02) compared to females on the shelf (1.44).

My estimates of foraging efficiency are much lower than the ratio of 23 reported for northern fur seals in the 1980s (Costa, 1993). However, this high foraging efficiency is based upon food intake that was indirectly derived (using an isotopic method to estimate changes in body water content, Costa 1993) and likely overestimated energy gain by a factor of 3 to 5 (diet of squids). Estimates of prey capture attempts and diet-related parameters carry the most uncertainty to the final calculation of foraging efficiency (Chapter 5). As a consequence, errors in terms of ingestion rates and on type of prey consumed could lead to a grossly overestimated final value such as theirs.

My results show that both on-shelf and off-shelf strategies led to average foraging efficiency above 1, indicating that the lactating females obtained enough energy to support their own physiological needs. However, ~ 30 % of the females foraging on the shelf lost more energy than they gained (ratio significantly lower than 1), and that 45 % seem to break even or were slightly above 1 (Table 6.3). Thus, a majority of females choosing this strategy would have had to rely heavily on internal reserves to support themselves and their pup, which was not the case for females foraging in the deep basin. Lactation and the cost of growing a pup is substantial (Goldsworthy et al., 2004). As foraging efficiency determines the amount of energy available for different physiological functions and as compromises are likely to be made on reproduction before one's survival (Bouten et al., 1994), females gaining 3 times more energy than what they spend are likely to be able to invest more energy in their pup than females that obtain only 1.5 times more.

I am aware that foraging efficiency of a single trip might not be representative of an entire breeding season. However, fur seals are known to remain faithful to their foraging

grounds and strategies over successive foraging trips unless a drastic change in environmental assemblage or physical features occurred (Call et al., 2008). This was confirmed by $\delta^{13}C$ and $\delta^{15}N$ stable isotopes ratios in plasma and RBC of the same individuals (Chapter 4).

It may seem surprising that females foraging on the shelf should continue foraging here despite the lower energetic efficiency of doing so compared to the females foraging off the shelf. However, presence/absence of prey is a better predictor of foraging habitat than prey density for northern fur seals (Benoit-Bird et al., 2013), and if prey are widely and predictably present on the Bering sea shelf, females might be inclined to keep foraging there. It is highly unlikely that individuals are 'aware' of their rate of energy gain at sea or the energetic values of their prey if they are feeding frequently in predictable patches. Larger size of females is usually an advantage when prey availability or accessibility is low because it provides them with a greater capacity to dive (higher ADL) and to buffer changes in conditions (greater body reserves) (Kooyman, 1989; Iverson et al., 1993). However, I did not find any relation between size of the females (or body condition) and choice in foraging strategy, foraging efficiency, or rate of energy gain. This indicates that prey are likely available and accessible in both foraging environments, but that the limiting factor is the difference in prey energy density.

There is a clear energetic disadvantage to foraging on the Bering Sea shelf compared to the deep basin despite the greater distance to the foraging grounds. Optimal foraging theory (MacArthur and Pianka, 1966) states that methods of searching and obtaining food should maximize foraging efficiency to optimize fitness of the animals. However, the on-shelf strategy does not seem to maximise foraging efficiency (or net energy gain) compared to the off-shelf strategy. This raises the question as to whether these foraging differences affect energy flow allocated to reproduction and thus fitness of individuals.

6.5.2 Conflict between time and energy currencies

Foraging efficiency of mothers is positively related to pup growth on Antarctic fur seals (Chapter 5), which means that females with greater foraging success produce bigger pups. The fact that pup mass at weaning is directly linked to pup survival in seals (Doidge

and Croxall, 1989; Baker and Fowler, 1992; Boltnev et al., 1998; McMahon et al., 2000; Hall et al., 2001; Beauplet et al., 2005) suggests that females with better foraging strategies that optimize foraging efficiency are likely to improve fitness, consistent with Optimal Foraging Theory. Applying this relationship to northern fur seals suggests that females foraging off the shelf would produce bigger pups and have greater reproductive success than females foraging on the shelf.

Maximising the rate of energy delivery to their pup rather than foraging efficiency (Costa, 1993) is another way for otariids to produce bigger pups (Gentry and Kooyman, 1986). Females foraging on the shelf perform significantly shorter foraging trips compared to females foraging in the deep basin. As foraging trip duration did not affect time spent ashore to feed pups (Antonelis et al., 1990), the females adopting the on-shelf strategy are likely to feed their pups ~ 20 – 25 % more frequently (considering a consistent 2-day difference in trip duration over the breeding season). Under this scenario, on-shelf females might not optimise foraging efficiency but rather the rate of delivery to pups to maximize their reproductive success. Rate of energy gain and time at sea were not significantly related in my study (*i.e.,* females with a greater capacity at obtaining energy while foraging did not perform shorter trips). There is disassociation between the 2 fitness-related currencies that are time and energy invested in foraging versus reproduction (Boggs, 1992; Ydenberg et al., 1992), and individuals compromised either on rate of energy gain (energy currency), or on delivery rate of milk to their pups (time currency). Both lead to a decrease in maternal investment to offspring. Northern fur seals thus seem to be conflicted by the trade-off between time away from their pups and the energy they gain foraging, while Antarctic fur seals seem to optimize both with short average foraging trips and high average FE (Table 6.1, Chapter 5).

Time and energy define the allocation of resources to growth and reproduction. Female fur seals can buffer fluctuations in these currencies by maintaining their body energy reserves when energy is in surplus, and can use them for reproduction investment or other purposes when energy intake exceeds costs (Trillmich, 1990). Sea bird parents have been shown to alternate long foraging trips that replenish their internal reserves with shorter foraging trips that maximise delivery of energy to chicks (Weimerskirch et al., 2003a). This shows the importance of body store usage to adjust and buffer energy expenditure and

acquisition during foraging for all allocation purposes. Female northern fur seals with lower body condition before a foraging trip tended to spend more time at sea compared to females in better body condition (Figure 6.2). This suggests that females likely make a trade-off between maintaining their own body condition or that of their fasting pups awaiting nursing, even though some have hypothesized that females can compensate for longer periods at sea by providing greater milk energy content (see section below). This relationship was not observed on Antarctic fur seals, which means that conditions on the Kerguelen plateau were favorable enough that compromises did not have to be made (Chapter 5), unlike in the Bering Sea.

The foraging strategies employed by northern fur seals were surprisingly similar to those of Antarctic fur seals inhabiting opposite hemispheres. Antarctic fur seals had similar time budgets as northern fur seals feeding on the Bering Sea shelf (*i.e.,*time at sea, distance traveled, allocation of time to different activities). However, parameters related to energy (*i.e.,*prey captures, diet and foraging efficiency, etc.) were similar between Antarctic fur seals and northern fur seals foraging off the shelf (Table 6.1). The degree of similarity between the sub-Arctic vs sub-Antarctic species provides insights into the physiological and behavioural flexibility of otariids breeding and foraging in high-latitude environments. On one hand, both face spatial and temporal constraints during the 4-month breeding season. On the other, northern fur seals must currently compromise on one of the limiting conditions (time allocated to nursing vs energy gained) whereas Antarctic fur seals do not. Whether this explains why one population is declining whereas the other is increasing remains unclear, but provides an interesting line for further investigation.

