Title

Dealing with a fast changing environment: the trophic ecology of the southern elephant seal (Mirounga leonina) and crabeater seal (Lobodon carcinophaga) in the western Antarctica Peninsula

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Publication Date

2012

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

Dealing with a fast changing environment: the trophic ecology of the southern elephant seal (*Mirounga leonina*) and crabeater seal (*Lobodon carcinophaga*) in the western Antarctica Peninsula

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

OCEAN SCIENCES

by

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June 2012

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ABSTRACT

Dealing with a fast changing environment: the trophic ecology of the southern elephant seal (*Mirounga leonina*) and crabeater seal (*Lobodon carcinophaga*) in the western Antarctica Peninsula

Luis A. Hückstädt

The foraging behavior of top predators is linked to the distribution and abundance of prey, which in turn is determined by oceanographic features. Thus, the identification of the specific foraging behaviors associated with different environmental conditions is of primary relevance to understanding the foraging behavior of top predators. The southern elephant seal (*Mirounga leonina*) and crabeater seal *(Lobodon carcinophaga*) are important top predators of the Southern Ocean, and as such, they can integrate information about several layers of primary and secondary productivity. Moreover, these two species are part of different trophic pathways of the Southern Ocean. Elephant seals are part of the northern slope and oceanic waters food web, where copepods, mesopelagic fish and squid occupy the mid-trophic levels. Crabeater seals are part of the southern food web, where the Antarctic krill, *Euphausia superba*, is considered the dominant species in the seasonal pack ice zone.

The main goal of my study was to determine what level of flexibility, if any, is displayed by the southern elephant seals and crabeater seals from the western

Antarctic Peninsula (wAP) in their foraging behavior and habitat utilization patterns, using a combination of stable isotope data ($\delta^{13}C$ and $\delta^{15}N$), satellite telemetry data (tracking and diving) and environmental data (from animal-borne sensors, oceanographic models and satellite oceanography) to address two main aspects of the ecology of the two species: (a) Feeding habits and trophic ecology, and (b) Habitat utilization in relation with the oceanography.

Combining stable isotope analysis and satellite telemetry, I studied the variability in individual foraging strategies of adult female southern elephant seals analyses (Chapter 1). Most individuals were specialists, with half of the individuals utilizing 31% or less of their available niche. I found 8 different foraging strategies for these animals. Hence, female elephant seals from the wAP are a diverse group of predators with individuals utilizing only a small portion of the total available niche, and therefore have the potential to expand their range to exploit new niches that will potentially become available as a consequence of environmental change.

Due to the high specialization of crabeater seal to forage on Antarctic krill *Euphausia superba*, the species is particularly vulnerable to the environmental changes that are already occurring in the Southern Ocean as a consequence of the climatic global change. Using stable isotopes, I studied the trophic ecology of crabeater seals from the western Antarctica Peninsula (Chapter 2). The median (range) contribution of Antarctic krill to the diet of the crabeater seal from the western Antarctica Peninsula (wAP) is 87.9 (81.2 – 94.8) %, however the results showed that crabeater seals are capable of displaying trophic plasticity, supplementing their diet with other prey that might be available in the environment (i.e. fish).

I also investigated the foraging behavior of adult female elephant seals from the wAP in relation with the *in situ* oceanographic conditions that they experience during their ca. 8-months post-molt migration at sea (Chapter 3). There was a wide diversity in the areas utilized by elephant seals contradicting the general idea of elephant seals as being part of the northern slope and oceanic waters food web of the Southern Ocean, where copepods, mesopelagic fish and squid occupy the mid-trophic levels, and extends their range into the southern/coastal food web, where the Antarctic krill, *Euphausia superba*, is considered the dominant mid-trophic species.

Finally I present a suit of habitat models for a conspicuous predator of the wAP: the crabeater seal, likely the largest consumer of krill in the world (Chapter 4). Crabeater seals from the wAP presented a coastal distribution, occupying water of the inner continental shelf preferably, and rarely venturing beyond the break of the continental shelf (1,000 isobath). The best habitat model, included variables associated with bathymetry and water column features. Crabeater seals preferred shelf areas between 100 and 200 km from the shelf break, with bathymetric slope of about 5° (~10%), and shallow depths (<500 m deep). As well I found a negative trend between crabeater seals and zones of intrusions of warm, off-shelf Circumpolar Deep Water (CDW).

ACKNOWLEDGEMENTS

Being one the of the few international students in the Costa Lab could have represented an interesting challenge (which it did, to some degree), yet more than anything I have to admit that this experience has brought me incredible opportunities to develop as a professional, offering insuperable opportunities to work in the field all over the world, and with several species of pinnipeds. It also gave me the opportunity to meet incredible people, friends and colleagues, which of course had something to do with me being able to pull this off.

I want to start off by thanking the people who helped me develop my obsession with field work. Samantha Simmons, Stella Villegas, Gitte McDonald, Patrick Robinson, Melinda Fowler, Cory Champagne, Carey Kuhn and Jason Hassrick. All of you were amazing teachers in the field, teaching me (well, I hope!) how to work with seals and sea lions, and are responsible for my inability to say “no” to field work. I also want to thank those of you who have offered me your incredible friendship during my time here, and have helped me at having fun (an important factor to consider), or even gave me a place to live for a while: Melinda Fowler, Samantha Simmons, Gitte McDonald, Stella Villegas, Mike Tift, Patrick Robinson, Kim Goetz, Nicole Teutschel, Autumn-Lynn Harrison, Brett Walker, Jenny Lehman, Rodrigo Beas, Alicia Abadia, Valentino Gonzalez, Feña Duran and Javiera Guedes. I also want to thank Sarah Peterson, Sara Maxwell, Michelle Kappes, Jennifer Maresh, Melinda Conners, Rachael Orben, Cory Champagne, Jason Hassrick, Andreas Walli, Mike Weise, Lisa Schwarz, Yann Tremblay, Greg Breed, Ken Yoda, Chandra Goetsch and others in the Costa Lab. All of you have been incredibly helpful at some point during my time here.

I want to express my gratitude to Dan Costa, my advisor. Dan took me into his lab without really understanding what I was capable (or not) of doing and, despite the fact that my initial research project proved to be a mere utopia, he offered me the opportunity to get involved in Antarctic science, the opportunity to explore new fields which I had no previous experience with, and he encouraged me whenever I had the misjudgment of adding more stuff to my to-do list. Dan can also be hold responsible for the incredible amount of miles that I have in my frequent flyer account. Thanks to Dan I have been part of the most amazing field projects with pinnipeds all over the world, and in the most incredible field sites, from Galapagos to Antarctica.

This project would have not been possible without my committee. Drs. Paul Koch, Raphael Kudela and Eileen Hoffman. The three of you were a very important part during my work at UCSC as a grad student, always been available when I organized a meeting to talk about my project or had some last minute questions about what I was doing (which was maybe a bit too often). You also gave me the opportunity to work with you, in your labs, giving me a hand to solve the random questions that I had through this process, and helped me with analyses and interpretation of the data I gathered.

Andrea Piñones, Mike Dinniman, Daniel Palacios, Kim Goetz, Patrick Robinson, Lisa Schwarz, Greg Breed, Brett Walker, Jenny Lehman, Dyke Andreasen, Leslie Roland and Sora Kim provided incredibly support and help during the tedious task of analyzing the data. Without their help this thesis would have been just a collection of cute pictures of seals. A critical part of this project was the field work which, to my regret, was not all conducted by me. Gitte McDonald has truly been a pivotal part of all this effort, spending months in the Antarctic deploying satellite tags on elephant seals in 4 consecutive years (2005 – 08), and she was also indispensable for the crabeater seals' field work in 2001, 02 and 07. Many others provided invaluable help in the field, and I specially thank Mike Goebel, Yann Tremblay, Cory Champagne, Jenn Burns, Mike Fedak, Dave Shuman, Tracey Goldstein, Stella Villegas, Patrick Robinson, and Samantha Simmons. Field work for the elephant seals deployments was conducted at the NOAA US-AMLR camp, Cape Shirreff, Livingston Island, and their field crews for 2005 to 2009 were essential in the field. I particularly want to acknowledge the 2009 field crew ("Grupo Elite de Captura de Focas"), which helped me when I was there, running the field season. I would also like to express my gratitude to the several crews of the *R/V Laurence Gould* (SO GLOBEC fall and winter cruises in 2001 and 2002, Crabeater seal cruise 2007) for their amazing support. Logistic support for all field work in the Antarctica was provided by National Science Foundation, United States Antarctic Program, Raytheon Polar Services and AGUNSA (Chile).

The Chilean inside me won't let me forget to express my deepest gratitude to my family: Carlos L. Huckstadt, Cecilia Figueroa, Lucia Figueroa, Carlos R. Huckstadt, Andrea Zambrano, Roman Huckstadt and the new addition, Luciano Saavedra. Ustedes siempre están conmigo, son parte de mi. As well, my friends from Chile … You guys have always been there for me.

Funding was provided by NSF (ANT-0840375, ANT-0440687, ANT-0523332 and ANT-0838937), NOPP (N00014-05-1-0645), Marine Mammal Commission, Friends of Long Marine Lab, and CDELSI-UCSC. LAH's doctoral studies were supported by Fulbright-CONICYT (Chile).

The text of this dissertation includes material of the following previously published material:

Hückstädt LA, PL Koch, BI McDonald, ME Goebel, DE Crocker & DP Costa (2012) Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. Oecologia 169(2): 395-406

Hückstädt LA, JM Burns, PL Koch, BI McDonald, DE Crocker & DP Costa (2012) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Marine Ecology Progress Series 455: 287-301.

DEDICATION

In memory of my aunt, Lucia E. Figueroa

“I’m never going to forget what you said… Wait, what did you say?”

SYNTHESIS

The foraging behavior of top predators is linked to the distribution and abundance of prey, which in turn is determined by oceanographic features that increase the availability of prey by physically forcing prey aggregations and, thus, creating areas where foraging efficiency can be increased (Hui 1979, Schneider 1982, Haney 1991, Costa 1993, Elphick & Hunt 1993, Bonadonna et al. 2001). Thus, the identification of the specific foraging behaviors associated with different environmental conditions is of primary relevance to understanding the foraging behavior of top predators, the processes that lead to their high abundances and how these organisms may be affected by annual and long-term changes in the ocean climate (Boyd 1999, Simmons et al. 2007).

The western Antarctica Peninsula (wAP) (Fig. 1) has been recognized as one of the areas of particular interest in the context of climate change, since it is experiencing one of the fastest rates of environmental change in the world (Atkinson et al. 2004, Schofield et al. 2010). Recent studies have linked climatic change with alterations at different levels of the trophic web in the Southern Ocean, from long-term declines in the biomass of the keystone species Antarctic krill (*Euphausia superba*), to important changes in the range and population numbers of different species of top predators (Fraser & Hofmann 2003, Atkinson et al. 2004, Clarke et al. 2007). Among the responses that top predators might exhibit under the current conditions of rapid climate change are changes in their foraging behavior and patterns of movement and at-sea distribution (Trathan et al. 2007, Moore & Huntington 2008).

Southern elephant seals (*Mirounga leonina*) (Fig. 2) are top predators of the Southern Ocean and adjacent ecosystems, where they potentially play an important ecological role over large spatial scales (millions of km^2) as major consumers of squid and fish in the Southern Ocean (Bradshaw et al. 2003, Daneri & Carlini 2002). Female southern elephant seals are pelagic, foraging in wide pelagic areas over the Southern Ocean, although they do venture into the continental shelf waters of the Antarctic Peninsula (McConnell et al. 1992, McConnell & Fedak 1996, Field et al. 2001). On the other hand, crabeater seals (*Lobodon carcinophaga*) (Fig. 3), the most abundant species of phocid in the world, are distributed throughout the coast of the Antarctic continent, closely associated with the pack ice. This species is a specialist predator of Antarctic krill, although some fish can be included in the diet as well (Knox 1994, Zhao et al. 2004). This high level of specialization, along with their high biomass, makes the crabeater seals the largest consumer of krill in the world.

The main goal of my study was to determine what level of flexibility, if any, is displayed by the southern elephant seals and crabeater seals in their foraging behavior and habitat utilization patterns. For this study, I used a combination of stable isotope data, satellite telemetry data (tracking and diving) and environmental data (from animal-borne sensors, oceanographic models and satellite oceanography) to address two main aspects of the ecology of the two species: (a) Feeding habits and trophic ecology, and (b) Habitat utilization in relation with the oceanography.

Feeding habits and trophic behavior

In **Chapter 1**, I present a study that combines stable isotope analysis and satellite telemetry to study the variability in individual foraging strategies of adult female southern elephant seals (*Mirounga leonina*). My hypothesis is that female elephant seals from the Western Antarctica Peninsula (WAP) display individual specialization in their diets. Adult female elephant seals ($N = 56$, 2005 - 09) were captured at Livingston Island (Antarctica), and instrumented with SMRU-CTD satellite tags, and blood, fur, and vibrissae samples were collected for $\delta^{13}C$ and $\delta\ ^{15}N$ analyses. The mean values for all vibrissae were -21.0 ± 0.7‰ for $\delta^{13}C$, and 10.4 ± 0.8‰, for $\delta\ ^{15}N$. The between-individual variability of $\delta\ ^{13}C$ (60%) was more important than the within-individual variability (40%) in explaining the total variance observed in these data. For $\delta\ ^{15}N$, the results showed the opposite trend, with the within-individual variability (64%) contributing more to the total variance than the between-individual variability (36%). Most individuals were specialists, with half of the individuals utilizing 31% or less of their available niche. I found 8 different foraging strategies for these animals. Female elephant seals from the wAP are a diverse group of predators with individuals utilizing only a small portion of the total available niche. Hence, elephant seals have the potential to expand their range to exploit new niches that will potentially become available as a consequence of environmental change.

Despite of being described as one of the most abundant consumers of Antarctic krill *Euphausia superba*, the diet of crabeater seal *Lobodon carcinophaga* has been rarely studied throughout its range. However, this high specialization could make the species particularly vulnerable to the environmental changes that are already occurring in the Southern Ocean as a consequence of the climatic global change. **Chapter 2** presents a study of the trophic ecology of crabeater seals from the western Antarctica Peninsula in 2001 (n = 14), 2002 (n = 29) and 2007(n = 10), 31 females and 22 males, by measuring $\delta^{13}C$ and $\delta^{15}N$ values in vibrissae samples, and used those data to reconstruct the diet of the seals using the Bayesian mixing model MixSir 1.0 v1.0. I observed a wide variability in individual seal mean $\delta^{13}C$ values, which ranged between -24.9‰ and -19.8‰, whereas $\delta^{15}N$ mean value per individual varied between 5.3 and 7.9‰. By using Mixed Effect Models, I identified a positive significant effect of seal mass on $\delta^{13}C$, as well as a significant seasonal effect (higher $\delta^{13}C$ values in Winter compared with Fall). Crabeater seals' $\delta^{15}N$ values, on the other hand, were affected by year, with individuals in 2002 presenting a higher $\delta^{15}N$. Diet reconstruction based on stable isotope analysis showed that the median (range) contribution of Antarctic krill to the diet of the crabeater seal from the western Antarctica Peninsula (wAP) is 87.9 (81.2 – 94.8) %. The higher $\delta^{15}N$ of individual crabeater seals in 2002, likely the consequence of a higher consumption of fish during that year, implied the reduction of krill contribution to the diet that same year to 84.5 (75.1 – 92.4) %, when krill biomass in the study area was at one of its lowest levels during the last two decades. My findings indicate that the crabeater seal is capable of displaying trophic plasticity, supplementing their diet with other prey that might be available in the environment (i.e. fish). However, it is unknown to what extent and at what rate crabeater seals might be able to switch from a krill-dominated diet to a more generalized one, under the current scenery of rapid environmental change that is affecting wAP.

Habitat utilization in relation with the oceanography

In **Chapter 3**, I investigated the foraging behavior of adult female elephant seals from the wAP in relation with the *in situ* oceanographic conditions that they experience during their ca. 8-months post-molt migration at sea.

Adult female southern elephant seals (n = 57) were captured and instrumented with Conductivity – Temperature - Depth (CTD) Satellite Relay Data Loggers (SRDL) (Sea Mammal Research Unit, University of St Andrews). In order to identify foraging areas of importance for the elephant seals, I calculated residual First Bottom Time (*rFBT*) (Bailleul et al. 2008), a scale-dependent measure of search effort derived from two dimensional movement data (Fauchald & Tveraa 2003), which incorporates the vertical dimension in a diving predator. My analysis revealed existence of at least two foraging strategies (Chapter 1, Costa et al. 2010): shelf and pelagic foraging and, consequently, I constructed statistical models for each strategy using Non Parametric Multiplicative Regression (NPMR). There was a wide diversity in the areas utilized by elephant seals along the wAP. Animals identified as shelf foragers were the most diverse in terms of patterns of habitat utilization, ranging from foraging at the shelf break north of the South Shetland Islands, to individuals reaching the shelf break in the Amundsen Sea, whereas pelagic foragers also showed a wide diversity in their patterns of habitat utilization, with animals foraging along the Polar Front, in association with the ice edge off the Amundsen and Ross Seas, or in association with seamounts.