6.5.3 Maternal investment

Allocation of energy to the pup is mediated through milk provisioning in fur seals. Factors such as maternal foraging trip duration, diet, mother's mass, time ashore and days postpartum affect milk composition and overall energy transfer to pups (Oftedal, 1984; Trillmich and Lechner, 1986; Arnould and Boyd, 1995b; Arnould and Hindell, 1999; Georges et al., 2001; Goebel, 2002; Banks, 2012). In my case, I measured milk composition in females in mid-lactation, and recaptured females as soon as possible after their return on

land post feeding, so both days postpartum and time ashore were standardized as much as possible. Foraging trip duration and maternal diets are thus the 2 main parameters that differed between my 2 groups.

Foraging trip duration has been shown to be positively related to milk lipid and protein content in Antarctic and Australian fur seals (Arnould and Boyd, 1995a; Arnould and Hindell, 1999). In these cases, females that spend more time at sea are thought to compensate for longer fasting of their pups by producing energy richer milk. However, this relationship has not been found in northern or sub-Antarctic fur seals (Georges et al., 2001; Goebel, 2002). Another study on northern fur seal lactation even showed a negative relationship between foraging trip duration and milk lipid content, but attributed it to mammary gland involution when intervals between 2 suckling bouts are too long (Banks, 2012). In my study, I found the relationship between the lipid content of milk (post-foraging) and the duration of the foraging trip was positive. However, my results should be viewed cautiously because I only collected 5 milk samples after the females returned to land. The relationship between foraging duration and milk composition is thus unclear, although it seems that females might be able to at least partly compensate for longer trips by increasing the energy content of their milk. However, it has been suggested that the increase per additional day of absence from the pup to provide an identical milk energy yield would be physiologically unrealistic to achieve (Trillmich, 1990), and that the outcome of increased time at sea (assuming similar diets) would be a lowered growth rate of young (Gentry and Holt, 1986).

Milk composition of fur seals usually reflects what they fed on prior to the nursing bout (Goebel, 2002), which means that greater foraging efficiency should result in higher energy allocation for milk production. This is consistent with lactating females on Bogoslof Island—known to feed on high energy density prey located close to breeding grounds—having significantly greater milk lipid content than females from St. Paul Island (Banks, 2012). Assuming this difference was diet related means that the milk lipid content of my females foraging off the shelf should have been greater than the on shelf females. My results the difference was not significant (~ 50 % vs ~ 46 %), possibly due to my low sample size and reduced statistical power.

Once again, it is difficult to tease apart the impacts that difference in diets and foraging trip durations have on energy allocation to milk, as they seem to be confounding factors. Females foraging off the shelf have longer trips (that tend to increase milk lipid content) and feed on a diet that would logically provide them with a greater energy overhead available for reproduction. However, their pups would be fed less often and likely still grow slowly. On the other hand, if females foraging on the shelf gained only slightly more energy than what they spent foraging, they would feed their pups more often. However, their allocation to milk would likely involve mobilizing body reserves to produce milk of adequate fat content for fur seals (Jensen, 1996), and would thus require greater subsequent foraging efficiency to replenish these reserves. As females come ashore, body reserves are drained through suckling and the metabolic costs of fasting on land until low body reserves induces the female to return to sea to forage (Trillmich, 1990). I did not find any clear differences in body condition between females from the 2 groups, or between body condition and milk composition, but females with the lowest fat content in milk before their foraging trip tended to spend more time at sea during the following trip (n = 5).

Foraging efficiency defines allocation trade-offs of energy to milk or to body reserve and allocation of time to maternal investment or to replenishing body condition, and females might alternate between priorities to maximize both their body integrity and future survival and pup chances of survival. I did not obtain data from individual mother-pup pairs to determine reproductive success but randomly captured pups on the colony as a population index of pup growth and maternal investment of the colony compared to growth rates previously recorded. Pup mass and body condition at weaning are known to define survival of pups during their first year at sea, which links reproductive investment of females to survival of pups, and thus to population demography.

There were no significant differences between pup mass-at-age in the different available datasets (from the 1980s – Boltnev et al. (1998); from 1996 – Donohue et al. (2000); from 2011 – this study; Figure 4). However, analysis of variances on the slopes of these models showed that the growth rates of the pups in 2011 were slower than pups in the 1980s or in 1996 ($p < 10^{-5}$ in all cases). This difference might reflect a difference in the range of age collection (*i.e.,*I collected data from age 42 to 76 d, while Boltnev et al. (1998)

collected from 0 to 140 d and Donohue et al. (2000) from 15 to 104 d). However, the data I compared my results to were taken during years when the population was not declining (Angliss and Allen, 2009). This might thus highlight a mechanistic influence of lower provisioning from mothers in recent years.

6.5.4 Conclusions

Despite the limitations of my study, my results provide interesting clues into the states of the mother-pup energy transfer on St. Paul Island and highlight the importance of taking a further step towards investigating the series of events that link environmental conditions, animal behaviors, energy balance, fitness of individuals, and demographic parameters. It is interesting to note that females from an increasing population (Antarctic fur seals) can on average simultaneously maximise foraging efficiency and frequency of feeding their pups, while females from a declining population (northern fur seals) are faced with a trade-off between the two. Having a significant proportion of breeding mothers adopt a strategy that does not maximise their offspring's chances of surviving might significantly affect population recruitment. Ultimately, this could lead to northern fur seals producing a significant portion of smaller pups at weaning, with lower survival during their first year and thus a lower recruitment in the population (Baker and Fowler, 1992). If my study provides evidence of such a possibility, there is a need to investigate whether one foraging strategy yields a lower reproductive success via lower pup survival of the young compared to the other to fully understand whether this is a potential cause for the population decline. The next step would be to estimate the survival rate of juveniles over the first few years of their pelagic life at sea, and how it relates to the foraging strategies of their mothers during their first 4 months of life.

Chapter 7: General conclusion

The main objective of my thesis was to determine how foraging strategies of lactating northern and Antarctic fur seal females affected their foraging efficiencies and ultimately their fitness. In this way, I sought to link environmental and prey conditions with the population dynamics of the two species. I used a quantitative approach based on energetic flows that standardized for the differences between foraging habitats. I also used state of the art technology to investigate the foraging locations and behaviours for single foraging trips of 20 mature lactating fur seals from both species, and determined how much energy they spent and how much energy they extracted from the sea. I then linked foraging strategies and efficiencies of individual mothers with the growth of their respective pups for Antarctic fur seals, and with milk samples and the mass of random pups on the colony for northern fur seals to investigate how these parameters affected reproductive success. Trade-offs in energy and time during the nursing season affect the fitness of females and ultimately the survival of their pups during their first year at sea. Ultimately, changes in survival of the young and thus of recruitment can alter the dynamics and trajectories of populations.

Studying large and elusive mammals in the marine environment is inherently difficult and resulted in some unavoidable caveats. However, my individual energetic-based approach revealed robust and quantitative connections between the environment and the population dynamics of the two species. The results have advanced understanding of how animals cope with their environment and their adaptive limits to changes or sub-optimal or changing conditions. My study emphasizes the importance of considering individual variability and individual-based studies given that individual performance and plasticity link the environment with population trends. It also shows the importance of basing studies on robust science, such as energetic-flows and thermodynamic laws, to draw mechanistic, process-driven relationships and understand and predict population changes. Ultimately, my study highlights the potential vulnerabilities of fur seal populations to current or future changes in their environments and provides information to direct spatial and temporal conservation efforts towards the most sensitive part of the population. However, my study left a number of questions unanswered and revealed new ones that need further investigation.

7.1 Summary of findings

Chapters 2 and 3 sought to develop, test and validate methods to predict foraging energy costs using acceleration data. In Chapter 2, I investigated foraging energy expenditure of northern and Antarctic fur seal females given their time-activity budgets at sea. To do so, I used field measurements of metabolic rates at sea from the doubly- labeled water method as a reference for energy expenditure, which, when linked to fine-scale time-activity budgets of individuals, allowed me to calculate activity-specific metabolic rates. I tested whether tri-axial dynamic body acceleration was accurate at predicting energy spent at sea in free-ranging animals over a full foraging trip or separated by types of activities they displayed at sea. My results show that time-activity budgets affected energy expenditure at sea of individuals. They also show that diving is the most expensive activity followed by transiting at the surface. Dynamic body acceleration (VeDBA) also needs to be separated by type of activity to accurately predict energy expenditure at sea.

I feel that Chapter 2 represents my most significant contribution to the field of marine mammal ecology as I showed how combining behavioural information from GPS, time-depth recorders and high-resolution accelerometers with metabolic measures of energy expenditure can be used to determine and partition fine-scale behaviours and their associated metabolic rates in a free-ranging animal. This approach opens new perspectives to the field of free-ranging energetics to gain a greater understanding concerning how changes in foraging strategies, via time-activity budgets, can impact foraging costs. The doubly-labeled water method indirectly measure respirometry exchanges and is consequently based on more robust physiological and energetic grounds than acceleration. However, it is very expensive to perform on large animals, only provides a single measurement over the duration of the foraging trip, and is biased at the individual level. Accelerometers are a cheaper and easier tool to employ in field studies, and their strength lies in their potential to provide energetic information at the activity level. However, acceleration is a measure of body movement and not of gas exchange, and limitations to its use also remain, mostly at the full trip level. Future research should thus take into account the pros and cons of each technique depending on the focus of the study to decide on a methodology.

In Chapter 3, I investigated similar questions and employed a similar approach as in Chapter 2, but focused on the cost of transport rather than tri-axial dynamic body acceleration. I developed a method to detect flipper strokes from acceleration data and tested whether their number, rate, or amplitude could accurately predict energy expenditure at sea. I also calculated energetic cost of stroking flippers for fur seals, and the cost to travel a given distance under water. My results show that flipper strokes could only be detected when animals were diving, and when they were transiting at a fast rate. Flipper strokes were accurate at predicting energy expenditure during diving and to a lesser extent during transiting, but not as well during an entire foraging trip. My results also show that tri-axial dynamic body acceleration is a better predictor of energy spent while foraging when separated by activities than are flipper stroke metrics.

In Chapter 4, I focused on determining accurate diet composition of northern fur seals, an essential component of energy gained from foraging. I employed modern molecular methods to improve detection of prey from scats compared to more traditional hard-part based methods. My results show that despite inherent biases from both methods, DNA meta-barcoding provides a finer more complete list of prey. Concurrent measures of C and N blood stable isotopes on 20 individual females from the colony where the scats were collected, indicated that northern fur seals foraged in two different locations (on shelf versus deep basin) and had two different diets. Presence of these two diets was confirmed by a cluster analyses of prey associated within scats, but were not represented in the same proportion as was indicated by stable isotopes. This work represents the first step towards determining the energy gained by females as a function of the prey they consumed.

Chapters 5 and 6 integrated results from Chapters 2 and 4 to investigate differences in foraging strategies and their respective foraging efficiency, and discussed their impacts on reproduction success. I estimated foraging strategies (from foraging locations and time-activity budgets at sea), foraging costs (from the DLW measure of energy expenditure) and foraging benefits (from diet composition), size of prey (from scat hard-part remains), and number of prey capture attempts (from acceleration data). Chapter 5 focused on Antarctic fur seals and linked foraging parameters of mothers to the growth of their respective pups from birth to weaning. The results showed that the quality of mothers as foragers was directly

linked to the size of their pups at weaning, and thus of the probability of their pups surviving during their first year at sea. Better foragers were capable of increasing their rate of energy gain without increasing their overall energy expenditure, and spent overall less time at sea compared to less efficient females. Thus, increased fitness through higher maternal investment was achieved by maximising both foraging efficiency and their frequency of feeding their pup.

Chapter 6 focused on the northern fur seal population, and showed that the two foraging strategies described in Chapter 4 resulted in different foraging efficiencies. Both groups of females spent similar energy to forage, but females foraging in the on-shelf neritic habitat had lower foraging efficiencies as they captured bigger prey of lesser energetic quality and did so less often compared to females foraging in the off-shelf pelagic area. They however spent less time at sea overall, which meant that they returned to land to feed their pups more frequently. So unlike Antarctic fur seals, female northern fur seals compromised either their foraging efficiency or the frequency with which they fed their pups. My results indicate that females foraging for longer periods of time might compensate for greater fasting duration of their pups by increasing milk energy content, but the extent of this compensation is likely limited. There were also limited clues that the growth rate of NFS pups of the colony might be lower than in the pre-decline time. In conclusion, compromising on either foraging efficiency or on time spent nursing their pup might result in lower pup growth rates on the colony and ultimately declines in population size, even if the direct link between foraging strategies and individual pup growth rates could not be made.

7.2 Evaluation of research hypotheses

My general research hypothesis was that females from the declining population used foraging strategies that increased energy expended during foraging and minimise their foraging success due to prey being less accessible and of poorer quality, and therefore have lower foraging efficiencies compared to females from the increasing population. They therefore have less energy and time to allocate to reproduction, and produce pups that grow at slower rates. As mass at weaning is critical for survival during their first year at sea, this might lead to lower recruitment in the declining population.

My results did not show clear inter-specific differences in foraging strategies. As species, northern and Antarctic fur seals were similar in their average trip durations, distances traveled and time-activity budgets. They allocated the same proportion of time to diving, transiting and resting during their foraging trips at sea—even though Antarctic fur seals tended to perform more dives, but of shorter duration than northern fur seals. However, I found a significant intra-specific dichotomy in foraging strategies between northern fur seals. Forty percent of the females foraged in a pelagic habitat within the deep basin of the Bering Sea, while 60% remained in the neritic habitat of the shallow shelf. Females foraging on the shelf had similar trip durations and distances traveled as Antarctic fur seals, but their diving behaviours were different. Alternatively, female northern fur seals foraging in the deep basin displayed diving behaviours very similar to those of Antarctic fur seals, but performed trips of longer duration and traveled longer distances.

Contrary to my initial hypothesis, female northern fur seals also did not spend more energy to forage compared to Antarctic fur seals. Field metabolic rates of the northern fur seals foraging on the shelf were greater than those of the females foraging off the shelf. They were also greater than the metabolic rates of the Antarctic fur seals. However, spending less time at sea resulted in similar total energy expenditure between and within species. As expected, however, my results showed that northern fur seals as a population have a lower rate of energy gain and foraged less efficiently than Antarctic fur seals. Females foraging on the Bering Sea shelf captured prey of lower energy density and less frequently than Antarctic fur seals, which significantly reduced foraging efficiency. However, female northern fur seals whose strategy was to forage in the deep basin showed similar numbers of prey capture attempts, rates of energy gain and foraging efficiencies as did Antarctic fur seals. Consequently, the overall lower foraging efficiency of northern fur seals was not due to an increase in foraging cost, but reflected a decrease in the foraging success.