My modeling approach resulted in model with very low predictive power, as indicated by their low xR^2 values (maximum of 0.09). My study presents strong evidence that contradicts the general idea of elephant seals as being part of the northern slope and oceanic waters food web of the Southern Ocean, where copepods, mesopelagic fish and squid occupy the mid-trophic levels, and extends their range into the southern/coastal food web, where the Antarctic krill, *Euphausia superba*, is considered the dominant mid-trophic species (Kock & Shimadzu 1994). Thus, my study suggests that the high variability in the patterns on habitat usage of individual seals affects the performance of statistical models, decreasing the likelihood of identifying general patterns in the data as a consequence of the wide spectrum of variables and interactions among these that the elephant seals experience during their post-molt foraging trip.

In **Chapter 4**, I present a suit of habitat models for a conspicuous predator of the wAP, the crabeater seal (*Lobodon carcinophaga*), a highly specialized specialist predator of Antarctic krill (*Euphausia superba*), and likely the largest consumer of krill in the world. The characteristics of the species, such as its rather limited feeding niche, relatively low mobility, and high dependence on sea ice as substrate, make the crabeater seal a species of high interest in studies of impacts of climate change, since it is likely that this species will be highly impacted by the drastic environmental changes predicted for the area.

A total of 42 crabeater seals were tagged in 2001, 2002 and 2007, which transmitted data between 4 and 189 days. Mean transit rate for seals in this study was 1.8 ± 0.6 km h^{-1}, whereas mean total distance travelled was 2586.6 ± 1720.8 km. Crabeater seals in my study dived to an average depth of 102.3 ± 94.0 m, reaching a maximum depth of 713 m, whereas the mean dive duration was 353.8 ± 195.3 sec, with the longest dive lasting for a little over half an hour (1890 sec, longest dive ever recorded). Crabeater seals from the wAP presented a coastal distribution, occupying water of the inner continental shelf preferably, and rarely venturing beyond the break of the continental shelf (1,000 isobath). Most individuals' movements occurred between Anvers Island and Alexander Island, including Marguerite Bay, with few exceptions of animals heading north of this area to reach the area of the Brandsfield Strait and the South Shetland Islands. I constructed 8 different habitat models using Non Parametric Multiplicative Regression.

The best habitat model, as selected based on log*B* and AUC values corresponded to the model including bathymetric and water column features. Crabeater seals preferred shelf areas between 100 and 200 km from the shelf break, with bathymetric slope of about 5° (~10%), and shallow depths (<500 m deep). As well I found a negative trend between crabeater seals presence and the maximum temperature below 100 m , suggesting that crabeater seals avoid zones of intrusions of warm, off-shelf Circumpolar Deep Water (CDW), as well as sea surface temperatures above the freezing point for sea water (> -0.5°C).

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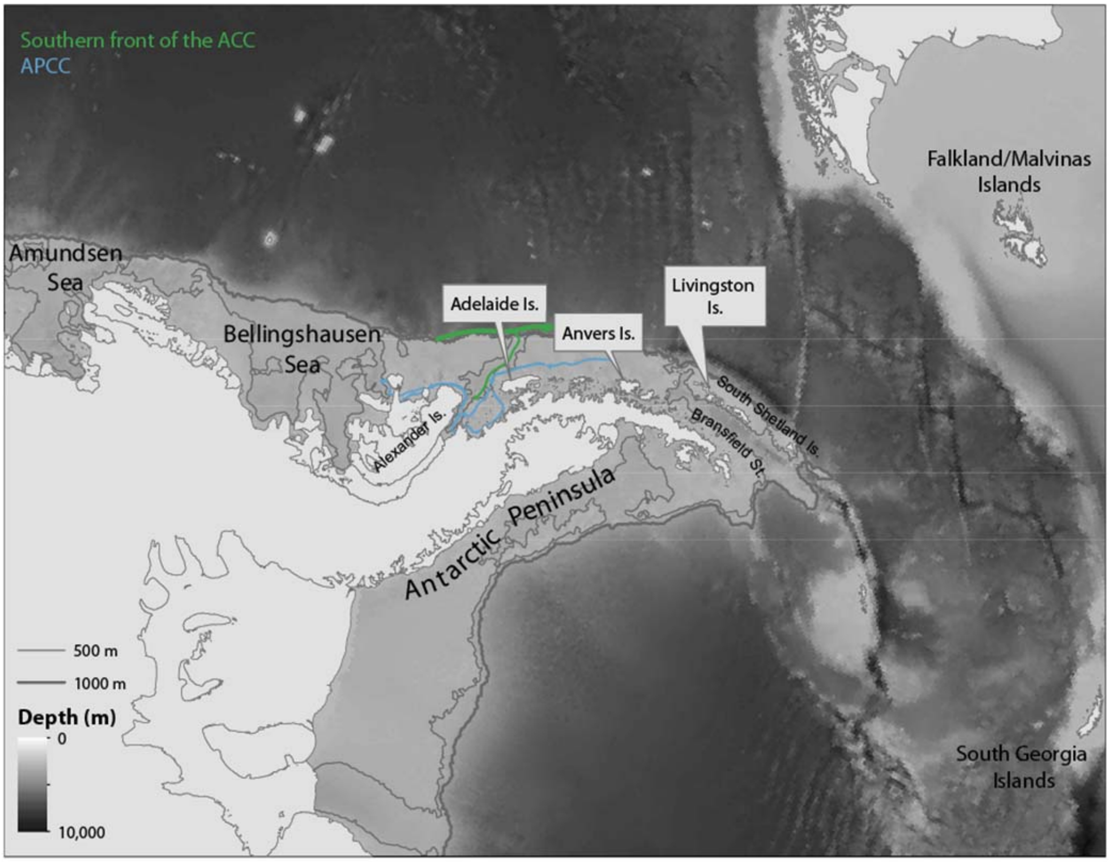

Figure 1. Map of the western Antarctica Peninsula (wAP). The figure shows the location of important landmarks in the study area, as well as the break of the continental shelf (illustrated as the 1,000 m isobaths), and the location of the southern front of the Antarctic Circumpolar Current (ACC, green), and the coastal Antarctic Peninsula Counter- Current (APCC) (modified from (Moffat et al. 2008)).

Figure 2. Southern elephant seal *Mirounga leonina* (Photo by Michal Goebel)

Figure 3. Crabeater seal *Lobodon carcinophaga* (Photo by Daniel Costa).

Chapter 1 STABLE ISOTOPE ANALYSES REVEAL INDIVIDUAL VARIABILITY IN THE TROPHIC ECOLOGY OF A TOP MARINE PREDATOR, THE SOUTHERN ELEPHANT SEAL

Luis A. Hückstädt

Introduction

Knowledge about the food habits of marine top predators is critical for understanding their role in marine ecosystems because it provides information on feeding locations, seasonal prey utilization and prey availability. Marine predators must be able to acquire food resources in highly heterogeneous and unpredictable environments and their foraging behavior is inextricably linked to prey distribution and abundance (Harcourt et al. 2002; McCafferty et al. 1998). We could expect that, in response to the low predictability of the marine environment, individuals from the same species should tend to reduce intra-specific competition by displaying resource partitioning in order to maximize their foraging success.

A specialist species is composed of individuals that consume the same type of prey, i.e. very low or none variation among individuals. However, there are at least two potential mechanisms that can explain a generalist strategy for a species (i.e. wide niche). A generalist species could be composed of: (a) generalist individuals, or individuals exploiting a wide variety of prey, displaying large within-individual variation, and (b) specialists individuals, each individual specialize on a restricted and particular subset of resources that is different from what is being used by other individuals of the same species, displaying large between-individual variation (Araujo et al. 2007; Bearhop et al. 2004; Bolnick et al. 2007; Newsome et al. 2009; Woo et al. 2008). Thus, the identification of foraging strategies of individuals is critical to our understanding of the ecology of a particular species, and can provide tools to understand and predict possible ecological responses to environmental change.

Naturally occurring stable isotopes of carbon ($^{13}C/^{12}C$, or $\delta\,^{13}C$) and nitrogen ($^{15}N/^{14}N$, or $\delta\,^{15}N$) are commonly used to study trophic relationships and feeding habitats of marine mammals (Hirons et al. 2001a; Hobson et al. 1996; Vander Zanden and Rasmussen 2001). As well, large-scale variations in $\delta\,^{13}C$ and $\delta\,^{15}N$ values allow us to reconstruct migratory movements of animals, and provide a useful metric to determine foraging grounds in animals whose foraging habitats range on the order of hundreds of kilometers (Kelly 2000; Newsome et al. 2007; Newsome et al. 2006). Given the variability in tissue-specific metabolic turnover rates, we can also gain information from different time scales by analyzing isotopic ratios on different tissues (Hobson et al. 1996; Kelly 2000). The study of metabolically slower and continuously growing tissue, such as vibrissae or nails, will not only integrate information on the feeding ecology on scales of several months to years, but provides a temporal (longitudinal) record of dietary change since these tissues can be serially sampled

(Cherel et al. 2009; Newsome et al. 2009).

A less explored application of stable isotopes in ecology is their utilization to study individuality in niche width and foraging strategies (Araujo et al. 2007; Bearhop et al. 2004; Jaeger et al. 2010; Newsome et al. 2009). Briefly, we can use the total variance in stable isotopes between individuals as an indicator of the dietary variation among individuals in a population, while the variance along a continuously growing inert tissue (i.e. vibrissae) can be considered an indicator of dietary variation of a particular individual (see Bearhop et al. 2004 and Newsome et al. 2009 for assumptions).

Studies based on at-sea movement and diving patterns of pinnipeds have successfully identified the existence of different individual foraging strategies (Lea et al. 2002; Villegas-Amtmann et al. 2008; Weise et al. 2010). Whereas studies have shown separation in space according to foraging strategies (Villegas-Amtmann et al. 2008), others have shown spatial overlap among strategies, indicating a degree of niche separation among individuals from the same sex or age class that effectively occupy the same areas (Weise et al. 2010). However, the study of individuals strategies in pinnipeds (and other cryptic species) can greatly benefit from using a combination of telemetry data with stable isotopes analysis, since this will provide us with complimentary information on behavior, habitat use and dietary preferences from the level of individuals up to populations, and on a range of scales (Bailleul et al. 2010; Newsome et al. 2010).

Southern elephant seals *Mirounga leonina* play an important ecological role in the Southern Ocean and adjacent ecosystems as major consumers of fish and squid (Bradshaw et al. 2004a; Daneri and Carlini 2002). Differences in foraging strategies and niche separation have been well documented in southern elephant seals from different age and sex groups (Bailleul et al. 2010; Lewis et al. 2006; Newland et al. 2009). Some studies have demonstrated different individual strategies in adult males (Lewis et al. 2006) and juvenile southern elephant seals (Eder et al. 2010). Considering their intrinsic importance for the population and the extensive literature on their foraging ecology as a group, the existence of differences among individual adult female elephant seals has been somehow less explored, despite the fact that significant inter-individual variation can occur within sex, age, or other *a priori* morphological groups (Bolnick et al. 2003).

Along the western Antarctic Peninsula (wAP) southern elephant seals often venture into the continental shelf waters (Costa et al. 2010; Field et al. 2001; McConnell and Fedak 1996). Adult female elephant seals utilize some islands of the wAP as haul out sites, mainly during the molting season (January – February), but also during the reproductive season (October – November), when adults give birth to a fluctuating number of pups every year. Recent tracking data suggest the existence of at least two main foraging strategies of adult females elephant seals tagged in the wAP: about 85% of instrumented adult females display benthic foraging associated with the shelf break along the wAP and the Bellingshausen Sea, while the remaining

15% have an open water mesopelagic foraging strategy (Costa et al. 2010).

Since the majority of the individual adult female elephant seals from the wAP utilize common foraging areas, we can expect them to exhibit mechanisms to minimize competition among individuals. Hence, I hypothesize that shelf foraging elephant seals, which represent the majority of the wAP animals, will display high individual specialization in their diets, as observed from the stable isotopes record along their vibrissae. It follows that, pelagic foragers, a much smaller fraction of the individuals from the wAP, will have a more generalist strategy. Further, I hypothesize the existence of different foraging strategies for shelf foraging elephant seals, as defined from the stable isotope values, movement patterns and diving behavior. Specifically, my aims are (1) to describe the individual variations in the use of resources (i.e. individual specialization or individual generalization), and (2) to identify foraging strategies used by female southern elephant seals from the wAP.

Materials and methods

Animal handling and sample collection

Animal captures were conducted under National Marine Fisheries Service permit No. 87-1851-00. All animal procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at University of California Santa Cruz. Adult female southern elephant seals (*n* = 56) were captured and instrumented during the late molting season (January-February) at Cape Shirreff, Livingston Island (62°39’S; 60°46’W), South Shetland Islands (Fig. 1.1), between 2005 and 2009 (Table 1.1). Animals were immobilized with tiletamine HCl/zolazepam HCl (Telazol ®) administered intramuscularly (1.0 mg/100 kg) and immobilization was maintained with intravenous injections of Ketamine (100 mg/ml, Ketaset, Fort Dodge Animal Health). Females were weighed (Measurement Systems International, capacity 1000 ± 1 kg) and measured.

During the capture, the longest vibrissae for each animal was selected and collected for analysis by pulling it from the root using a pair of tweezers. Samples were washed with distilled water and detergent and allowed to air dry, and then rinsed in an ultrasonic bath with petroleum ether for 15 minutes in order to extract lipids and debris. Vibrissae were measured to the nearest cm, and cut into 1 cm segments, identifying the distal and proximal ends. Each segment was sub-sampled for stable isotope analyses, obtaining a 0.5 ± 0.05 mg sample from the proximal end of the segment. Blood samples were collected from the extradural vein using serum vacutainers. After centrifugation, serum samples were frozen until analysis (-20°C). Samples were freeze-dried and lipids were extracted in petroleum ether using an accelerated solvent extractor (Dionex, Light Stable Isotope Lab, UCSC). Lipid-free samples were then weighed (0.5 ± 0.05 mg) for stable isotope analysis.

In addition to vibrissae and serum, in 2009 (n_{2009} = 15) I also collected fur, serum and red blood cells (RBC, from heparinized vacutainers) to determine variability in $\delta^{13}C$ and $\delta^{15}N$ in tissues of differing metabolic activity. Fur samples were cleaned following the same protocol as with vibrissae samples, whereas RBC samples were treated the same as serum. Six of the females in my sample were recaptured one year after the first handling, when a second vibrissa sample was collected to examine between-year variability in foraging strategy of adult female southern elephant seals.

As part of a concurrent study (see Chapter 3), the females were instrumented with Conductivity – Temperature - Depth (CTD) Satellite Relay Data Loggers (SRDL) (Sea Mammal Research Unit, University of St Andrews). These instruments allowed us to track individual seals and monitor their diving behavior during their post-molt foraging migration following their capture (ca. 8 months later) see Costa et al. (2010).

Sample analysis

Vibrissae samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Carbo-Elba elemental analyzer interfaced with a Finnigan Delta Plus XP mass-spectrometer (Light Stable Isotope Lab, UCSC). Experimental precision, estimated as the standard deviation of replicates of our within-run standards (Pugel) was 0.06‰ for $\delta^{13}C$ and 0.1‰ for $\delta^{15}N$ ($n = 209$).

Data analysis

All data were tested for normality and homogeneity of variance before analysis. When assumptions of normality and homogeneity of variance were not satisfied, and transformations did not improve our data, we used non-parametric statistics. For all statistical tests significance level was set at 95%. Results are reported as mean ± Standard Deviation (SD), unless otherwise stated.

Individual variation (specialization)

I used a Mixed-Effect Model Variance Component Analysis to determine the source of the observed variability in isotopic values (Table 1.1). In my model, I selected year as a fixed variable, and individuals nested within year and Body Condition Index (mass/length^2, BCI) as random variables. The error (residual) term in the model corresponds to the intra-individual variability in $\delta^{13}C$ and $\delta\ ^{15}N$.

To evaluate the individual variability in trophic niche of elephant seals, I followed the approach proposed by Bearhop et al. (2004), and used by Newsome et al. (2009) on sea otters (*Enhydra lutris*) and Jaeger et al. (2010) on procellariiforms. The Between Individual Component (BIC) was estimated as the total standard deviation in the isotopic values of our sampled population. The Within Individual Component (WIC) was the along-vibrissae standard deviation in isotopes for a particular individual. Given the confounding factors that might affect $\delta\ ^{15}N$ (i.e.

periods of fasting, which affect the $\delta^{15}N$ values), I only used the standard deviation of $\delta^{13}C$ for this part of our analysis. The degree of individual specialization (*S*) was calculated according as *S* = *WIC/TNW*, where, *S* is the Specialization Index, and *TNW* is the Total Niche Width (*WIC* + *BIC*). Lower values of *S* indicate higher specialization, while higher *S* values indicate generalist individuals. For this dataset, I defined an extreme specialist as an individual occupying less than 20% of the available niche ($S \leq 0.2$), whereas those occupying 50% or more of the niche ($S \geq 0.5$) were defined as generalists.

Foraging strategies

Tracking data from elephant seals were filtered using a particle filter (Tremblay et al. 2009). Diving locations were then estimated by interpolation along the resultant filtered track. Water column depth for each dive was obtained for each dive location using cubic interpolation from the ETOPO 1-min dataset. Six different parameters were obtained from the SRDLs: (1) Dive depth (m), (2) Bottom time (%, percentage time that the seal spent within 80% of its maximum dive depth), (3) Dive ratio (ratio between the dive depth and bathymetry at that location), (4) transit rate (km h^{-1}), (5) angle between successive locations, and (6) distance to rookery (km). I calculated utilization distribution probabilities (kernel analysis) based on the tracking data (see Costa et al. 2010), weighed by tracking effort. Smoothing parameters for the kernel analyses were calculated using *ad-hoc* method, href.

I used a complimentary approach based on the use of both tracking and diving, and isotopic data to investigate the individual variability in foraging strategies of adult female southern elephant seals from the wAP. After checking for cross-correlation among variables (Pearson correlation), variables were analyzed using Principal Component Analysis (PCA), Varimax rotation. Seven Principal Components (PCs) accounted for 84.7% of the variance, and were loaded into a Hierarchical Cluster Analysis (HCA), using Ward Linkage and Euclidean distance. The optimal number of clusters obtained was determined using a combination of the Root Mean Square Standard Deviation (RMSSTD) and Pseudo-*F* indices.

Vibrissae and foraging ecology

The variation of stable isotopes along the vibrissae of mammals has been used by several authors in studies of trophic ecology of different species (e.g. Cherel et al. 2009; Eder et al. 2010; Lewis et al. 2006; Newland et al. 2011; Newsome et al. 2009), yet there are several unknowns regarding growth rate and retention of vibrissae, which complicates the interpretation of the results of such studies. Some attempts have been conducted to estimate a rate of growth of vibrissae in both otariids and phocids, with values that range between 0.1 and 0.8 mm d^{-1} (Greaves et al. 2004; Hall-Aspland et al. 2005; Hirons et al. 2001b). If I apply these rates to elephant seals, then the time period reflected in vibrissae samples (mean length 11.1 cm) ranges between 139 and 1110 days (mean of 246 d). Additionally, the shedding pattern of vibrissae is not synchronic (Greaves et al. 2004; Hirons et al. 2001b; Newland et al. 2011), and it is likely phocids do not grow their vibrissae continuously, nor retain them between years (as opposed to otariids), which makes attempts to trace back the changes in diet using vibrissae isotopic data problematic. However, for the purposes of my study, I assumed that the along-vibrissae isotopic data represent tissue metabolized during the previous period (year) at sea, as suggested by Newland et al. (2011).

Results

A total of 745 vibrissae segments were analyzed for δ^{13}C and δ^{15}N. Mean vibrissae length was 11.1 ± 2.5 cm. The mean values for all vibrissae (including the basal segment) were -21.1 ± 0.8‰ for δ^{13}C, 10.5 ± 0.9‰ for δ^{15}N. The C:N ratio (% weight) was 3.0 ± 0.1. I found significant variation in the C:N ratio (% weight) along the vibrissae (Kruskal-Wallis, $H = 232.659$, $p < 0.001$), due to a significantly higher C:N ratio of the proximal segment compared with the rest of the vibrissae (post-hoc Dunn's method), and consequently I eliminated this segment from further analysis. Additionally, it is likely that this proximal segment is not pure keratin, but a combination of different tissues that form the follicle. After eliminating the basal segment from my sample ($n = 683$), mean values were -21.0 ± 0.7‰, 10.4 ± 0.8‰, and 2.9 ± 0.1, for $\delta^{13}C$, $\delta^{15}N$ and C:N ratio respectively.

A multi-tissue comparison of individuals captured in 2009 ($n_{2009} = 15$) provided further evidence of the different isotopic values at the base of the vibrissae. Based on tissue-specific turnover rates, serum represents a period of days prior to its collection (i.e. fasting period), while RBCs are representative of a longer period of time, on the order of weeks to a month (i.e. foraging at-sea) (Dalerum and Angerbjorn 2005; Hobson and Clark 1992; Kelly 2000). Fur is grown during the fasting period on land just prior to sampling. Both serum and fur are enriched in $\delta^{15}N$ compared with RBC. The base of the vibrissae lines up with serum and fur in $\delta^{15}N$ (Fig. 1.2), suggesting that this section corresponds to the fasting period, not the foraging period that we are interested in for the purposes of this paper.

Individual variation (specialization)

I analyzed the between-year variability in the foraging strategies of individual adult female elephant seals in a subsample of animals that were opportunistically recaptured the year after the initial sampling ($n = 6$). My results showed that only one individual significantly differed between years for both isotopic systems, while the rest presented no difference in the along-vibrissae values for either $\delta^{13}C$ of $\delta^{15}N$ (Table 1.2). The $\delta^{13}C$ and $\delta^{15}N$ values did not vary significantly between years

(Table 1.1, ANOVA $\delta^{13}C$ $F_{4,50}$=0.89, $p = 0.47$; $\delta^{15}N$ $F_{4,50}$=1.13, $p = 0.35$), and consequently data were pooled together for further analysis. There was a negative relationship between $\delta^{13}C$ and mass ($R^2 = 0.096$, p =0.025), and length ($R^2 = 0.01$, p = 0.019); whereas $\delta^{15}N$ was positively related to mass (R^2= 0.123, $p = 0.011$), and length ($R^2 = 0.023$, $p = 0.001$), although in all cases mass and length only accounted for a small amount of the variation.

I found that most of the differences in $\delta^{13}C$ values are primarily associated with the between-individual variation instead of within-individual variability, which would indicate that female elephant seals are a group of generalist predators composed of individuals that specialize on subset of resources (Fig. 1.3). The results from my Mixed-Effect Model Variance Component Analysis indicate that neither Year nor Body Condition Index were significant in explaining the variance of either isotopic system (Table 1.3). The between-individual variability of $\delta^{13}C$ (60%) is relatively more important than the within-individual variability (40%) in explaining the total variance observed in our data. For $\delta^{15}N$, the results showed the opposite trend, with the within-individual variability explaining 64% of the variance of this isotope, while the between-individual variability accounted for 36% of the variance (Table 1.3).

The calculation of the degree of individual specialization *S*, revealed that adult female elephant seals from the wAP are mostly specialists (Fig. 1.4). Half of the individuals included in this study had specialization indices of 0.31 or less (Fig. 1.4).

My analysis indicated the presence of seven extreme specialists ($S \leq 0.2$), while five individuals (9.3% of individuals in our sample) were identified as generalists ($S \geq 0.5$).

Foraging strategies

I identified 8 groups within the data, which varied in size between 1 and 18 individuals (Fig. 1.5) using PCA and HCA. Seven Principal Components (PCs) explained 84.7% of the variation observed in my data. PC1, PC2, and PC3 are associated with three different sets of variables (movement pattern, diving behavior and stable isotopes values, respectively), while PCs 4 through 7 correspond to a combination between these sets (Table 1.4). Movement patterns (PC1) explained 24.8% of the variance, while diving (PC2) explained 18.1% and stable isotopes (PC3) 12.6% of the variance. The groups identified in my analysis showed differences in both their isotopic values, as well as their foraging behavior, as observed from the telemetry data. There is a clear distinction between Cluster 1 ($n_{Cluster\ 1} = 8$) and the rest of the groups found in my analysis. Cluster 1 is characterized by animals that fed pelagically, as evident from their home range (Fig. 1.5b), transit rate, diving behavior, and particularly their very low dive ratio (Fig. 1.6c-d), with a median $\delta^{13}C$ of -20.6‰, and the lowest median $\delta^{15}N$ (9.8‰). All remaining clusters but Cluster 2 and Cluster 6 corresponded to animals that foraged along the shelf break (500 m isobath), or on the shelf of the wAP and Bellingshausen Sea (Fig. 1.5c-i, as observed from their relatively high dive ratios (Fig. 1.6d).

A clear structure is observed in the dendrogram for these ‘shelf-break’ groups (Fig. 1.5a), and spatial differences in their home ranges and hot spots are evident (Fig. 1.5c-i). For instance, Cluster 3 has two primary core areas in the northern half of the wAP, while having the shallowest dive depths of all clusters (median 304 m) and the second lowest δ^{15}N (median 10.1‰). Cluster 4 has a well-defined and restricted hot spot on the continental shelf west of Alexander Island, while having the highest δ^{15}N (median 10.7‰, Fig. 4d) and the deepest dives (median 423 m). Individuals from Clusters 5 presented relatively high variability in their δ^{13}C values, and were among the more generalist groups after Clusters 1 and 8 (median $S = 0.4$), with a core area that extends along the shelf break from Marguerite Bay south, and into the Bellingshausen Sea. Cluster 7 included specialist individuals (median $S = 0.3$) with the highest median δ^{15}N values among all clusters (10.8‰), and were clearly restricted to the mouth of Marguerite Bay on the wAP. Cluster 8 included animals that focused their foraging on a restricted section beyond the shelf break west of Alexander Island (and west of the core area of Cluster 4) in the Bellingshausen Sea, had the lowest δ^{13}C values of all clusters (median δ^{13}C = -21.7‰), and included the most generalist individuals among the shelf foragers (median $S = 0.4$).

The only two exceptions within my model of pelagic versus shelf foragers corresponded to Clusters 2 and 6. Cluster 2 included the most extreme generalist individuals of my study animals (median *S* = 0. 6, Fig. 1.6e), with the second highest $\delta^{13}C$ (median $\delta^{13}C$ = -20.1‰, Fig. 1.6a), the largest core area along the wAP expanding well beyond the shelf break, and some secondary core areas as far as Bellingshausen/Amundsen transition, and the Falkland Islands. Finally, Cluster 6 constitutes a clear outlier within our model. This group corresponded to one individual (SE06-12) that fed on the Drake Passage. This individual presented the highest $\delta^{13}C$ value among all individuals included in this study ($\delta^{13}C$ = -19.4‰), one of the lowest transit rates (0.7 km h^{-1}) and despite diving to a mean depth of 457 m, it presented a low dive ratio (33.4%), indicating a pelagic behavior.

Discussion

I present evidence on the existence of marked individual variability in the trophic ecology of adult female elephant seals from the wAP, as observed from stable isotopes analysis ($\delta^{13}C$ and $\delta^{15}N$) of vibrissae samples, and supported by diving and tracking data. My data support the idea of female elephant seals as a diverse group of predators, whose variability can be explained as differences within and between individuals.

Vibrissae and foraging ecology

I did not observe a cyclical pattern for vibrissae δ ^{13}C or δ ^{15}N (Fig. 1.3) like the one described for Antarctic fur seals (Cherel et al. 2009), which would indicate that, at most, the vibrissae was limited in its growth to the time elapsed between two fasting periods. A cyclical pattern (i.e. presence of several peaks in δ ^{15}N associated with fasting) is also absent in the data presented by Newland et al. (2011) for several vibrissae collected from the same animal, reinforcing the idea that the information derived from an elephant seal vibrissae does not expand for longer than a year. On the other hand, the lack of a secondary peak in δ ^{15}N before the proximal end (i.e. most recent) would also suggest that the two fasting periods (breeding and molting) could be confounded into one high δ^{15}N value at the base of the vibrissae, indicating a very limited growth for whiskers between these two periods. Yet, further investigation is necessary to clarify this.

I was able to recapture a subset of six individuals one year after the original vibrissae sampling. The comparison of the isotopic data from vibrissae collected in successive years can be used to provide an insight into the inter-annual variability of foraging habits of the same individuals and can validate my approach of comparing isotopic data (i.e. reflecting the foraging behavior of the individual before the collection), with satellite telemetry data (i.e. obtained for the year following the sample collection). Only one animal presented significant differences in both δ^{13}C and δ^{15}N between sampling years (SE07-07), although these differences were associated with a smaller SD in both isotopes for the sample collected in early 2007 (i.e. representing the foraging activity of that individual in 2006) compared with the sample collected in 2008. This particular individual was among the smallest seals included in our sample (mass = 317 kg, length = 272 cm), and presumably one of the youngest animals included in this study.

My findings on general fidelity to foraging ground in elephant seals, as revealed from the consistency in isotopic values for animals recaptured in consecutive years, confirm previous results obtained from tracking data. Satellite telemetry tracking data obtained from individual northern elephant seals followed during two or more foraging migrations in the North Pacific indicate a high degree of fidelity, not only with respect to foraging areas, but also to migratory routes (Simmons 2008), and similar consistency has been observed for individual female southern elephant seals from the wAP captured in different years (Hückstädt et al. unpublished). Furthermore, it has been observed that adult female southern elephant seals demonstrate a high degree of fidelity to foraging grounds between years, with an overlap of foraging areas of about 65% between successive foraging grounds (Bradshaw et al. 2004b).

Fasting and $\delta^{15}N$

The interpretation of δ^{15}N values from fasting animals is complicated by the fact that animals “feed on themselves”, which results in an artificially high δ^{15}N value as a consequence of the preferential excretion of ^{14}N from the already ^{15}N-enriched consumer's body (Cherel et al. 2005; Hobson et al. 1993; Kelly 2000). The magnitude of this enrichment, however, is tissue-dependent (Cherel et al. 2005), which adds uncertainty to the analysis of feeding habits of consumers based on δ^{15}N values of tissues that are affected by a fasting signal.

For the adult female elephant seal, blood serum (with a turnover rate of days) and fur (which grows rapidly during the haul out molting period) can be assumed to represent isotopic values corresponding to the fasting period. I observed that both tissues have high δ^{15}N values (12.0 and 11.6‰, respectively, Fig. 1.2). RBCs, on the other hand, represent a period of weeks to months of active foraging at sea, and its lower δ^{15}N value (10.5‰) is indicative of foraging, not fasting. The root of the vibrissae (i.e. most recent deposition) presented δ^{15}N values higher than the rest of the vibrissae (11.7 versus 10.6‰), indicating that this segment grew while the animals were fasting, and therefore the root was discarded from further analyses. Additionally, the C:N ratios were higher at the base of the vibrissae, even after lipid extraction, indicating a different tissue composition. It is likely that the base of the sample includes some skin and parts of the follicle that are not pure keratin. Thus, future studies should consider this variability in isotopic values along samples like vibrissae or feathers, whether associated with metabolic processes like fasting or different tissue composition, when using them to describe the foraging behavior or ecology of a particular species.

Individual specialization and foraging strategies

Individual seals included in my study are part of the South Georgia stock, the largest stock of the species throughout its range (app. 54% of the world's population), which has been suggested as stable after experiencing a rapid recovery following the cease of the sealing activities in the mid 1900's (Boyd et al. 1996; Laws 1994). It includes colonies and haul out sites in the South Georgia and Falkland archipelagos and other Sub-Antarctic Islands in the Atlantic sector of the Southern Ocean, as well as the South American and Antarctic continents. Given the large population size of this stock, we can expect individual seals to exhibit mechanisms to minimize competition with conspecifics.

$\delta^{13}C$ presents a latitudinal variation (lower values in high latitudes) as a consequence of biochemical processes at the level of primary producers, which is ultimately reflected throughout the trophic web (Goericke and Fry 1994; Graham et al. 2009; Popp et al. 1999), thus becoming a powerful indicator of habitats used by consumers, particular in the Southern Ocean where this latitudinal variation is more accentuated. Hence, the low $\delta^{13}C$ values observed in the animals included in our sample confirm that female elephant seals from the wAP utilize Antarctic waters, as observed from satellite telemetry (Costa et al. 2010, this study). Taking into consideration the differential trophic enrichment between whole blood and vibrissae

(Hobson et al. 1996), we can compare our results with isotopic data on adult female elephant seals from other colonies.