My hypothesis that females with lower foraging efficiency would have less energy to invest into pup rearing was validated on Antarctic fur seals. Females with a greater foraging efficiency produced bigger pups at weaning, which would thus be expected to have a higher survival probability during their first year at sea. I was however unable to make the direct link and comparison between fur seal species as I could not follow pup growth on the

northern fur seal colony. My results showed that females from the increasing population were capable of high foraging efficiency and high rate of milk delivery to their pups, while females from the declining population have had to compromise either on foraging efficiency or on the frequency with which they fed their pups. Females unable to optimise both of these parameters might not produce pups big enough to survive their first year at sea, which in turn could reduce recruitment and negatively affect the population trend.

Overall, my initial hypothesis was partly validated. The reason why northern fur seals have a lower foraging efficiency than Antarctic fur seals was different than I initially expected. However, there are indications that lower foraging efficiency might indeed be a limiting factor linked to their decline. The consistency in foraging costs between and within species might suggest that females from both species forage at their metabolic ceiling and that they have limited plasticity to modulate it. Fur seals are flexible in their foraging behaviours and choices of strategies at sea, but if environmental conditions change such that they do not allow a rate of energy gain sufficient to match their high and seemingly hard-wired energy costs of foraging, they might be at risk of being in a negative balance and reducing their fitness.

One of my research objectives was to also test and validate new methods to determine energy expenditure at sea, and whether this could be achieved at the activity-specific level in free-ranging fur seals. My hypothesis was that accuracy of acceleration would be limited in free-ranging setting when animals spend time at the interface between two media (*i.e.,* when they are at the surface). My results showed partial validation of my hypothesis as acceleration metrics (VeDBA or flipper stroke) were poor predictors of energy expenditure over a full foraging trip. However, when separated by type of activities performed at sea, both VeDBA and to a lesser extent flipper stroke metrics accurately predicted energy spent (*i.e.,* activity-specific metabolic rates calculated from best fit models). Consequently, acceleration can be used in fur seals to predict energy expenditure at sea provided time activity budget of individuals are taken into account.

7.3 Caveats and limitations

My study was integrative and exhaustive, but the constraints of data collection on large remote animals and the overall protocol came with some caveats that need to be acknowledged. One of the major caveats around foraging efficiency is that all my analyses were individual-based, and yet diet compositions of individuals were estimated from population estimates. I also assumed that females foraging off the shelf had similar diet as females breeding on Bogoslof island based on stable isotopes and foraging habitat, even though they likely differ (albeit probably slightly). Stable isotopes only provide an overall trophic level of the predator, even though careful mixing models can provide greater taxonomic resolution. Different prey species can have similar isotopic signatures and yet different sizes and energy densities, which would likely change my final calculations. In addition, the Bogoslof diet I used was collected 2 years before my field season with potentially different yearly conditions. Estimating diets of wild animals is inherently difficult and cannot at this point be estimated per individual animal. I however used the best and latest methods in combination to increase the precision of the final outcome.

My selection of females for the study was likely biased towards more successful individuals. For northern fur seals, I only selected healthy-looking females with a confirmed pup at mid-lactation (*i.e.*, individuals already successful at rearing a viable pup for 2 months). The 20 Antarctic fur seal females were selected as part of a pool of 36 females whose pups were tagged at birth among the first born on the colony. More experienced—and thus more successful—females tend to pup earlier in the season (Lunn and Boyd, 1993), so my data is likely skewed towards the best individuals. In addition, as I needed to glue 3 different data loggers on the back and head of each animals, I tended to select females towards the heaviest range (although not exclusively) to minimise the impact of drag on the animals. Indeed, presence of these tags on animals affects streamlining and buoyancy and increases drag during swimming (Wilson et al., 1986; Boyd et al., 1997). Fur seals also rely exclusively on their dense fur to thermoregulate. Gluing tags on their fur disrupts the boundary layer and affects their thermal integrity. They can compensate behaviourally for the added drag (Boyd et al 1997), but ultimately, presence of data loggers increases their energy expenditure at sea (Wilson et al 1986) and will consequently lower foraging

efficiency estimates more so for smaller females, which means the error might not be consistent between all individuals.

Financial and logistic constraints allowed me to only follow females for a single foraging trip. My results thus provide only a narrow window of information into the foraging ecology of these animals. Even though there is evidence that females are consistent within a year in terms of their foraging behaviours (Call et al., 2008) and foraging efficiencies (my study), extending my conclusions beyond the timescale of my measurements should be taken cautiously. Individuals might adjust their foraging behaviours to find better conditions in subsequent trips if conditions are suboptimal during the preceding one. Better quality Antarctic fur seals seem consistently more efficient over the breeding season in their uniform foraging habitat, but it might not be the case for northern fur seals that can alternate between two different habitats and diets. It is uncertain whether females with low foraging efficiencies during the measured trip would still be in low balance in following trips—or whether females with short foraging trips will consistently make short trips. Flexibility or adaptability of females to environmental conditions likely operates at the timescale of a breeding season rather than a single foraging trip. Therefore, my short time window only allows educated inferences and conjectures regarding the consequences of foraging efficiency on fitness of individuals.

My inferences were stronger for Antarctic fur seals as I could follow growth of pups associated with the tracked females over a full nursing period. Unfortunately, this was not feasible on the northern fur seal rookery. The biggest caveat and missing piece of this puzzle was that I could not estimate from my data whether female northern fur seals with greater foraging efficiencies or females that feed their pup more frequently produced bigger pups at weaning, whether both produced small pups given their compromise on either time or energy allocated to maternal investment, or even whether this compromise affected pup growth at all. As these two parameters were confounded in Antarctic fur seals, it was difficult to estimate their respective contribution to the overall reproduction success. In addition, determining whether compromising on time or energy allocated to reproduction impacts population dynamics of northern fur seals would require comparing present pup information with pre-decline data. I could only collect morphometric measures of random pups 3 times at

mid-breeding season, so the comparison was very limited—especially since I could not obtain masses at weaning. Consequently, my data highlight possible reasons for why the northern fur seal population has declined based on comparisons with Antarctic fur seals, but this would need to be explicitly uncovered for northern fur seals.

Interspecific comparisons such as I undertook is a common approach in physiological ecology to elucidate the processes that animals use to adapt to environmental conditions. Northern and Antarctic fur seals undoubtedly share many similarities despite their opposite ranges. However, comparisons between only two species that involve correlations between individual characteristics and the environment raise several logical and statistical problems. Garland and Adolph (1994) argue that concluding significant differences between two species would not be statistically meaningful as they are expected due to genetic divergence resulting from differential environmental selective pressures. The null hypothesis should thus be that species are different, and not similar. So inferring mechanistic processes in northern fur seals based on results from Antarctic fur seals should be taken cautiously. Garland and Adolph (1994) thus advise making comparisons between more than two species and between populations from the same species. In this case, differences uncovered are less a result of genetics and are more readily related to the environments in which the populations evolved.