Previous studies on the trophic ecology of adult female elephant seals from the Eastern Pacific showed a squid-dominated diet of pelagic animals versus a fish-dominated diet of shelf foragers (Bradshaw et al. 2003). As well, studies on the feeding habits of elephant seals from the Kerguelen Islands (Indian Ocean) using stable isotopes found that the diet of the species was dominated by myctophid fishes rather than squid (Cherel et al. 2008). Individuals in my sample have $\delta^{13}C$ values similar to animals from Sub-Antarctic colonies known to forage in Eastern Antarctic waters (Bailleul et al. 2010; Cherel et al. 2008; Ducatez et al. 2008), while the $\delta^{15}N$ values of seals in my sample is about 1‰ lower. I propose that these small differences, likely due to problems associated when interpreting isotopic data collected from different tissues (i.e. whole blood versus vibrissae) are indicative of female elephant seals occupying similar environments/feeding on similar prey throughout their Antarctic distribution.

Despite the mentioned similarity of isotopic values among individuals seals exploiting resources in different sectors of the Antarctic continent, female elephant seals from the wAP present a characteristic foraging behavior, with about 85% of the foraging in continental shelf waters of Antarctica (Costa et al. 2010; Field et al. 2001; McConnell et al. 1992; McConnell and Fedak 1996, Fig. 1.1, Chapter 3), as opposed to the most common pelagic foraging strategy of individuals from other sites. Yet, the lack of isotopic data of elephant seal prey for the entire spatial range utilized by individuals in this study, prevents us from linking their relative low $\delta^{15}N$ with the potential dominance (or absence) of squid in the diet of elephant seals. Hence, the question remains open for seals from the wAP, although differences in the diet of open water and shelf foragers is highly likely, including the possibility of a squid dominated diet for open water foragers.

Individuals included in our study presented a wide variability in their $\delta^{13}C$ and $\delta^{15}N$ values (-22.65 to -18.47‰ and 8.79 to 12.75‰, respectively). The wide ranges observed indicates that adult female elephant seals from the wAP are a diverse group of predators, exploiting prey in different areas of the Southern Ocean and at least at two different trophic levels. For $\delta^{13}C$, 60% of the variation observed in our data is associated with differences among individuals (Table 1.3), indicating that individual adult female elephant seals are exploiting different habitats, water column depths, and ultimately prey sources throughout their range.

The existence of niche partitioning among different age and sex classes has been described for both southern and northern elephant seals *M. angustirostris* (Bailleul et al. 2010; Bradshaw et al. 2004b; Eder et al. 2010; Le Boeuf et al. 2000; Lewis et al. 2006). Evidence of inter-individual niche differences of adult female elephant seals has also been studied in recent years using fatty acids and stable isotopes analyses (Bradshaw et al. 2003; Ducatez et al. 2008; Lewis et al. 2006), yet the topic of individuality, in terms of individual niche width relative to the population's niche width, is not well understood despite the fact that it can help discern variability among species, conspecifics populations, and even among individuals within a population (Bolnick et al. 2003).

My data provided evidence that adult female elephant seals are specialized individuals, with a rather limited individual niche width relative to the total niche available for them as a group. Half of the individuals sampled for this study occupied less than 31% of the total niche width (Fig. 1.4) and, more interestingly, we identified extreme specialists in our sample. A similar study on sea otters (*Enhydra lutris*) found individuals as having low intra-individual variability (WIC), while having high inter-individual variability (BIC), confirming previous observational studies indicating that individual sea otters have highly specialized and constant diets through time (Newsome et al. 2009). Despite this similarity with our study, our data from recaptured animals showed that elephant seals are capable of feeding plasticity. One individual in our study (SE07-07) switched from an extreme specialized strategy in one year (2006, $S = 0.13$), to a relatively more generalist strategy two years later (2008, $S = 0.37$) (Table 1.2).

We found a clear distinction between animals that foraged on the shelf of the wAP (Fig. 1.5c-i) and those who preferred open waters (i.e. pelagic animals) (Fig.1.5b). Furthermore, the diversification identified among the individuals that used the shelf as their habitat is particularly interesting. Cluster 2 (generalists) included animals with movement patterns and diving behavior indistinguishable from the other shelf foragers (Fig. 1.6c-d), yet it included individuals with the highest *S* (i.e. generalists), the second highest $\delta^{13}C$ values (indicating a 'northern' foraging range) and the smallest body sizes (Fig. 1.6f).

We found some evidence of ontogenetic changes in foraging strategy which is consistent with previous studies where they observed as juvenile males switch from a 'female-like' strategy to a more defined 'adult male strategy' with age (Bailleul et al. 2010). It has been shown that there is a sigmoidal relationship between age and standard length of adult female elephant (Bell et al. 2005), suggesting that the smallest seals (Cluster 2) were likely the youngest in our sample. Coincidentally, these individuals were also the more generalist seals in our sample (Fig. 1.6e). On the other hand, we found the opposite results for individuals from Cluster 7, with the longest mean body size (i.e. oldest) and highest specialization (lowest *S*, Fig. 1.6e, f), suggesting an ontogenetic change in foraging strategies of females. However, we did not find a relationship between body length and Specialization Index when data for all individuals were pooled together. Thus, we propose that, instead of a constant trend towards specialization with age, female elephant seals go through an exploratory phase in terms of their foraging habits when they exhibit maximum generalization, until they reach an age after which they consistently display the same foraging strategy (more specialized), a pattern similar to the ontogenetic changes in foraging behavior observed in males (Bailleul et al. 2010). Evidence of this consistency on adult female foraging strategies has also been observed for northern elephant seal females (Simmons 2008).

The trophic ecology of southern elephant seals is particularly difficult to describe using traditional techniques (i.e. stomach content and scat analyses), since individuals from both sexes engage in long-scale migration (in the order of thousands of kilometers in distance and months in time), making it highly unlikely that the scats or stomach samples collected on land are representative of the entire foraging trip. Stable isotope analysis of metabolically slow tissue (i.e. vibrissae) offers an excellent alternative, as it provides information both on the foraging ecology integrated over months (Hobson et al. 1996, Kelly 2000, Hall-Aspland et al. 2005, Newsome et al. 2009), as well as a record of the dietary variability of individuals over that time scale.

The relative proportion of individual specialists and generalists varies widely among species and even among populations of the same species (Bolnick et al. 2003). Our sample consisted exclusively of individual elephant seals captured in the Antarctic continent, where most of them feed. Most colonies of the species, however, occur in Subantarctic Islands, and consequently animals must travel considerable distances to forage in Antarctic waters, and are exposed to different environments during their post-molt migration. Given the variability in foraging behavior observed in this study, it would be instructive to examine the individual variability of the species throughout its range, which will provide a better understanding of the ability of southern elephant seals to cope with environmental change.

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Table 1.1. Vibrissae stable isotope values ($\delta^{13}C$, $\delta^{15}N$), C:N ratio, body mass and length of adult female *Mirounga leonina* from the Western Antarctica Peninsula, 2005-2009.

Year	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N	Mass (kg)	Length (m)
2005	6	-21.23 ± 0.69	10.38 ± 0.26	2.98 ± 0.06	419 ± 98.67	2.86 ± 0.14
2006	12	-21.11 ± 0.8	10.43 ± 0.5	2.94 ± 0.03	362.17 ± 65.21	2.73 ± 0.18
2007	12	-21.24 ± 0.55	10.35 ± 0.37	2.99 ± 0.02	343.09 ± 35.6	2.71 ± 0.08
2008	11	-20.9 ± 0.5	10.28 ± 0.43	2.97 ± 0.02	344.6 ± 51.55	2.67 ± 0.1
2009	15	-21.28 ± 0.31	10.64 ± 0.66	2.96 ± 0.02	422.92 ± 67.85	2.79 ± 0.11

Table 1.2. Variability in isotopic values of vibrissae samples of adult female *Mirounga leonina* collected in consecutive years from the same individuals. Bolded values indicate significant differences between years.

	$\delta^{13}C$		$\delta^{15}N$	
Individual	F-ratio	*p*	F-ratio	*P*
SE06-01	2.42	0.15	0.013	0.91
SE06-08	1.62	0.22	0.2	0.66
SE06-12	0.285	0.6	0.116	0.74
SE07-01	0.031	0.86	1.235	0.283
SE07-03	1.65	.22	0	0.98
SE07-07	**15.469**	**.001**	1.341	.262

Table 1.3. Variance component analysis for vibrissae $\delta^{13}C$ and $\delta^{15}N$ data of adult female *Mirounga leonina* from the Western Antarctica Peninsula (ANOVA estimation method, Type III sums of squares)

	$\delta^{13}C$	$\delta^{15}N$
Effect	Variance explained (%)	Variance explained (%)
Year	NS†	NS
Individual (Year)	60	36.02
BCI	NS	NS
Intra-Individual	40	63.98

†NS: Non significant effect

Table 1.4. Principal Component Analysis rotated loading matrix for 14 variables used to identify foraging strategies in adult female *Mirounga leonina* from the Western Antarctica Peninsula.

	PC1 (24.8%)	PC2 (18.1%)	PC3 (12.6%)	PC4 (11.1%)	PC5 (7.6%)	PC6 (5.6%)	PC7 (4.9%)
$\delta^{13}C$	-0.201	-0.167	**0.363**	-0.220	0.055	**-0.698**	0.120
SD $\delta^{13}C$	-0.113	-0.048	**0.451**	**0.471**	-0.095	-0.164	-0.006
$\delta^{15}N$	0.251	0.203	0.171	**0.394**	-0.123	**0.267**	0.153
SD $\delta^{15}N$	-0.087	-0.147	**0.518**	0.159	0.129	**0.271**	**-0.561**
Mean dive depth	**0.315**	**0.430**	0.104	-0.174	0.030	-0.031	-0.043
SD of dive depth	0.069	**0.415**	0.191	**-0.401**	0.186	0.146	-0.004
Mean bottom time	0.256	**-0.445**	-0.119	-0.049	-0.065	0.189	**-0.169**
SD bottom time	-0.215	**-0.377**	-0.121	**-0.346**	**-0.213**	0.180	**-0.194**
Mean dive ratio	0.260	-0.001	-0.139	0.187	**-0.675**	**-0.240**	0.030
Mean transit rate	**-0.413**	0.241	0.039	-0.052	**-0.360**	0.085	**-0.180**
Mean turning angle	**-0.367**	0.091	-0.270	0.237	**0.237**	-0.070	0.066
SD turning angle	**0.344**	-0.088	**0.314**	**-0.329**	-0.202	-0.080	-0.029
Distance to colony	**-0.353**	**0.315**	0.010	-0.136	**-0.411**	0.071	-0.161
Body length	0.213	0.190	**-0.314**	0.124	0.137	**-0.412**	**-0.718**

Figure 1.1. Satellite tracks (yellow) from 56 adult female southern elephant seal (*Mirounga leonina*) from the Western Antarctica Peninsula between 2005 and 2009. The star (inset) indicates the sampling location (Cape Shirreff, Livingston Island, South Shetland Islands). The thick lines show the typical location of the Polar Front Zone (PFZ), bound roughly between the 5°C (SubAntarctic Front, SAF, light blue) and 2°C (Polar Front, PF, dark blue) isotherms. The gray thin line represents the 500 m isobath (shelf break for the Antarctic Continent).

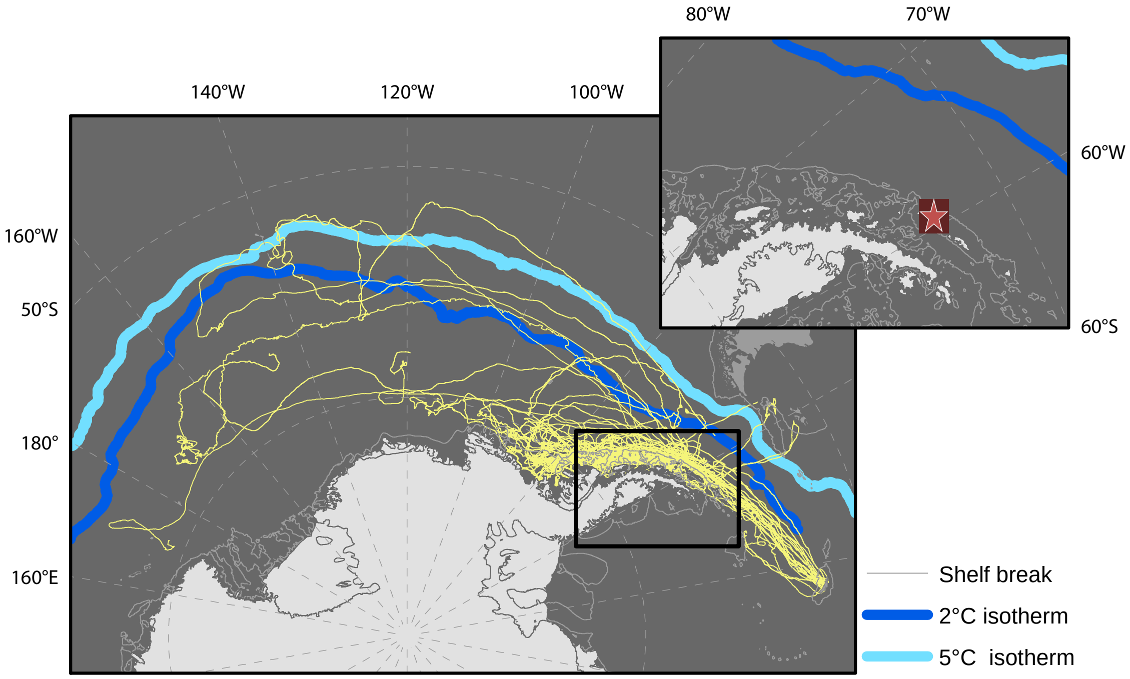


Figure 1.2. Multi-tissue comparison of $\delta^{13}C$ and $\delta^{15}N$ values of adult female southern elephant seals *Mirounga leonina*. Symbols represent mean values and bars represent Standard Deviations (SD). Grey symbols correspond to tissue grown during the molting fast. Black symbols correspond to tissue metabolized previous to fasting (i.e. at-sea foraging).

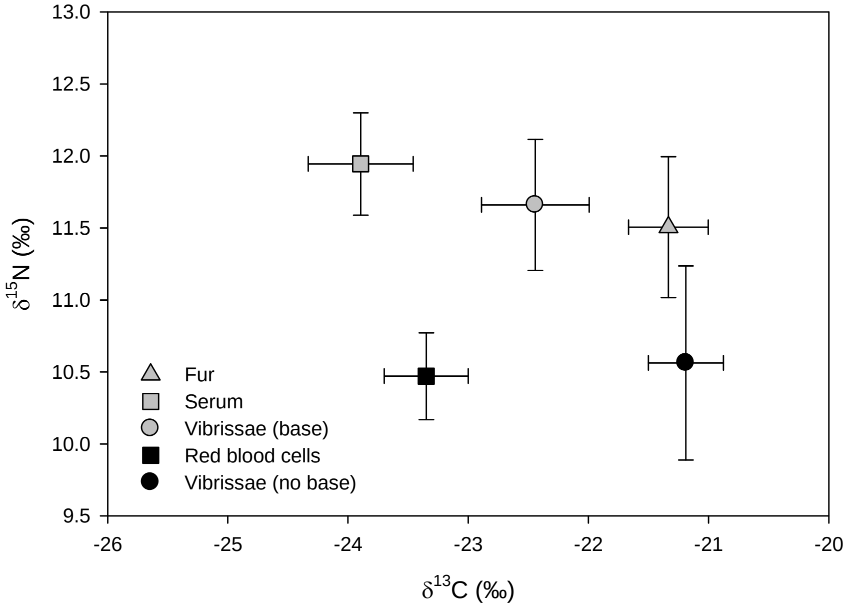


Figure 1.3. Variation of $\delta^{13}C$ along vibrissae samples from a subset of individual adult female southern elephant seals (*Mirounga leonina*) from the Western Antarctica Peninsula. Gray lines represent the three most generalist individuals in the sample (highest along-vibrissae variability in their $\delta^{13}C$). Black lines correspond to the three most extreme specialist individuals in the sample (lowest along-vibrissae variability in their $\delta^{13}C$ values).

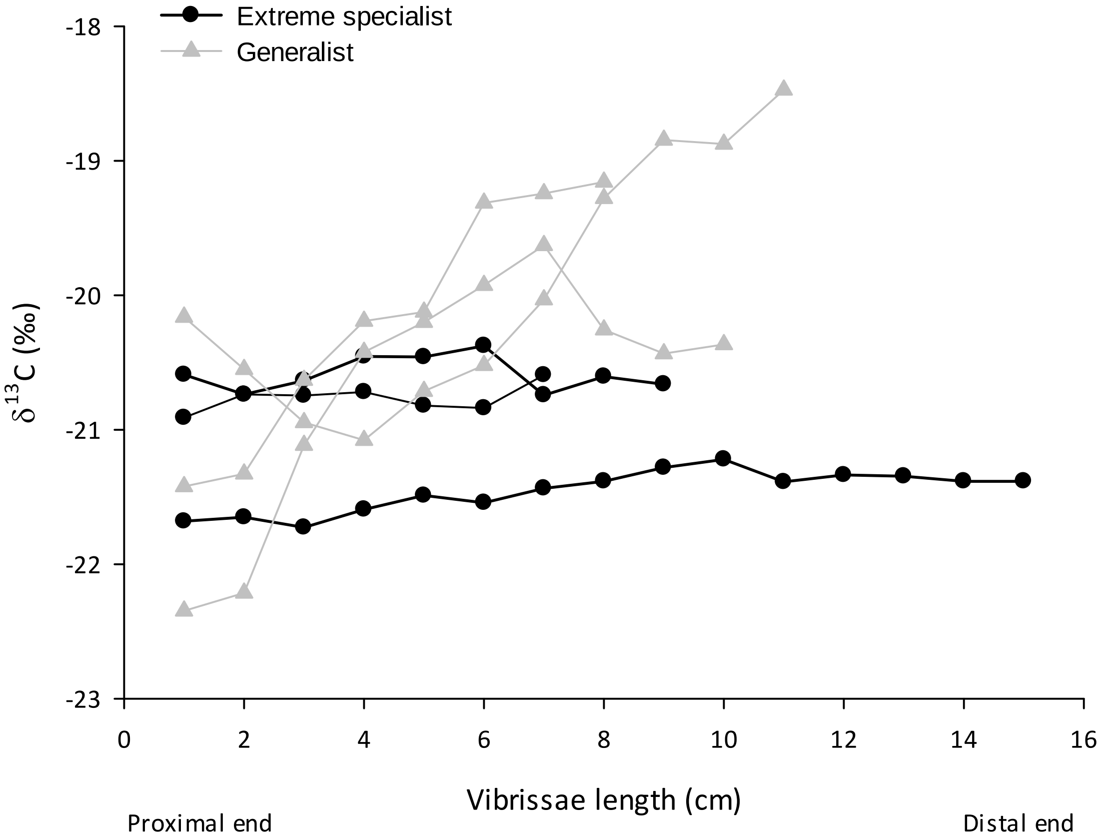


Figure 1.4. Frequency distribution of the Specialization Index (S) of adult female elephant seals *Mirounga leonina* from the Western Antarctica Peninsula (N = 56).

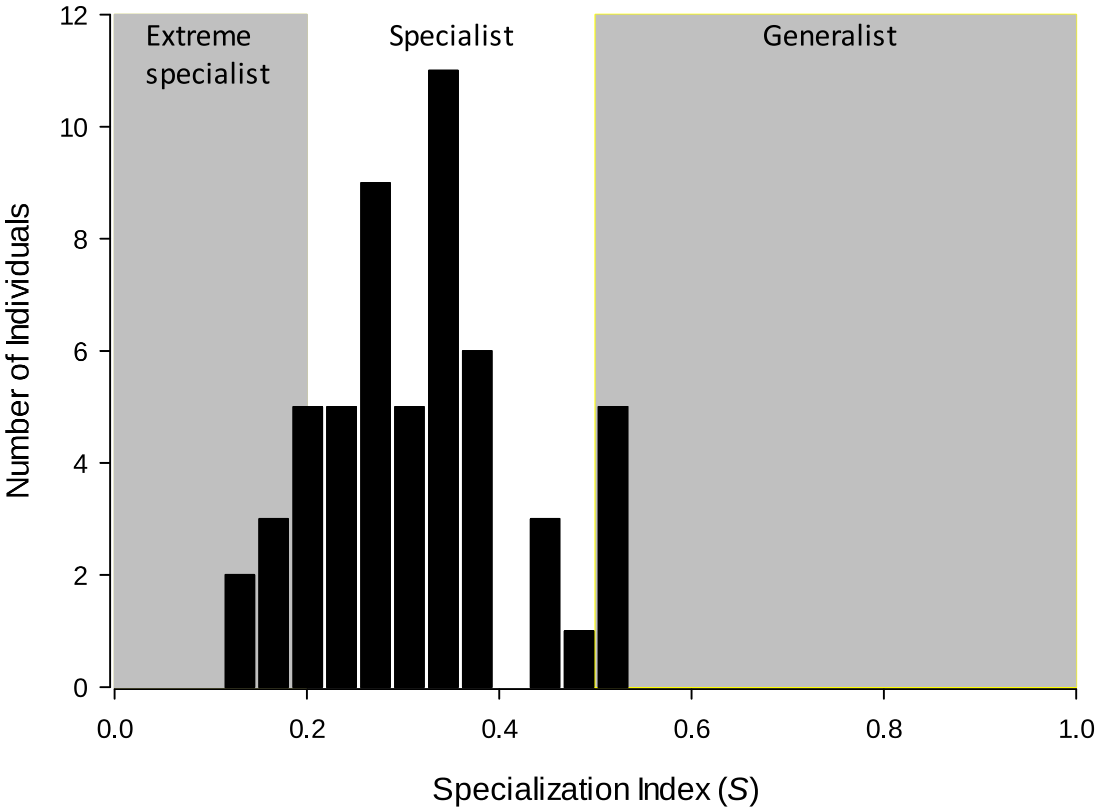


Figure 1.5. Dendrogram of foraging strategies of adult female elephants seal *Mirounga leonina* from the Western Antarctica Peninsula.

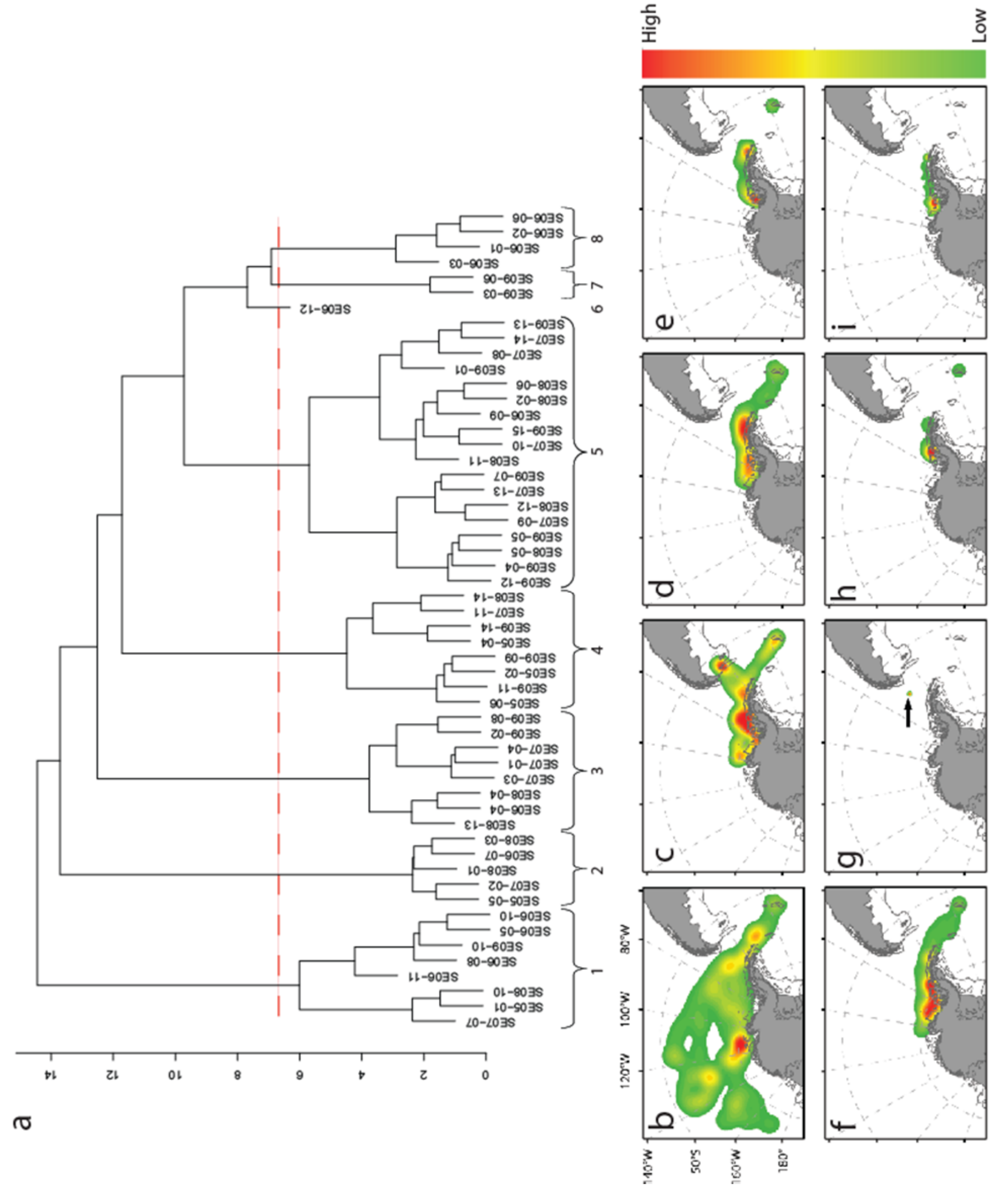
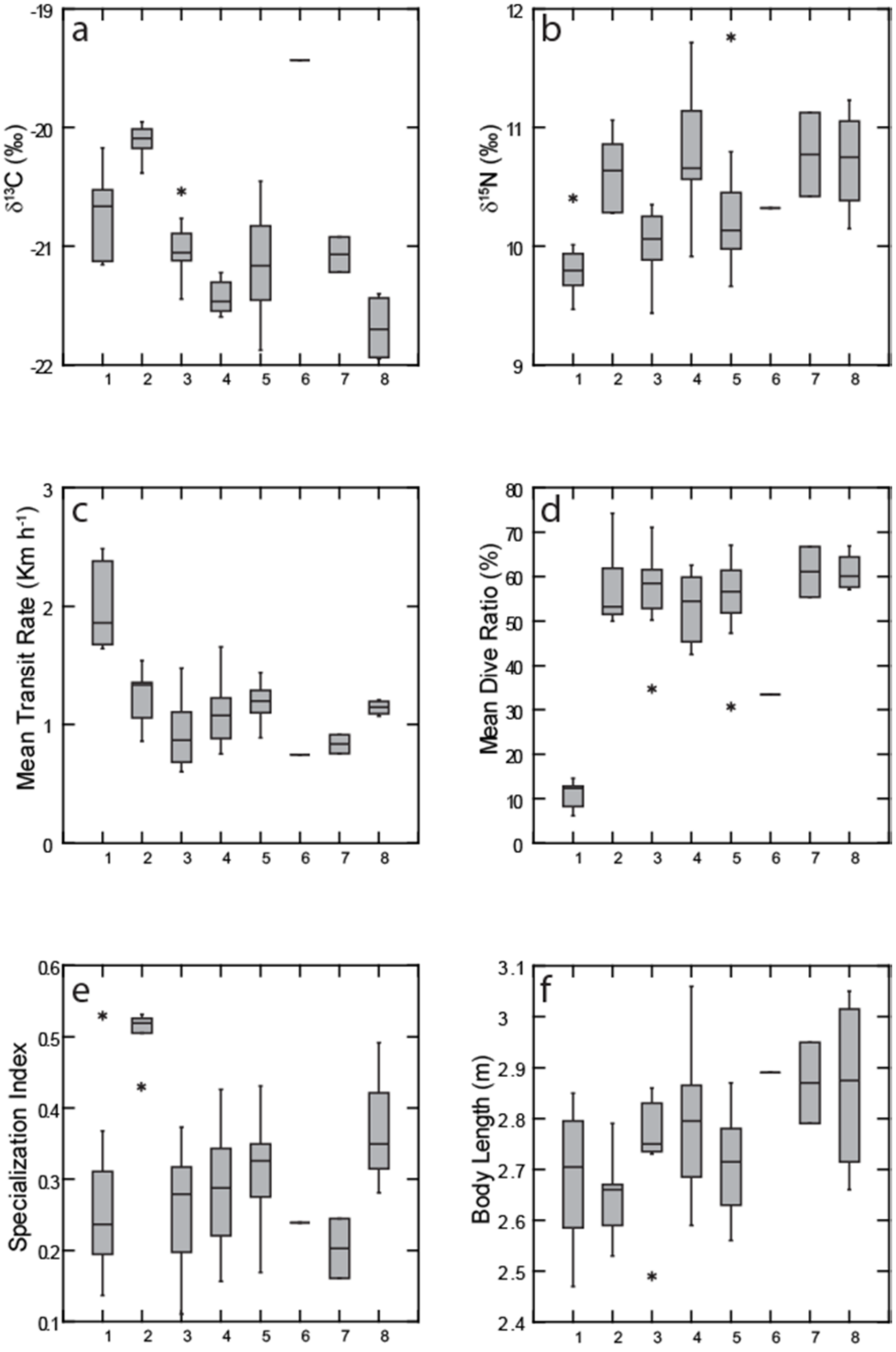


Figure 1.6. Differences in the foraging strategies of adult female elephant seal *Mirounga leonina* from the Western Antarctica Peninsula.



Chapter 2 BEING A SPECIALIST IN A CHANGING ENVIRONMENT: THE DIET OF THE CRABEATER SEAL ALONG THE WESTERN ANTARCTICA PENINSULA

Luis Alfredo Hückstädt

Introduction

The western Antarctic Peninsula (wAP) is one of the most biologically productive areas of the Southern Ocean (Prezelin et al. 2000, Marrari et al. 2008). Mid-trophic level species shape the dynamics of the entire wAP ecosystem, forming two very distinctive trophic webs. Copepods, mesopelagic fish and squid, occupy the mid-trophic positions of the northern slope and oceanic waters food web along the wAP. Antarctic krill *Euphausia superba* is the dominant mid-trophic level species of the Southern food web in the pack ice zone, and therefore a major player in the entire ecosystem of the Southern Ocean (Kock & Shimadzu 1994, Hofmann & Hüsrevoglu 2003). Further, the wAP is an area of unusually high production of Antarctic krill (Atkinson et al. 2004, Howard et al. 2004, Moline et al. 2004). The large and persistent biomass of krill and other mid-trophic species in this region of the Southern Ocean sustains a large biomass of endothermic top predators (Costa & Crocker 1996, Ducklow et al. 2007), possibly the most important community of endothermic top predators in the world in terms of energy flux (Croxall 1992).

The wAP is a region with one of the greatest rates of environmental warming in the world, although the impacts of such rapid change on the marine ecosystem are still unclear (Atkinson et al. 2004, Stammerjohn et al. 2008). Recent studies have linked climatic change with perturbations at different levels of the trophic web, from long-term declines in krill biomass to shifts in the range and abundance of different species of penguins (Fraser & Hofmann 2003, Atkinson et al. 2004, Clarke et al. 2007, Costa et al. 2010). Top predators might also respond to climate change by alterations in their foraging behavior, movement patterns and at-sea distribution (Trathan et al. 2007). Because it is likely that climate change will primarily impact predators through alterations in prey distribution (Croxall 1992), shifts in the foraging behavior of top predators can provide us with an insight into the underlying changes of prey fields (Wall et al. 2007).

The crabeater seal *Lobodon carcinophaga* is one of the most abundant species of large mammals, with worldwide population estimates that vary between 14 and 30 million individuals (Erickson et al. 1990, Southwell et al. 2004, Knox 2007, Bengtson 2009). Endemic to Antarctic waters, the species is distributed along the coast of the continent, where it is considered a highly specialized predator of Antarctic krill, which accounts for over 90% of its diet, and the remainder made up of fish and other invertebrate (Laws 1977, Green & Williams 1986, Zhao et al. 2004, Knox 2007).

Such dietary specialization, along with their relative high biomass, makes the crabeater seal one of the largest consumers of krill in the world (Laws 1977, Hill et al. 2006, Hewitt & Lipsky 2009). On the other hand, however, this high level of specialization could make crabeater seals particularly vulnerable given the expected reductions in krill abundance as a result of the retreats in sea ice under the current conditions of rapid climate change (Loeb et al. 1997, Stammerjohn et al. 2008).

Despite its high abundance and its role as one of the most abundant consumers of Antarctic krill, there are only a handful of studies on the crabeater seal diet, based on stomach contents or scat analyses (Laws 1977, Green & Williams 1986, Lowry et al. 1988, Bengtson 2009). This approach is widely used in diet studies of marine mammals due to their high likelihood of finding samples with identifiable prey and its low cost, but these studies provide only a partial and/or snapshot view of the prey consumed (and not necessarily assimilated), and the results may be biased based on differential digestibility of prey taxa (Bowen 2000, Tollit et al. 2003). Hence, our knowledge of the variability of diets among individual crabeater seals at different temporal scales (from seasons to years) is limited or nonexistent.