My results are based on only two species, but they show that northern and Antarctic fur seals are strikingly similar in numerous behavioural and biological and ecological features despite having phylogenetically diverged 5 - 6 million years ago (Hoelzel, 2002). These similarities are thus more meaningful in terms of adaptation and evolution than any differences I could have found, and indicate that selective pressures might have been convergent despite their opposite hemispheric habitats. Physical, chemical and biological features are likely more important to define similarity in foraging habitats and thus behavioural responses of animals living in them rather than plain geographical location or coordinates. Both the Bering Sea and the Kerguelen plateau present very similar features, which likely explain the similarities between species (or dissimilarities between groups of the same species foraging in different environments). I also studied two populations within the northern fur seal species and two species overall (*i.e.,*three groups in total as advised by Garland and Adolph 1994), which increases the biological significance of the differences and

similarities I uncovered. Within species differences are usually expected to be less extreme than between species, but this was not the case in my study. This provides more grounds to my inter- and intra-specific approach, and to my energetic flows approach that synthesizes and standardizes different environments to a common thermodynamic framework.

I also assumed based on previous studies of different pinniped species that growth rates and mass at weaning of pups were linked to 1) their survival during the most critical period of their life and 2) to the fitness of females. If there is evidence of such links, they are seldom explicit. Consequently, conclusions in my study are based on strong assumptions, but not totally explicit relationships. Fitness is assessed over a lifetime and is a consequence of compromises between the individuals' own long term survival and their reproductive rate. Females that invest more into reproduction in a given year might jeopardize their future survival and thus opportunities to reproduce over a longer lifetime, especially if foraging conditions are challenging (Beauplet et al., 2006). Whether foraging efficiencies of mothers ultimately affect survival of pups during their first critical year needs to be further investigated. Larger body reserves at weaning likely provide a survival advantage for naïve and inexperienced young. However, it is vital to untangle whether lack of maternal investment or changes in environmental conditions that pups face during their first year at sea are responsible for a lack of recruitment in the declining population to conclude more assertively on the matter.

Finally, I used the increasing Antarctic fur seal population as a reference to understand what mechanisms could be involved in the decline of northern fur seals. However, it is important to keep in mind that population dynamics are a result of more than just birth and death rates as partially studied in my thesis. Predation, food supply, breeding site, diseases, inter- and intra-species competition for resources, environment variability and human activities all impact the abundance of individuals. Antarctic fur seals were hunted to near extinction, and it is possible that the population has not yet reached carrying capacity, and that the observed trend reflects this post-exploitation recovery. Post-exploitation recovery of Antarctic fur seals at other sites has shown population growth rates as high as 20% per year, slowing down to 5–6% close to a new equilibrium (Hucke-Gaete et al., 2004). Human activities and predation pressure are also likely heavier in the Bering Sea compared

to the Southern Ocean for example. Consequently, even if my study hypothesized that differences in population trends between northern and Antarctic fur seals are a result of the same mechanisms, it should be acknowledged that other—and probably different—factors are likely involved.

7.4 Future research

Diet composition is one of the most important parameters in ecological studies. Individual-based models would greatly benefit from focusing on developing new methods and technologies to determine the diets of individual animals rather than of populations. Such direct observations of prey ingestion would require technological advancements and miniaturisation of underwater cameras, which are currently limited in battery power, image resolution in dark environments, and physical memory space. It would be interesting to pair accelerometers with the cameras to trigger a still shot of prey when a PCA is initiated. On board processing of pictures could also be developed for tags that cannot be recovered or when memory space is limited. There are still some technical hurdles, but advancements in this field would greatly enhance understanding of predator-prey interactions, of individual energetics, and ecosystem dynamics.

Despite the advances in the understanding the mechanisms and processes involved in the decline of northern fur seals, and given the limitations mentioned in the previous section, future research should focus on more explicitly linking foraging strategies and efficiencies of mothers to respective growth and survival at sea of northern fur seal pups. It should expand from the work done here to uncover whether the foraging strategies chosen by females leads to different pup masses at weaning or not, and if so, which strategy produces bigger pups at the colony level. To do so, future research should build on the fact that foraging strategies of females are associated with different C and N stable isotopic signatures (Chapter 4), which will thus be transferred to their pups through nursing. Collecting mass and blood samples for isotopic signatures of pups close to weaning on a large scale would indicate which strategy their mother adopted during the breeding season—and whether she was consistent in her choice or not—and whether mothers adopting one strategy over another provide an advantage to their offspring before leaving the breeding site. Finally, survival of these known

pups during their first years at sea should be assessed through mark (before they have weaned) and recapture techniques (when they return on land for the first time). This would fill in the gap that my study left in the relationship between foraging strategies, efficiencies and fitness of the animals—and would provide a better mechanistic framework to understand why the population is declining.

Following the advice of Garland and Adolph (1994), future individual-based and quantitative work to link foraging efficiency and fitness should involve comparisons on a larger scale. Comparisons should also be undertaken using more populations within the northern and Antarctic fur seal species for more robust statistical significance. Pups from islands located on the Bering Sea shelf should be compared to pups from islands within or close to the deep basin such as Bogoslof Island or the Commander islands, or to San Miguel Island in California, which are sites of increasing populations. Alternatively, Antarctic fur seal colonies are present all around the Antarctic Peninsula with different environmental conditions and diets. Other species of mammals and seabirds are also subject to the same environmental changes and are faced with similar constraints in time and space during their reproductive cycles. Increasing the number of inter-specific comparisons with species such as penguins breeding at the same site in the southern hemisphere or alcids in the northern hemisphere to study individual strategies, efficiencies and adaptations to their environments could help to understand which species are less flexible and more susceptible to environmental changes. Such interspecies comparisons would also shed light on what coping mechanisms exist and whether general adaptation and evolutionary patterns can be uncovered.

Future research should also expand the physiological and energetic framework to investigate causes of individual variations in addition to their consequences. The personalities of individual animals likely affect their foraging strategies and decisions, capacities to forage efficiently and adaptability to changes in environmental conditions. Studies on albatrosses showed that bolder personalities for example are more prone to explore and discover new foraging grounds (Patrick et al., 2013). It would also be beneficial to understand how and why alternative strategies are maintained in the population, as well as the heritability of such traits. Linking individual personalities to foraging over one or more

breeding seasons would help to understand how choices are made, whether foraging strategies evolve within or between breeding seasons and what the environmental or physiological clues or thresholds are that trigger the changes in strategies.

To conclude, my study improved current understanding of the relationship between the foraging choices of two top marine predators, their fitness, and their population dynamics in relation to environmental conditions. It addressed the issue from an integrative, robust and comparative approach. In the context of global environmental changes and population collapses such as for northern fur seals and many others, the ecological energetics framework I used addressed real-world questions at spatial and temporal scales relevant to environmental issues. It allowed the integration of physiological requirements within ecological constraints and the interpretation of organismal energy dynamics within the broader template of ecology and environmental management. In an era of unprecedented environmental challenges, my results provide a mechanistic understanding of the drivers of threatened species. They allow process-based approaches to predict and measure the energetic responses of organisms to varying environmental conditions. Ultimately, my study provides a means to translate empirical behavioural or energetic measurements into practical, real-world outcomes on which to base management decisions for wildlife conservation.