Here, I present isotopic data ($\delta^{13}C$ and $\delta^{15}N$ values) from vibrissae samples collected from crabeater seals in 2001, 2002 and 2007 along the wAP, and use those data to reconstruct the diet of the species using the Bayesian mixing model MixSIR (Moore & Semmens 2008). Stable isotopes, particularly $\delta^{13}C$ and $\delta^{15}N$, are widely used in studies on feeding habits of animals since isotopic values in a given species are correlated with those of the prey items included in its diet; and food webs, given that isotopes either fractionate or change in a predictable fashion between trophic levels and thereby reflect trophic position (Deniro & Epstein 1978, Vander Zanden et al. 1997, Hirons et al. 2001a, Vander Zanden & Rasmussen 2001). By measuring isotopic values along the vibrissae my study (1) incorporates dietary information integrated over a time scale of months or years (Hobson et al. 1996, Hall-Aspland et al. 2005), and (2) examines within individual variability in the diet, since vibrissae contain a time series of information for the period during which it was formed (Cherel et al. 2009, Newsome et al. 2009).

Materials and methods

Sample collection

Adult crabeater seals (N = 53, Table 2.1) were captured in 2001 (*n* = 14), 2002 (*n* = 29) and 2007 (*n* = 10) during three cruises to the Crystal Sound/Lau Beeouf fjord/Marguerite Bay area along the wAP on board the *ARSV Lawrence M. Gould* (Fig. 2.1). Cruises in 2001 and 2002 were part of the US Southern Ocean GLOBEC (GLOBal ocean ECosystems dynamics) program (Hofmann et al. 2004) and data on habitat use, diving and foraging behavior, and body condition of these individuals have been published elsewhere (see Burns et al. 2004, Gales et al. 2004, Burns et al. 2008, McDonald et al. 2008, Costa et al. 2010).

Animals were sighted from the bridge of the vessel and approached by foot or inflatable boat, to deliver an intramuscular injection of Telazol (0.8 - 1.2 mg kg^{-1}, 2001) or Midazolam (0.5 - 0.75 mg kg^{-1}, 2002 and 2007), administered via a jab-stick or dart gun to sedate each animal. After the induction, animals were manually restrained with a hoop net, and isofluorane combined with oxygen was administered via a gas mask (Gales et al. 2005). Morphometric measurements were collected for each animal (mass and straight line length), and vibrissae were collected by plucking them.

Stable isotope analysis

Vibrissae samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ values. Two different protocols were followed for the treatment of samples in the laboratory: (1) vibrissae from 2001 and 2002 were washed with ethanol, allowed to air dry and then subsampled, so that an isotopic sample was collected, on average, every 0.9 cm (range 0.3 - 2.7 cm), with masses that varied between 0.2 and 0.84 mg; (2) vibrissae from 2007 samples were washed with distilled water and a mild detergent, and allowed to air dry for at least 24 hours. A second cleaning was conducted by rinsing whole vibrissae in an ultrasonic bath for 15 minutes in petroleum ether, and then vibrissae were subsampled every 0.5 cm, obtaining samples with masses of 0.5 ± 0.05 mg from the proximal end of each segment. Due to the confounding factors associated with the base of the vibrissae

(Zhao et al. 2006, Chapter 1), I eliminated all data from this segment from further analyses. Given the composition of the analyzed tissue (keratine), the lipid extraction technique is only a precautionary measurement to eliminate any lipids that might be have been attached during handling; thus, both approaches used in this study are appropriate, allowing us to compare the data despite the different treatment utilized.

Samples from 2001 and 2002 were analyzed using a Costech ECS4010 elemental analyzer coupled with a Finnigan Delta Plus XP mass spectrometer (Alaska Stable Isotope Facility, UAF), while samples collected in 2007 were analyzed using a Carbo-Elba elemental analyzer interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, UCSC).

The abundance of stable isotopes is expressed in δ notation, according to:

$$\delta^{h}X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000 \qquad (1)$$

where X is the element, h is the heavy atomic mass number, R is the heavy-to-light isotope ratio (i.e. $^{13}C/^{12}C$, $^{15}N/^{14}N$) in the standard or sample. The $\delta^{13}C$ standard is Vienna PeeDee Belemnite (VPDB), and $\delta^{15}N$ standard is atmospheric nitrogen (N_2). The units are parts per thousand (per mil, ‰) deviations from the standard. The experimental precision, estimated as the standard deviation of replicates of within-run standards (peptone for 2001 - 2002 samples, gelatin for 2007 samples), was 0.1‰ for $\delta^{13}C$ values and 0.2‰ for $\delta^{15}N$ values (2001 - 2002), and 0.1‰ for $\delta^{13}C$ and 0.1‰ for $\delta^{15}N$ values (2007).

Data analysis

To investigate if there were effects of year, season, sex or mass on vibrissae isotopic values, I used a suite of Linear Mixed Models with Individual as random effect using the package *nlme* in *R* (Pinheiro et al. 2011), followed by a Mixed Model Variance Component Analysis (MMVCA) using *ape* in *R* (Paradis et al. 2004), to estimate the percentage of observed variability associated with between- versus within-individual components. I selected the optimal model for each isotopic system (i.e. $\delta^{13}C$ or $\delta^{15}N$) using the likelihood ratio test (Zuur et al. 2009).

To analyze the contribution of prey items to the diet of crabeater seals, I used the Bayesian isotopic mixing model MixSIR v1.0 (Moore & Semmens 2008, Semmens & Moore 2008). A Bayesian approach is advantageous, since it allows for the estimation of the distributions of posterior probabilities for the proportional contributions of sources (i.e. prey items) to the mix (i.e. the consumer) through numerical integration (Semmens & Moore 2008), while incorporating uncertainties in the tissue-specific trophic discrimination factors (Martinez del Rio et al. 2009), as well as the uncertainty in consumer and prey isotopic data.

Previous studies have described the crabeater seal diet very broadly, only identifying prey as krill, fish and squid (e.g. Laws 1977, Green & Williams 1986, Lowry et al. 1988), and consequently I used non-informative source contribution priors when running the mixing model, using a number of iterations enough to render > 10,000 samples in the posterior distributions of the source contributions to the diet.

In my study, I included published isotopic data for Antarctic krill, the nototheniid *Pleurogramma antarcticum*, and the myctophids *Electrona antarctica* and *E. carlsbergi* for the study area (Polito & Goebel 2010, Polito et al. 2011, Table 2.2), as these prey have been observed in diets of other top predators that also specialize in krill in wAP area, specifically Antarctic fur seal, *Arctocephalus gazella* (Polito & Goebel 2010), and Adélie penguin, *Pygoscelis adeliae* (Polito et al. 2011). I used non-informative priors in the mixing model due to the limitations associated with the small number of earlier studies, differences among studies in methodologies and the way they report results, and an overall lack of knowledge about the contribution of different fish species to the diet.

I used vibrissae-specific isotopic fractionation values of 2.2 ± 0.7‰ for $\delta^{13}C$ and 3.5 ± 0.6‰ for $\delta^{15}N$ in the mixing model, as obtained from a study of the sea otter *Enhydra lutris* (Newsome et al. 2010a), since studies reporting the discrimination of carbon and nitrogen isotopes between diet and vibrissae for pinnipeds have not reported standard deviations (Hobson et al. 1996, Kurle & Worthy 2002, Lesage et al. 2002, Zhao et al. 2006). These values from Newsome et al. (2010a) are well within the range of mean enrichment factors estimated for pinniped vibrissae.

My approach allowed to sample different time periods in the foraging history of the seals, and consequently captured the variability in individual diets of crabeater seals. Assuming a growth rate similar to what has been described for the leopard seal

Hydrurga leptonyx of 0.01 mm d^{-1} (Hall-Aspland et al. 2005) would imply that vibrissae samples in this study represented an average record of 1170 days (3.2 years), which seems unlikely given the vibrissae growth pattern of phocids, which do not seem to retain vibrissae between years (Chapter 1, Hirons et al. 2001b, Greaves et al. 2004, Newland et al. 2011). New evidence from southern elephant seals *Mirounga leonina* suggests that at least part of the vibrissae is produced during the last weeks or few months (Newland et al. 2011). Yet, there is no certainty about the vibrissae growth rates for crabeater seals, and there are several unknowns about the pattern of vibrissae growth and shedding in phocids (Greaves et al. 2004). Therefore, I did not assign specific time frames for the different samples along the vibrissae, but rather treated them as relative terms of recent and past diet, and assumed that the isotopic information from vibrissae reflected the diet of the individual during year preceding the collection.

To assess the variability in the diet of crabeater seals at different levels I ran MixSIR as follows: Approach 1, using mean individual isotopic values, to address the diet of crabeater seals at the population level, Approach 2, using mean individual isotopic values separated by year, allowing us to investigate the difference in diet composition among sampling years (Fig. 2.3), Approach 3, using all serial samples for each individual, providing us information on individual variability in diet composition (Fig. 2.4), and Approach 4, using each vibrissae sample per individual, to assess the temporal variability in diet composition of each individual (Fig. 2.5).

Results for the posterior distributions of prey item contribution to the diet, as obtained from the output of the MixSIR model, are expressed as median (range).

I investigated the effect of year, season, sex and mass on the contribution of krill (%) to the diet of crabeater seals using a series of binomial Generalized Linear Mixed Effect Models (GLMMs) with a *logit* link function and the variable Individual as a random effect, using the package *lme4* in *R* (Bates et al. 2011). For these analyses, I used a subset of 10,000 randomly selected samples from each individual's posterior distributions as obtained from the MixSIR model. As previously, the optimal model was chosen using the likelihood ratio test (Zuur et al. 2009).

All statistical analyses were conducted in *R* (R Development Core Team 2011). Results are expressed as mean values ± SD unless otherwise noted, and the significance level was set at 95% for all tests.

Results

I measured $\delta^{13}C$ and $\delta^{15}N$ values in 389 samples obtained from 53 crabeater seals captured along the wAP (Table 2.1). The mean vibrissae length of my sample was 11.7 ± 1.8 cm, and I analyzed an average of 7.3 ± 3.3 segments per individual seal. My samples were from 31 females and 22 males, with a mean mass of 256 ± 54 kg. The mean C:N atomic ratio for the vibrissae samples was 3.4 ± 0.1 (Table 2.1).

Crabeater seals' individual δ^{13}C and δ^{15}N values were significantly positively correlated (Pearson correlation, $R = 0.53$, $p << .001$).

Crabeater seal vibrissae δ^{13}C values

The mean δ^{13}C value for all 389 samples was -22.4 ± 1.3‰. There was considerable variability in mean δ^{13}C values for individuals, which ranged between -24.9‰ for seal G018 to -19.8‰ for seal G001 (Table 2.1); the δ^{13}C SD for individuals varied by an order of magnitude, between 0.1‰ for seal G003, and 1.5‰ for seal G001 (Table 2.1).

Before fitting the models for δ^{13}C values, I transformed the data, as $log_{10}(\delta^{13}C + 30)$, to fulfill the assumption of residual normality. In the optimal model, δ^{13}C values of crabeater seal vibrissae were positively related to mass ($t = 2.12$, $p = 0.04$) and higher during the winter season compared with the fall ($t = 2.37$, $p = 0.02$). The results of MMVCA confirmed the importance of individual seals to the variability found in crabeater seal δ^{13}C values, 59.6% of which is associated with individual variability and approximately 40% is due to variability within individuals. Indeed, I could not identify common patterns among individuals with regards to the along-vibrissae variability in δ^{13}C values (Fig. 2.2).

Crabeater seal vibrissae $\delta^{15}N$ values

The mean δ^{15}N value for the 389 samples of crabeater seal vibrissae was 6.8 ± 0.8‰, whereas the mean value for individuals varied between 5.3‰ (seal G003) and 7.9‰ (seal G022). Similar to δ^{13}C results, the SD for different individuals ranged from 0.1‰ (seal G001) to1.3‰ (seal G017) (Table 2.1).

Since my data did not fulfill the assumption of homogeneity of variance for the variable year, my suite of models for δ^{15}N values included a variance structure (*VarIdent*), allowing each year to have different variance in the models. The optimal model included only the effect of the year in the δ^{15}N values (individuals in 2002 had higher δ^{15}N values, $t = 2.52$, $p = 0.02$). The variance in δ^{15}N values was, however, evenly split between the individual (49.3%) and the within-individual (50.7%) components, according to the MMVCA and, as with δ^{13}C, no common patterns were identified among individuals in the vibrissae variability in δ^{15}N values (Fig. 2.2).

Diet composition: Population versus individuals

The high carbon values for seal G001 (Table 2.1) indicate that this individual foraged north of the Polar Front/Sub-Polar Front (see Discussion for explanation), so it was not included in the analysis.

A limitation of using stable isotopes for diet analysis is that it is not possible to reconstruct the diet without knowledge of the isotopic composition of potential or actual prey items for a consumer (Kelly 2000, Newsome et al. 2010b). Furthermore, isotopic mixing models cannot differentiate between the contributions of different prey unless prey isotopic values are significantly different (Phillips 2001, Phillips et al. 2005, Moore & Semmens 2008). While I included three fish species in the mixing models (Table 2.3), *P. antarcticum* and *E. antarctica* have very similar δ^{13}C values (-24.7 ± 0.4‰ and -25.1 ± 0.9‰, respectively) and identical δ^{15}N values (9.4 ± 0.5‰ and 9.4 ± 0.6‰, respectively), preventing me from distinguishing the contribution of each species to the diet. I therefore pooled the results for all three fish species by adding their posterior distributions in all further analyses.

My analysis demonstrated that Antarctic krill were the predominant prey taxa in the diet of crabeater seals from the wAP (Approach 1). Krill accounted for 87.9% (81.2 – 94.8%) of the diet of the crabeater seals, whereas the cumulative contribution of all three species of fish was 12.1% (5.2 – 18.8%) of their diet (Table 2.3). There was a decrease in the contribution of krill to crabeater seal diet in 2002, compared with 2001 and 2007 (Approach 2, Table 2.3). This was confirmed by the GLMM, which identified year (2002) as the only significant variable ($z = -2.0$, $p = 0.04$).

As expected, and in agreement with the results obtained from the MMVCA, I observed a high degree of variability in the diet of individual seals (Fig. 2.4). The median contribution of krill varied among individual seals (Approach 3) between 60.8% (40.6 – 80.7%, seal G022) and 98.3% (92.5 – 99.9%, seal G102). At the individual level there was an increase in the uncertainty of the model results, with the contribution of krill to diet ranging by as much as 67% in the diet of particular individuals (i.e. seal G024, Fig. 2.4).

Temporal variability in the diet of crabeater seals

I was able to identify differences in the diet of seals with time (as obtained from the longitudinal record of isotopic values along the vibrissae, Approach 4) (Fig. 2.5). Whereas most individuals showed low variability in the median contribution of krill to their diets (Fig. 2.5), some individual diets fluctuated through time. In 20 seals (38.5% of sampled individuals) the median krill contribution to the diet dropped below 75% of the diet at least once in the time period recorded in the vibrissae, in some cases dropping as low as 48.6% (seal G030, Fig. 2.5).

Discussion

This is the first study using stable isotopes to examine the diet composition of crabeater seals in the western Antarctica Peninsula. My approach allowed me to evaluate dietary information assimilated over a time scale of, at least, months based on the analysis of a slow-growing tissue (i.e. vibrissae), rather than the instantaneous snapshot from scats, or stomach content analysis (Kelly 2000, Crawford et al. 2008). My data clearly demonstrated the predominance of krill in the diet of crabeater seals from the wAP (~88% of its diet), in agreement with previous studies (Laws 1977, Green & Williams 1986, Lowry et al. 1988, Hewitt & Lipsky 2009). My study also showed clear individual and temporal variability in the contribution of krill to the diet of crabeater seals, highlighting the importance of understanding the responses of this highly specialized predator to the environmental variability of its prey, especially in light of the rapid and drastic environmental changes in the study area (Atkinson et al. 2004, Stammerjohn et al. 2008).