The declining population of northern fur seals has experienced significant environmental changes around their breeding grounds. These changes appear to affect individual fitness and population dynamics through the relationship I quantified between mother's foraging efficiency and pup mass at weaning, but also most likely through lower survival of naïve young of the year that have limited diving capacities. The presence of the two northern fur seal foraging strategies might indicate that they have been maintained in the population because they have similar net fitness outcomes—which would be an evolutionary stable strategy (ESS). However, neither strategy currently appears to be efficient in terms of time or energy spent and delivered. This might reflect differences in environmental conditions now compared to when the two foraging strategies evolved. Assessing the respective contributions of the two foraging strategies to the decline of northern fur seals is difficult. Either one of the foraging strategies could contribute more to the decline of the

population than the other—or the difference between them might simply be averaged in terms of fitness over several generations.

In contrast, the population of Antarctic fur seals breeding on Kerguelen is currently healthy, although increases are occurring in the frequency and intensity of anomalous conditions in the Southern Ocean caused by oceanic warming that might trigger a southward shift of the Polar Front (Moore et al., 1999). Such a change would mean that dense and predictable prey patches will be located further from the colony and likely at deeper depths. Less accessible and predictable prey implies greater energetic costs to access prey for lower energy benefits of foraging per unit of time, which can impact foraging efficiency and reproductive success (Inchausti et al., 2003).

Climatic anomalies affecting food availability (Loeb et al., 1997; Waluda et al., 2004) create more challenges for lactating fur seals (Lescroël et al., 2010); Lea et al. (2006) that might not be able to absorb the extra foraging effort required without compromising either reproduction or survival. Climatic anomalies have been hypothesized to be responsible for the decrease in reproduction success in seabirds (Weimerskirch et al., 2003b) and may have more pronounced effects on less adaptable central place foragers already operating close to their metabolic ceiling such as fur seals. Consequently, my study not only provides a greater understanding of ongoing processes to potentially explain population trends of fur seals today, but also a mechanistic framework to build predictive scenarios of the effects of environmental changes on future population dynamics.

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Appendices

Table A.1: Additional models of energy expenditure per time-activity budget for energy expenditure calculated with the 3 equations that yielded less accurate results than the equation from (Speakman et al., 1993).

	Equation	Parameter	Estimate (MJ/d)	SE	P value	R^2	AIC	Estimate (MJ/d)	SE	P value	R^2	AIC
EE at sea (MJ)	Speakman 1993	Foraging	31.51	5.82	$<2.10^{-5}$	0.70	266.1	31.44	5.66	$<2.10^{-5}$	0.70	264.1
		Transiting	19.73	6.84	0.009			19.58	6.52	0.006		
		Surf. Mov.	15.09	8.01	1.887			14.63	6.22	0.028		
		Resting	-2.97	30.90	-0.096							
	Speakman 1997	Foraging	34.50	6.25	$<2.10^{-5}$	0.70	269.8	34.46	6.08	$<10^{-5}$	0.70	267.8
		Transiting	23.67	7.34	0.003			23.57	7.00	0.003		
		Surf. Mov.	16.00	8.58	0.075			15.68	6.68	0.028		
		Resting	-1.64	33.15	0.949							
	Coward et al. 1985	Foraging	27.92	6.85	0.001	0.61	274.6	27.95	6.67	$<10^{-3}$	0.61	272.6
		Transiting	20.33	8.06	0.019			20.39	7.68	0.014		
		Surf. Mov.	11.13	9.42	0.250			11.33	7.33	0.136		
		Resting	1.22	36.39	0.973							
REE at sea (MJ/d)	Speakman 1993	Foraging	32.39	6.76	$<10^{-4}$	0.	165.8	32.68	6.44	$<10^{-4}$	0.	163.9
		Transiting	21.05	7.93	0.015			21.31	7.64	0.010		
		Surf. Mov.	10.55	7.53	0.175			11.09	6.81	0.117		
		Resting	4.62	24.51	0.852							
	Speakman 1997	Foraging	35.35	7.16	$<10^{-4}$	0.	168.8	35.73	6.83	$<10^{-4}$	0.	166.9
		Transiting	24.79	8.40	0.007			25.14	8.10	0.005		
		Surf. Mov.	11.64	7.98	0.159			12.35	7.22	0.101		
		Resting	6.10	25.97	0.816							
	Coward et al. 1985	Foraging	29.04	8.00	0.001	0.	174.7	29.51	7.63	0.001	0.	172.7
		Transiting	22.70	9.39	0.024			23.12	9.06	0.018		
		Surf. Mov.	5.67	8.92	0.532			6.54	8.08	0.426		
		Resting	7.44	29.04	0.800							

Table A.2: Details of the best models predicting energy expenditure (in MJ or in MJ/kg).

Model/Eq.	Parameters	Estimates	SE	*p*	R^2	AICc
2.11	Intercept	16.160	14.170	0.268	0.89	241.2
	$Int.DBA_{Transit}$	-3.10^{-7}	7.10^{-8}	$< 10^{-4}$		
	Dive.NB	-0.041	0.010	$< 10^{-3}$		
	$Time_{Dive}$	0.026	0.006	$< 10^{-3}$		
	$Int.DBA_{Rest}$	-2.10^{-6}	8.10^{-7}	0.021		
	Total.Time	0.021	0.003	$< 10^{-6}$		
2.12	Intercept	8.238	13.75	0.556	0.89	241.9
	$Int.DBA_{Transit}$	-4.10^{-7}	7.10^{-8}	$< 10^{-4}$		
	Dive.NB	-0.041	0.010	$< 10^{-3}$		
	$Time_{Dive}$	0.047	0.006	$< 10^{-6}$		
	$Time_{Tramsit}$	0.019	0.003	$< 10^{-4}$		
	$Time_{Surf.mov}$	0.024	0.004	$< 10^{-5}$		
2.13	Intercept	10.990	14.220	0.449	0.88	242.8
	$Int.DBA_{Transit}$	-4.10^{-7}	7.10^{-8}	$< 10^{-4}$		
	Dive.NB	-0.041	0.001	0.001		
	$Time_{Dive}$	0.025	0.007	0.002		
	$Time_{Rest.}$	-0.035	0.016	0.039		
	Total.Time	0.024	0.003	$< 10^{-6}$		
2.14	Intercept	87.030	26.690	0.004	0.88	243.1
	$Int.DBA_{Transit}$	-3.10^{-7}	7.10^{-8}	$< 10^{-4}$		
	Dive.Rate	-5.882	1.533	0.001		
	$Time_{Dive}$	0.027	0.006	0.002		
	$Int.DBA_{Rest}$	-2.10^{-6}	8.10^{-7}	0.039		
	Total.Time	0.014	0.003	$< 10^{-4}$		
2.15	Intercept	2.314	0.629	0.001	0.86	73.0
	$Int.DBA_{Transit}$(/kg)	-3.10^{-7}	8.10^{-8}	0.001		
	Dive.rate	-0.178	0.044	$< 10^{-3}$		
	$Time_{Dive}$	$8.\ 10^{-4}$	$1.\ 10^{-4}$	$< 10^{-4}$		
	$Int.DBA_{Total}$(/kg)	-2.10^{-6}	5.10^{-7}	$< 10^{-3}$		

Table A.3: Frequency of occurrence (FO) and split-sample frequency of occurrence (SSFO) of different prey item in northern fur seals diets measured either by morphological identification of hard-part remains or by DNA sequences analyses in scats collected on Reef rookery (St. Paul Island, Bering Sea, Alaska) during the breeding season 2011.The mean percent of DNA sequences specific to each prey in the scats (Perc. seq.) is also indicated.

		Hard-parts		DNA			Combined	
Group	Species/taxon name	FO (%)	SSFO (%)	FO (%)	SSFO (%)	Perc. seq. (%)	FO (%)	SSFO (%)
Gadid	Walleye pollock	75.00	62.75	96.94	51.11	70.42	96.94	46.14
	Pacific cod	8.33	7.00	18.37	4.70	2.99	22.45	6.06
	Pacific hake			21.43	5.08	2.54	21.43	4.89
Cephalopod	Unidentified squid/Octopus	20.00	12.28				12.24	2.97
	Boreopacific armhook squid			2.04	0.51	0.07	2.04	0.51
Salmon	All salmon	15.00	6.03	52.04	13.47	6.94	3.06	0.71
	Chum salmon			27.55	7.70	5.21	27.55	7.11
	Pink salmon			10.20	2.95	0.82	10.20	2.60
	Chinook salmon			7.14	1.40	0.51	7.14	1.37
	Coho salmon			5.10	0.92	0.33	5.10	0.92
	Sockeye salmon			2.04	0.49	0.07	2.04	0.49
Hexagrammid	Atka mackerel	10.00	2.92	5.10	0.78	1.15	8.16	1.63
	Kelp greenling	3.33	0.72	15.31	3.14	3.13	15.31	2.89
	Whitespotted greenling			1.02	0.26	0.03	1.02	0.20
	Lingcod			1.02	0.17	0.07	1.02	0.15
Mesopelagic	Northern smoothtongue	5.00	2.42	4.08	0.84	1.52	5.10	1.11
	Northern lampfish			1.02	0.15	0.02	1.02	0.13
	Northern lanternfish			1.02	0.15	0.02	1.02	0.13
Forage	Pacific herring			30.61	9.08	4.87	30.61	8.46
	Pacific sand lance	1.67	0.83	6.12	1.51	0.50	6.12	1.33
	Pacific sandfish	1.67	0.42	2.04	0.51	0.80	2.04	0.46
	Capelin	1.67	0.28				1.02	0.17
Flatfish	Pacific halibut			15.31	3.30	1.50	15.31	3.18
	Arrowtooth flounder	1.67	0.28	9.18	2.04	0.75	9.18	1.84
	Dover sole			1.02	0.17	0.07	1.02	0.15
Other	Rockfish	1.67	0.33				1.02	0.20
	Pacific staghorn sSculpin			5.10	1.17	0.53	5.10	1.17
	Shiner surfperch			6.12	1.02	0.56	6.12	0.97
	Crescent gunnel			2.04	0.71	1.51	2.04	0.71
	Sablefish			1.02	0.15	0.04	1.02	0.13
	Non-fish	3.33	2.50				2.04	0.51
	Worm	3.33	1.25				2.04	0.71

Table A.4: Stable carbon and nitrogen isotope values in plasma and red blood cells of 20 lactating northern fur seals breeding on St. Paul Island, Bering Sea.Blood samples were taken either before or after a single foraging trip at sea.

Sampling time	Tissue	ID	Foraging location	$\delta^{13}C$	$\delta^{15}N$	$\%^{13}C$	$\%^{15}N$	C/N ratio
Before	Plasma	1	on-shelf	-18.73	16.46	45.80	12.40	3.69
Before	Plasma	5	on-shelf	-18.81	16.79	45.48	12.05	3.77
Before	Plasma	6	on-shelf	-19.69	14.23	46.14	12.21	3.78
Before	Plasma	7	on-shelf	-18.37	18.16	45.46	11.94	3.81
Before	Plasma	8	on-shelf	-18.94	17.35	46.06	12.03	3.83
Before	Plasma	9	on-shelf	-18.54	17.56	45.08	12.04	3.74
Before	Plasma	12	on-shelf	-19.37	16.56	43.23	11.37	3.80
Before	Plasma	13	on-shelf	-18.47	17.41	46.36	12.17	3.81
Before	Plasma	14	on-shelf	-19.38	14.96	46.18	12.40	3.73
Before	Plasma	17	on-shelf	-18.62	16.81	45.91	12.32	3.73
Before	Plasma	18	on-shelf	-18.33	17.52	43.87	12.19	3.60
Before	Plasma	19	on-shelf	-18.74	17.43	44.01	11.52	3.82
Before	Plasma	2	off-shelf	-19.69	13.89	45.33	12.15	3.73
Before	Plasma	3	off-shelf	-19.65	15.03	46.13	12.13	3.80
Before	Plasma	4	off-shelf	-19.54	14.60	45.97	12.07	3.81
Before	Plasma	10	off-shelf	-19.13	15.91	45.89	12.48	3.68
Before	Plasma	11	off-shelf	-19.78	14.90	44.60	11.43	3.90
Before	Plasma	15	off-shelf	-19.32	14.90	46.93	12.80	3.67
Before	Plasma	16	off-shelf	-19.44	15.05	47.06	12.78	3.68
Before	Plasma	20	off-shelf	-19.56	15.13	44.15	11.58	3.81
Before	RBC	1	on-shelf	-19.34	15.36	56.92	17.05	3.34
Before	RBC	5	on-shelf	-19.33	15.11	50.64	15.09	3.36
Before	RBC	6	on-shelf	-19.94	12.08	50.73	15.24	3.33
Before	RBC	7	on-shelf	-18.78	16.25	48.03	14.11	3.40
Before	RBC	8	on-shelf	-19.16	15.73	50.41	15.06	3.35
Before	RBC	9	on-shelf	-18.92	15.34	50.58	15.10	3.35
Before	RBC	12	on-shelf	-19.54	14.38	52.00	15.56	3.34
Before	RBC	13	on-shelf	-18.88	15.89	51.15	15.23	3.36
Before	RBC	14	on-shelf	-19.70	14.87	50.18	14.93	3.36
Before	RBC	17	on-shelf	-19.24	13.77	49.91	14.95	3.34
Before	RBC	18	on-shelf	-19.12	16.01	49.86	14.86	3.36
Before	RBC	19	on-shelf	-19.52	14.95	47.12	13.98	3.37
Before	RBC	2	off-shelf	-20.01	11.70	50.90	15.12	3.37
Before	RBC	3	off-shelf	-19.60	14.46	51.45	15.32	3.36
Before	RBC	4	off-shelf	-19.90	12.47	51.10	15.23	3.36
Before	RBC	10	off-shelf	-19.70	15.55	50.17	15.01	3.34
Before	RBC	11	off-shelf	-19.89	12.90	50.99	15.05	3.39