Crabeater seal $\delta^{13}C$ and $\delta^{15}N$ values

Despite its importance as one of the major consumers of Antarctic krill in the Southern Ocean (Laws 1977, Hill et al. 2006, Hewitt & Lipsky 2009), there are relatively few studies on the trophic ecology of crabeater seals and most have been based on stomach content and scat analysis. To my knowledge, only two studies have measured isotopic values of crabeater seals (Rau et al. 1992, Zhao et al. 2004) from blood or muscle samples. These tissues integrate dietary information on a scale of days (blood serum) to months (muscle, Hobson et al. 1996, Dalerum & Angerbjorn 2005, Kurle & Gudmundson 2007), but these samples do not provide a way to address temporal variability of an individual by themselves if samples are taken at one particular time only, as in the case of these studies where either serum or muscle samples were collected from particular individuals. However, if the variability in δ^{13}C and/or δ^{15}N values is quantified between different tissue samples (e.g. muscle and blood serum) collected from the same individual at the same time, individual and temporal variability in the diets of individuals, as detected by stable isotope analysis, can be investigated due to differences in the reflection of an individual's diet attributed to differences in the turnover rate of different body tissues (e.g. Bearhop et al. 2004, Quevedo et al. 2009, Matich et al. 2011).

Crabeater seals from the wAP showed greater variability in both $\delta^{13}C$ and $\delta^{15}N$ values than that found by Rau et al. (1992) in the Weddell Sea and by Zhao et al. (2004) in the Ross Sea. For instance, Rau et al. (1992) reported $\delta^{13}C$ values for muscle that varied by about 4‰ among individuals, whereas Zhao et al. (2004) reported individual values that varied by 3.7‰ for lipid-extracted blood serum. Individual mean $\delta^{13}C$ values showed greater variability in my study (4.8‰, Table 2.1). Yet I also found an important contribution from the within-individual variability in $\delta^{13}C$ values, which explained about 40% of the variance of the isotope. Thus, when considering all samples in this study, the variability of crabeater seal $\delta^{13}C$ values increased to 7.9‰. Similarly, mean individual $\delta^{15}N$ values varied by 2.7‰, whereas all samples varied by 5‰, compared to ~1.2‰ in the Weddell Sea (Rau et al. 1992), and ~2.3‰ in the Ross Sea (Zhao et al. 2004).

Several factors might contribute to the differences in variance between my study and the previously published studies of crabeater seals. First, measuring isotopic values along a metabolic inert tissue, such as a vibrissae, offered a continuous and time-integrated record of the seals foraging ecology, sampled at relatively high resolution (Hall-Aspland et al. 2005, Newsome et al. 2009, Eder et al. 2010, Newland et al. 2011). Regardless of the time period integrated in one sample of serum (days) or muscle (months), these tissues only provide one data point in time unless a longitudinal study of the same individual can be conducted, which is not realistic in the case of the wild animals as those in my sample. One vibrissa, on the other hand, offers a stratified record in time, therefore providing several samples for the same individual, as opposed to the unique value that one muscle or serum sample can provide.

Second, isotope values at the base of trophic webs vary regionally, due to differences in oceanographic parameters such as temperature, productivity, physiology and identity of primary producers, vertical mixing, and isotopic differences in the main sources of carbon and nitrogen (Somes et al. 2010). At a global scale, $\delta^{13}C$ decreases towards the poles and because this isotopic gradient is more pronounced in the Southern Ocean (Goericke & Fry 1994, Popp et al. 1999, Graham et al. 2009), the North-South orientation of the wAP, spanning 12° in latitude, is of particular relevance when comparing isotopic variability. This is ultimately reflected throughout the trophic web, which could explain the high range of $\delta^{13}C$ values in my data compared to other sites. On the other hand, $\delta^{15}N$ values also decrease towards the poles (Jaeger et al. 2010a, Somes et al. 2010), although this relationship is harder to evaluate in consumers as variations in $\delta^{15}N$ values are also associated with changes in trophic level.

Third, Zhao et al. (2004) suggested that the gradient in $\delta^{13}C$ values between onshore and offshore waters contributed to the wide range of $\delta^{13}C$ values they observed in crabeater seals from the Ross Sea. Tracking data show, however, that along the wAP crabeater seals are restricted to shelf waters (Burns et al. 2004, Burns et al. 2008, Costa et al. 2008, Costa et al. 2010), consequently an onshore-offshore $\delta^{13}C$ gradient is unlikely to contribute to the isotopic variability in my data.

Despite these possible explanations, I propose that the high variation in crabeater seals' isotopic values is likely associated with the high variability of isotopic values at the base of the food web. The isotopic composition of krill varies as they switch from grazing between pelagic and sea ice diatoms, which are typically enriched in ^{13}C and ^{15}N (Wada et al. 1987). These differences are integrated by krill and other phytoplankton consumers (Schmidt et al. 2003), and are then transferred up through the food web to crabeater seals. These changes in baseline isotopic values, a consequence of the shift between a pelagic and sea ice phytoplankton community, could also explain the significant effect that season had on $\delta^{13}C$ values of crabeater seals. Finally, despite being a highly specialized predator, crabeater seals do consume prey other than krill (Laws 1977, Green & Williams 1986, Lowry et al. 1988, Hewitt & Lipsky 2009), and therefore we can expect changes in their isotopic values as they incorporate more than one prey in their diet (see *Diet of crabeater seals*).

Sub Antarctic foraging by a crabeater seal

Based on the relationship between latitude and $\delta^{13}C$ values, it is possible to identify oceanographic features utilized by top predators in the Southern Ocean, such as the Polar Front, with $\delta^{13}C$ values measured in penguin and fur seal blood of -22.9 to -22.5‰; and the Sub-Polar Front, with $\delta^{13}C$ values of -20.1 to -19.7‰ in the same type of samples (Cherel & Hobson 2007, Jaeger et al. 2010b). Crabeater seals have rarely been observed in Sub Antarctic latitudes, and most reports consist of juvenile or injured animals (Knox 2007, Bengtson 2009). However, one individual in my study, G001, had $\delta^{13}C$ values that ranged between -21.5 and -17.6‰ (Table 2.1, Fig. 2.2), which indicates that this individual foraged north of the Sub-Polar Front. The maximum $\delta^{13}C$ value for this individual (-17.6‰) is higher than vibrissae $\delta^{13}C$ values of female southern elephant seals *Mirounga leonina* from the wAP (Chapter 1), which reportedly feed as far north as the Sub-Polar Front (Costa et al. 2010, Chapter 1, 3), and was within the range of $\delta^{13}C$ values reported for other species that forage north of the Polar Front, such as rockhopper penguins *Eudyptes chrysocome* (Cherel et al. 2007), macaroni penguins *E. chrysolophus*, Antarctic fur seals *Arctocephalus gazella* (Cherel & Hobson 2007), and Wilson's storm petrel *Oceanites oceanicus* (Quillfeldt et al. 2005).

A closer look at $\delta^{13}C$ values along the vibrissae profile (Fig. 2.2), provides evidence of individual G001 transiting back and forth between an area north of the Polar Front and the Antarctic continental margin, as observed from the two peaks in

$\delta^{13}C$ (north foraging), and the low values (Antarctic foraging). A final transit to the Antarctic continent (not seen in the vibrissae isotopic data) is evident since the individual was captured along the wAP. Thus, this constitutes the first record of a crabeater seal successfully transiting between Sub Antarctic and Antarctic foraging grounds.

Diet of crabeater seals

Although most studies on diet of crabeater seals have distinguished between krill and unspecified fish species, I included three different species of fish that occur in the diet of other krill specialists in the same study area (Polito & Goebel 2010, Polito et al. 2011, Table 2.3). However, due to the similarity in isotopic values for two of the fish species included in my analysis, I combined the diet contributions obtained from the mixing model for all three species of fish (Table 2.3, Fig. 2.3). Not surprisingly, my results showed that the diet of the crabeater seal along the wAP is largely dominated by krill, which accounts for 88% of the diet when considering individual isotopic mean values (Approach 1). My results for fish species, on the other hand, are more difficult to interpret.

My data showed that crabeater seals display some trophic plasticity, likely a response to fluctuations in the availability of their primary prey, Antarctic krill. Large fluctuations in the biomass of Antarctic krill in the wAP have been described (Siegel

& Loeb 1995, Hewitt et al. 2003, Reiss et al. 2008), and linked to environmental variations at different scales, from local fluctuations in sea ice extent (Loeb et al. 1997), to global-scale perturbations such as ENSO (Loeb et al. 2009). My study included samples collected during the austral fall and winter of 2002, presumably reflecting krill consumption during the austral summer 2001-02. This particular year was characterized by a one of the lowest recorded biomasses of krill for the northern wAP (Hewitt et al. 2003, Reiss et al. 2008). My analysis revealed that the contribution of krill to the diet of crabeater seals was significantly lower in 2002 compared with 2001, whereas no difference was evident between 2001 and 2007 (Figs. 2.3 and 2.4). Seals sampled in 2002 had the lowest median contribution of krill to diet, with about half of the individuals in my sample having median contributions to diet of less than 75% at least once along their vibrissae (Fig. 2.5). Fish are enriched in $\delta^{15}N$ compared to Antarctic krill (Cherel & Hobson 2007, Cherel et al. 2007, Polito & Goebel 2010, Polito et al. 2011); and this higher proportion of fish in the diet of the seals is not surprising considering that my results indicated that seals in 2002 have significantly higher $\delta^{15}N$ than other years.

Seasonal fluctuations in biomass and vertical distribution of Antarctic krill have also been observed for the wAP, with less dense (< 10 g m^{-3}) and deeper aggregations during the fall – winter period compared with high density (>100 g m^{-3}) and shallow aggregations observed in summer (Lascara et al. 1999). Regardless, crabeater seals are able to prey on krill throughout the fall – winter season, as their vertical distribution remains well within the diving range of crabeater seals (Burns et al. 2004). Further, deeper krill aggregations are likely to be denser, making up for the deeper and therefore longer dives that would be required to obtain them (Burns et al. 2004, Burns et al. 2008). Nonetheless, the variations observed in the median contribution of krill along vibrissae (Fig. 2.5) can be interpreted as a change in the diet of crabeater seals as they respond to changes in the availability of their prey (krill and fish).

Evidence from tagging studies of crabeater seals in the wAP indicates that their foraging behavior switches from shallow – short dives in summer, to deeper – longer dives in the winter, likely in response to changes in vertical distribution of their prey (Burns et al. 2004). Yet, they are capable of maintaining, or even increasing their body mass during winter (McDonald et al. 2008). Burns et al. (2004) suggested that, regardless of the crabeater seals' high level of specialization on a single prey, they display behavioral plasticity to forage successfully in winter, when there is less availability of their main prey. My study offers evidence that their plasticity is not only related to changes in patterns of habitat utilization and diving behavior as previously suggested (Burns et al. 2004), but also the inclusion of other prey (i.e. fish) in their diet. Similar findings have been described for Adélie penguins along the wAP, whose diet shifts from primarily krill in the summer breeding season to include >50% fish during winter (Lynnes et al. 2004, Polito et al. 2011) . It is unknown, however, to what extent and at what rate crabeater seals might be able to switch from a krill-dominated diet to a more generalized one, under the current scenario of rapid climate change that is occurring along the wAP (Costa et al. 2010).

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Table 2.1. Individual mean ± standard deviation δ^{13}C and δ^{15}N values of 53 crabeater seals from the western Antarctica Peninsula, captured in 2001, 2002 and 2007. Individual ID, sex, and mass of each individual, as well as year and season of sampling, are also given.

ID	Year	Season	Sex	Mass (kg)	δ^{13}C (‰)	δ^{15}N (‰)	C:N
G001	2001	Fall	Female		-19.8 ± 1.5	7.1 ± 0.1	2.9 ± 0.4
G003	2001	Fall	Female	258	-22.1 ± 0.1	5.3 ± 0.7	3.0 ± 0.2
G004	2001	Fall	Male	342	-21.8 ± 0.5	6.7 ± 0.7	3.0 ± 0.1
G005	2001	Fall	Female	293	-21.9 ± 0.3	6.6 ± 0.5	3.0 ± 0.1
G006	2001	Fall	Female	413	-24.1 ± 0.5	6.2 ± 0.4	3.0 ± 0.1
G007	2001	Fall	Male	287	-21.8 ± 0.8	6.4 ± 0.5	2.9 ± 0.1
G008	2001	Fall	Female	355	-22.0 ± 0.3	6.8 ± 0.4	2.9 ± 0.1
G009	2001	Winter	Male	179	-23.4 ± 0.7	6.2 ± 0.3	2.9 ± 0.1
G010	2001	Winter	Female	307	-22.5 ± 0.7	6.5 ± 0.4	2.9 ± 0.0
G012	2001	Winter	Female	288	-21.5 ± 0.3	6.8 ± 0.7	3.0 ± 0.0
G013	2001	Winter	Male	234	-21.3 ± 0.9	6.7 ± 0.5	3.0 ± 0.1
G014	2001	Winter	Male	284	-21.6 ± 0.2	7.6 ± 0.7	2.9 ± 0.0
G015	2001	Winter	Male	234	-22.4 ± 0.3	7.3 ± 0.7	3.0 ± 0.1
G016	2001	Winter	Female	273	-21.1 ± 0.2	5.9 ± 0.4	3.0 ± 0.1
G017	2002	Fall	Female	118	-21.8 ± 0.4	6.8 ± 1.3	2.8 ± 0.1
G018	2002	Fall	Male	157	-24.9 ± 0.7	6.5 ± 0.6	2.8 ± 0.1
G019	2002	Fall	Female	156	-24.7 ± 0.6	6.6 ± 0.7	2.8 ± 0.0
G020	2002	Fall	Male	143	-24.5 ± 0.7	6.6 ± 0.7	2.8 ± 0.1
G021	2002	Fall	Male	271	-22.3 ± 0.7	6.7 ± 0.6	2.9 ± 0.1
G022	2002	Fall	Female	268	-20.9 ± 0.3	7.9 ± 0.5	2.9 ± 0.1
G023	2002	Fall	Male	174	-24.6 ± 0.6	6.4 ± 0.6	2.8 ± 0.1
G024	2002	Fall	Female	256	-21.8 ± 0.9	7.2 ± 0.5	2.8 ± 0.1
G026	2002	Fall	Female	266	-23.6 ± 0.2	6.5 ± 0.5	2.8 ± 0.1
G027	2002	Fall	Male	226	-22.3 ± 0.8	6.9 ± 0.5	2.8 ± 0.0
G028	2002	Fall	Female	314	-22.2 ± 1.1	7.1 ± 0.9	2.8 ± 0.1
G029	2002	Fall	Male	242	-21.6 ± 1.0	7.2 ± 0.9	2.8 ± 0.0
G030	2002	Fall	Male	250	-22.1 ± 1.0	6.9 ± 1.1	2.8 ± 0.0
G031	2002	Fall	Female	385	-21.2 ± 0.6	7.5 ± 0.6	2.8 ± 0.0
G032	2002	Fall	Female	230	-23.2 ± 0.7	7.0 ± 0.5	2.8 ± 0.0
G033	2002	Winter	Female	268	-21.1 ± 0.9	7.5 ± 0.9	2.8 ± 0.1
G034	2002	Winter	Female	295	-21.8 ± 0.6	6.7 ± 0.4	2.8 ± 0.1
G035	2002	Winter	Female	238	-21.6 ± 0.5	7.0 ± 0.6	2.8 ± 0.0
G036	2002	Winter	Female	207	-21.5 ± 1.0	7.3 ± 0.4	2.9 ± 0.1
G038	2002	Winter	Male	273	-22.0 ± 1.2	6.9 ± 0.5	2.9 ± 0.1
G039	2002	Winter	Male	247	-22.9 ± 0.4	7.3 ± 0.6	2.9 ± 0.1
G040	2002	Winter	Male	302	-23.7 ± 0.6	6.5 ± 0.5	2.9 ± 0.1
G041	2002	Winter	Male	269	-22.9 ± 0.5	6.7 ± 0.5	2.9 ± 0.1
G042	2002	Winter	Male	224	-21.6 ± 1.2	6.9 ± 0.5	3.0 ± 0.1
G043	2002	Winter	Male	224	-22.8 ± 0.8	7.4 ± 0.5	2.9 ± 0.1
G044	2002	Winter	Female	280	-21.8 ± 1.2	7.1 ± 0.8	3.0 ± 0.1
G045	2002	Winter	Female	221	-22.0 ± 0.3	7.6 ± 0.7	2.9 ± 0.1
G046	2002	Winter	Male	237	-21.7 ± 0.9	7.8 ± 0.6	2.9 ± 0.0
G047	2002	Winter	Male	254	-21.5 ± 1.2	7.1 ± 0.5	3.0 ± 0.1
G102	2007	Fall	Female	286	-23.8 ± 0.5	5.3 ± 0.3	
G104	2007	Fall	Female	197	-22.7 ± 0.7	6.9 ± 0.3	2.9 ± 0.1
G105	2007	Fall	Female	251	-22.3 ± 1.2	7.1 ± 0.5	
G106	2007	Fall	Female	207	-21.9 ± 0.7	7.1 ± 0.2	3.0 ± 0.0
G107	2007	Fall	Female	315	-23.3 ± 1.1	6.6 ± 0.2	
G108	2007	Fall	Female	207	-21.5 ± 1.6	7.5 ± 0.5	2.9 ± 0.1
G110	2007	Fall	Female	123	-23.1 ± 0.2	7.9 ± 1.0	
G112	2007	Fall	Female	252	-24.0 ± 0.5	5.4 ± 0.7	2.9 ± 0.0
G113	2007	Fall	Female	244	-23.3 ± 0.5	5.8 ± 0.4	3.0 ± 0.0
G114	2007	Fall	Male	304	-22.3 ± 1.2	7.1 ± 0.4	

Table 2.2. $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD) of potential prey for crabeater seal *Lobodon carcinophaga* along the western Antarctica Peninsula

	Prey	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Reference
Krill				
	Euphausia superba	-26.2 ± 0.9	3.2 ± 0.7	Polito et al. (2011)
Fish				
	Pleuragramma antarcticum	-24.7 ± 0.4	9.4 ± 0.5	Polito et al. (2011)
	Electrona antarctica	-25.1 ± 0.9	9.4 ± 0.6	Polito et al. (2010)
	E. carlsbergi	-22.6 ± 0.5	7.6 ± 0.3	Polito et al. (2010)

Table 2.3. Contribution of krill (%) to the diet of crabeater seals from the western Antarctica Peninsula, taking into account individual mean $\delta^{13}C$ and $\delta^{15}N$ values. Values represent median (range) of the posterior distributions obtained for each prey item included in the diet, as obtained from the Bayesian mixing model MixSIR v1.0 (Moore & Semmens 2008, Semmens & Moore 2008).