Sampling time	Tissue	ID	Foraging location	$\delta^{13}C$	$\delta^{15}N$	$\%^{13}C$	$\%^{15}N$	C/N ratio
Before	RBC	15	off-shelf	-19.28	15.10	49.96	14.92	3.35
Before	RBC	16	off-shelf	-19.46	14.95	50.06	14.98	3.34
Before	RBC	20	off-shelf	-19.53	15.11	46.20	13.69	3.37
After	Plasma	1	on-shelf	-18.85	16.49	45.53	12.24	3.72
After	Plasma	5	on-shelf	-18.55	16.85	46.16	12.44	3.71
After	Plasma	6	on-shelf	-19.72	15.04	47.61	12.43	3.83
After	Plasma	7	on-shelf	-18.20	18.01	46.17	12.13	3.81
After	Plasma	8	on-shelf	-18.85	17.78	45.47	11.84	3.84
After	Plasma	9	on-shelf	-19.19	17.08	45.20	11.95	3.78
After	Plasma	12	on-shelf	-19.02	16.89	47.08	12.20	3.86
After	Plasma	13	on-shelf	-18.74	17.62	43.22	11.36	3.80
After	Plasma	14	on-shelf	-19.00	16.76	45.51	12.18	3.74
After	Plasma	17	on-shelf	-18.82	17.00	43.67	11.28	3.87
After	Plasma	18	on-shelf	-18.32	18.58	45.38	12.16	3.73
After	Plasma	19	on-shelf	-18.93	17.71	44.20	11.30	3.91
After	Plasma	2	off-shelf	-19.79	14.04	46.04	12.01	3.83
After	Plasma	3	off-shelf	-19.60	15.17	38.27	10.00	3.83
After	Plasma	4	off-shelf	-19.58	14.48	43.69	11.49	3.80
After	Plasma	10	off-shelf	-19.63	14.98	47.07	12.61	3.73
After	Plasma	11	off-shelf	-19.64	14.76	46.90	12.33	3.80
After	Plasma	15	off-shelf	-19.49	14.58	47.60	12.70	3.75
After	Plasma	16	off-shelf	-19.28	15.58	45.29	11.92	3.80
After	Plasma	20	off-shelf	-19.51	15.33	44.15	11.72	3.77

Table A.5 Relative proportion (%), average prey mass (in g), prey energy density (ED in kJ/g), energy content (in kJ) of prey species in the diets of female northern fur seal breeding on St. Paul, and of females breeding on Bogoslof Island. Percent in diet (% SSFO) were obtained from morphological identification of hard part remains in our study and from collection of samples of Bogoslof Island rookeries in 2009 (Trites et al. 2015), and mass was calculated from size of hard part remains.

	Prey group	Prey species	% in diet	Mass (g)	ED (kJ/g)	EC (kJ)
ON-SHELF NFS	Gadid	Pollock	62.75	16.48 ± 1.11	3.57 ± 0.30	58.59 ± 0.20
		Pacific cod	7	6.76 ± 1.14	2.94 ± 0.12	19.72 ± 0.11
	Caphalopod	Cephalopod	12.28	3.74 ± 0.29	4.76 ± 0.11	17.79 ± 0.04
	Salmon	Salmon	6.03	797.78 ± 53.65	5.53 ± 0.30	4425.00 ± 9.80
	Hexagrammid	Atka mackerel	2.92	18.69 ±2.37	4.02 ± 0.08	75.19 ± 0.29
		Kelp Greenling	0.72	NA	3.45	NA
	Mesopelagic	Northern smoothtongue	2.42	3.87 ± 0.25	5.67 ± 0.25	21.91 ± 0.05
	Forage	Sand lance	0.83	12.76 ± 0.05	5.06 ± 0.12	64.55 ± 0.05
		Sandfish	0.42	8.01 ± 1.04	3.55 ± 0.13	28.52 ± 0.12
		Capelin	0.28	8.49 ± 0.31	4.35 ± 0.35	36.95 ± 0.11
	Flatfish	Arrowtooth flounder	0.28	3.78 ± 0.01	5.14 ± 0.75	19.45 ± 0.08
	Other	Rockfish sp.	0.33	3.78 ± 0.06	2.97	NA
		Non-fish	2.5	NA	NA	NA
		Worm	1.25	NA	NA	NA
OFF-SHELF NFS	Gadid	Pollock	0.86	16.48 ± 11.45	3.57 ± 0.30	58.59 ± 0.20
	Caphalopod	Octopus sp.	42.70	3.74 ± 0.29	4.76 ± 0.11	17.79 ± 0.04
	Salmon	Salmon	3.87	797.78 ± 8.92	5.53 ± 0.30	4425.00 ± 9.80
	Hexagrammid	Atka mackerel	0.60	18.69 ± 2.37	4.02 ± 0.08	75.19 ± 0.29
	Mesopelagic	Northern lampfish	2.75	2.02 ± 1.01	8.98 ± 1.74	17.84 ± 0.30
		Northern smoothtongue	46.22	3.87 ± 0.25	5.67 ± 0.25	21.91 ± 0.05
	Forage	Pacific herring	0.52	23.49 ± 5.75	6.3 ± 0.22	147.76 ± 1.14
		Sand lance	1.03	12.76 ± 0.05	5.06 ± 0.12	64.55 ± 0.05
	Other	Sablefish	0.86	NA	NA	NA
		Polychaete unident.	0.34	NA	NA	NA
		Threespine stickleback	0.26	NA	NA	NA

Equations to estimate body length and mass of fish and squid

The following equations used to convert the lengths of otolith and squid beaks into body length and mass for nine species consumed by northern fur seals:

Walleye pollock. $FL = 0.50\ OL^2 + 15.74\ OL + 13.3$ (Zeppelin et al., 2004) and $BM = 0.0077 \times FL^{2.906}$ (Frost and Lowry, 1981). Walleye pollock were separated into age classes using the cutting length of 100mm below which they were considered of age-0+ and above which they were of age-1+ (Whitman, 2010; Honkalehto et al., 2012).

Salmon. $BM = 0.0103 \times FL^{3.092}$ (Harvey et al., 2000) . *Simulations*: 31.75 ± 0.14 cm and 797.78 ± 8.92 g (from 55% of fish between 16-24 cm, and 45% between 35 - 59cm).

Atka mackerel. $FL = 8.40\ OL - 4.99$ and $BM = 0.0034 \times FL^{3.401}$ (Harvey et al., 2000) .

Northern smoothtongue. $BM = 0.0106 \times FL^{2.85}$ (Orlov and Binohlan, 2009).

Capelin. $FL = 3.45\ OL + 3.62$ and $BM = 0.0054 \times FL^{3.160}$ (Harvey et al., 2000) .

Pacific herring. $FL = 5.24\ OL - 1.85$ and $BM = 0.0044 \times FL^{3.398}$ (Harvey et al., 2000) .

Arrowtooth flounder. $FL = 4.75\ OL - 2.96$ and $BM = 0.0093 \times FL^{2.999}$ (Harvey et al., 2000). *Simulations*: 6.00 ± 0.005 cm and 3.78 ± 0.006g (from 100% of fish between 5 - 7 cm)

Pacific sand lance. $FL = 4.06\ OL - 2.01$ and $BM = 0.0063 \times FL^{2.790}$ (Harvey et al., 2000). *Simulations*: 15.00 ± 0.02 cm and 12.76 ± 0.05g (from 100% fish between 11 - 19 cm).

Squid. Measures of lower beak rostrum length (LRL) were converted into squid mass using the equations $\ln(BM) = 2.52 + 1.99 \times \ln(LRL)$ (Clarke, 1962).