	Fish			**Total Fish (%)**	**Krill (%)**
	P. antarcticum (%)	*E. antarctica* (%)	*E. carlsbergi* (%)		
2001	0.8 (0 – 8.3)	0.8 (0 – 9.0)	5.9 (0.01 – 20.7)	**8.4** **(0.9 – 21.4)**	**91.6** **(78.6 – 99.1)**
2002	0.6 (0 – 5.9)	0.6 (0 – 6.2)	14.0 (3.6 – 24.7)	**15.5** **(7.6 – 24.9)**	**84.5** **(75.1 – 92.4)**
2007	1.5 (0 – 16.9)	1.4 (0 – 13.1)	4.2 (0 – 20.5)	**8.9** **(0.4 – 22.0)**	**91.1** **(78.0 – 99.6)**
All Data	0.4 (0 – 5.4)	0.3 (0 – 3.4)	11.2 (3.5 – 18.3)	**12.1** **(5.2 – 18.8)**	**87.9** **(81.2 – 94.8)**

Figure 2.1. Sites of capture of crabeater seals along the western Antarctica Peninsula. Adult crabeater seals were captured in 2001 (n = 14, blue), 2002 (n = 29, green) and 2007 (n = 10, red) during different Fall/Winter cruises to the Crystal Sound/Lau Beouf fjord/Marguerite Bay area on board the *ARSV Lawrence M. Gould*.

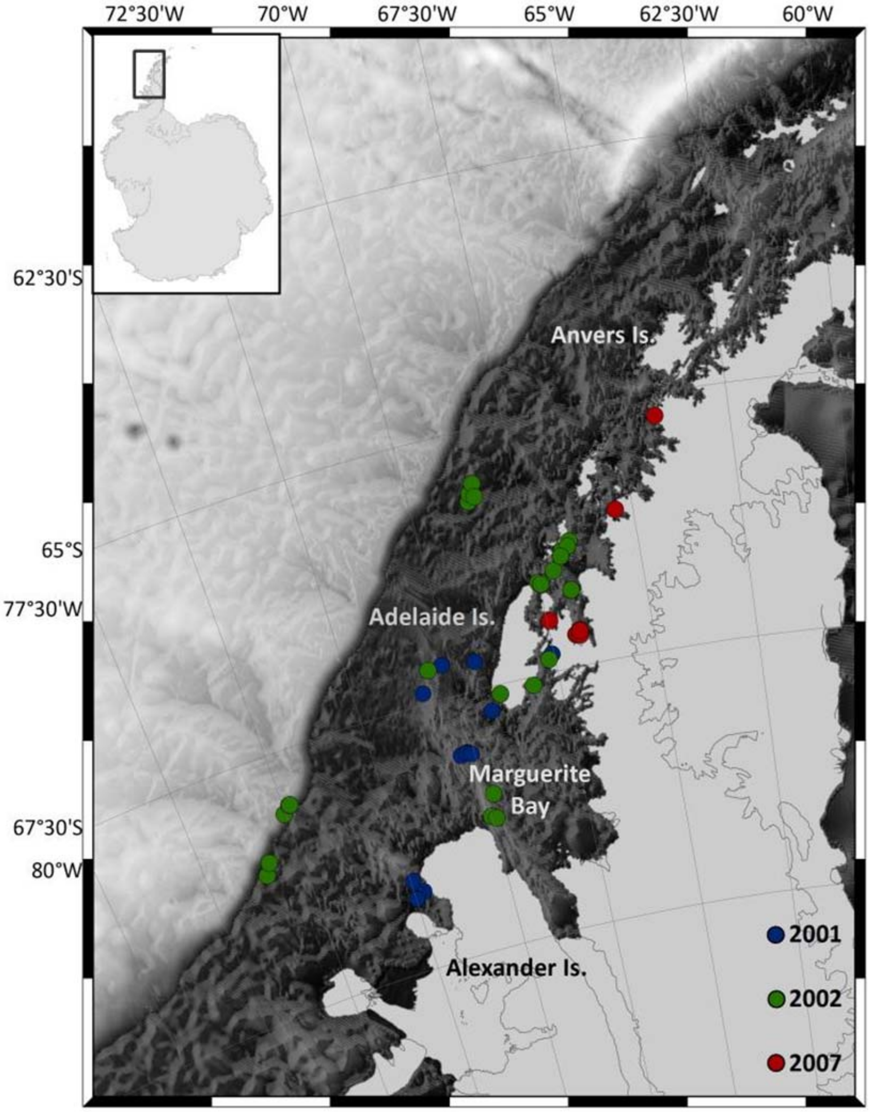


Figure 2.2. Variation of $\delta^{13}C$ (solid line) and $\delta^{15}N$ (dashed line) along vibrissae of crabeater seals captured along the western Antarctica Peninsula in 2001, 2002 and 2007. White panels symbolize fall captures, whereas gray panels represent winter sampling.

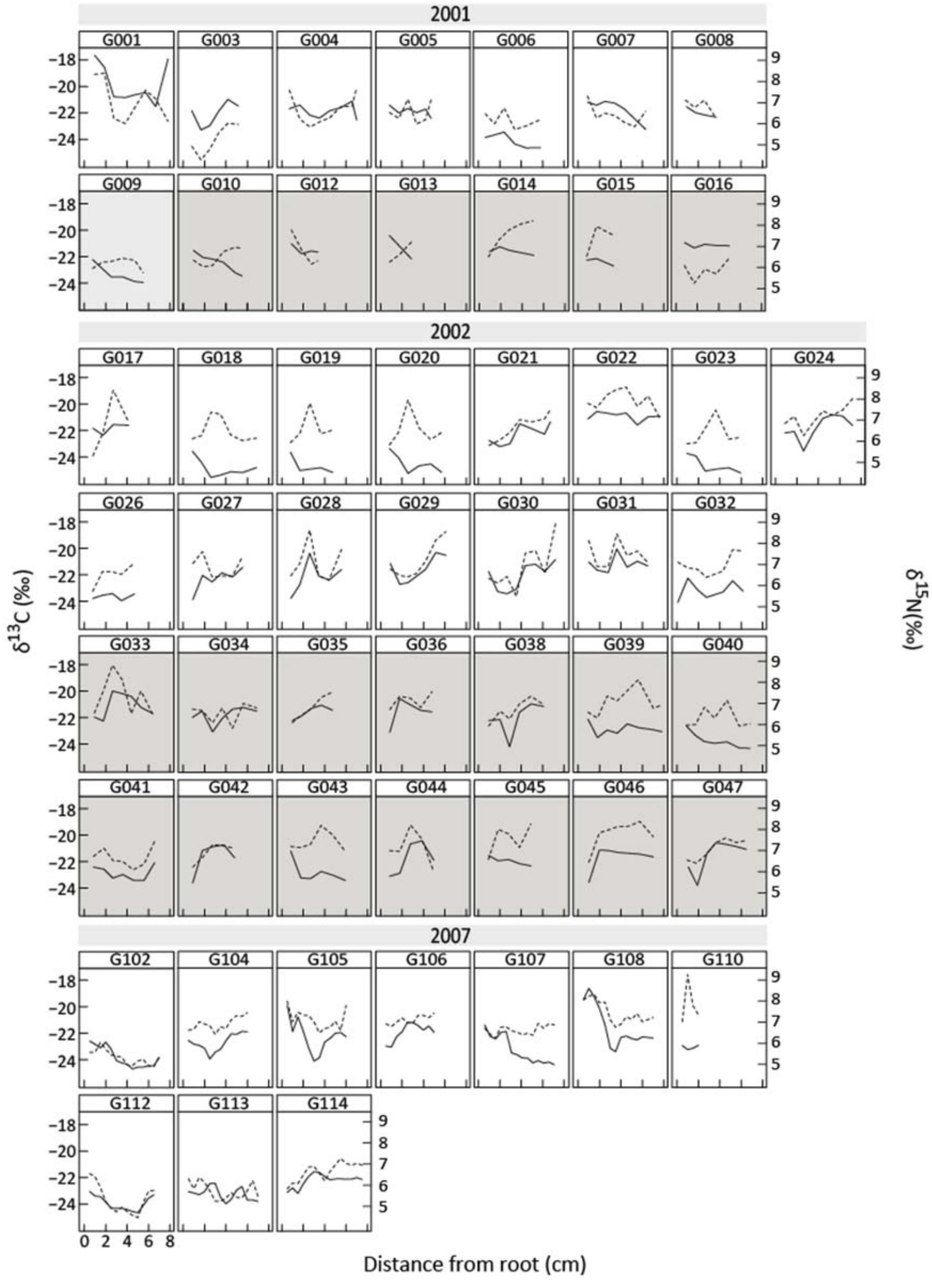


Figure 2.3. Contribution of prey items to the diet of crabeater seals from the western Antarctica by year (2001, 2002 and 2007). Prey contribution to the diet was calculated based on vibrissae $\delta^{13}C$ and $\delta^{15}N$ values, using the Bayesian mixing model MixSIR. Dark gray bars correspond to the diet contribution of Antarctic krill *Euphausia superba*, and light gray bars correspond to the combined contribution to the diet of the fish species *Pleuragramma antarcticum*, *Electrona antarctica* and *E. carlsbergi*. The dashed lines correspond to the median contribution for both krill and fish.

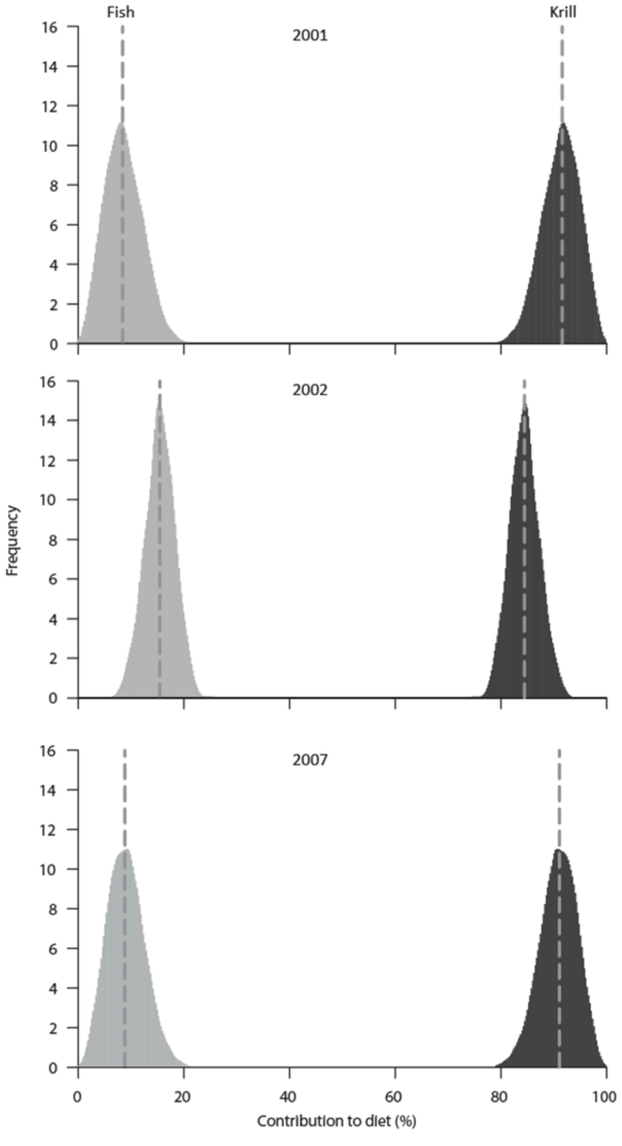


Figure 2.4. Individual variation in diet composition of crabeater seals from the western Antarctica Peninsula. Dark gray bars correspond to the posterior distribution of the contribution of Antarctic krill *Euphausia superba* to the diet of individual crabeater seal, and the light gray dots correspond to the individual median. Light gray bars correspond to the posterior distribution of the contribution of fish to the diet of individual crabeater seal, and the dark gray dots correspond to the individual median

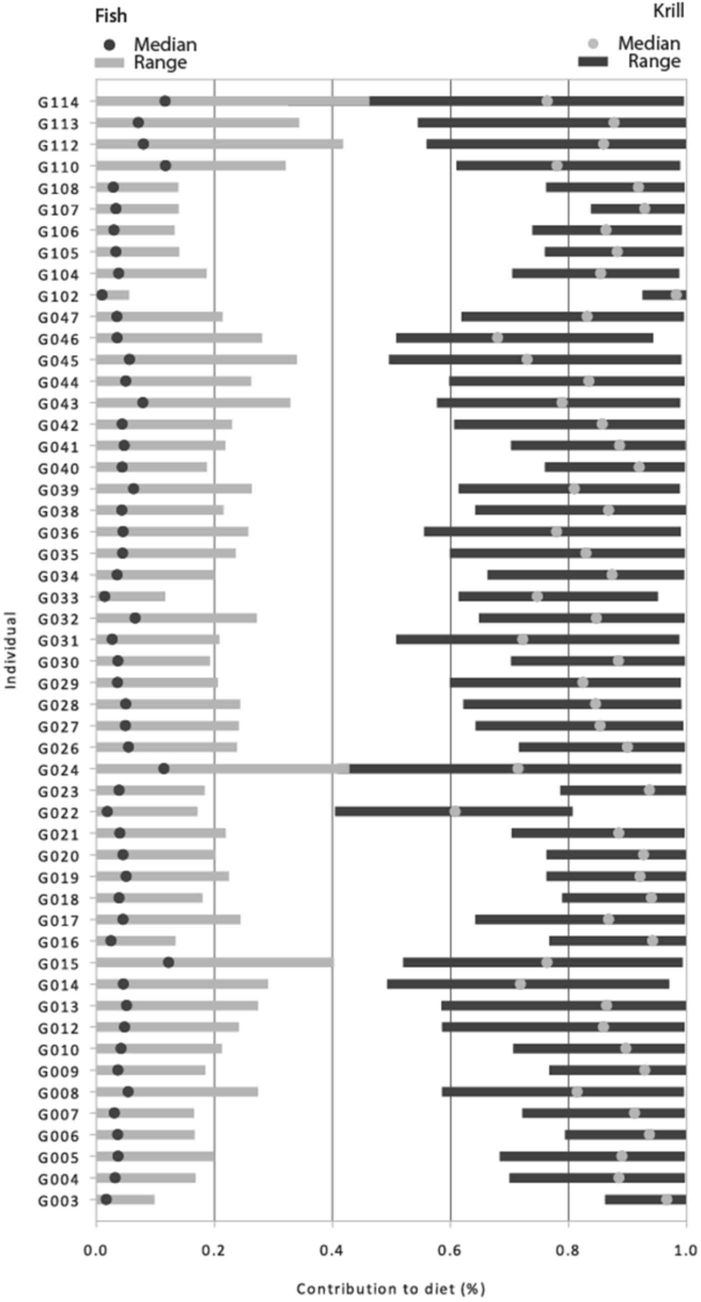
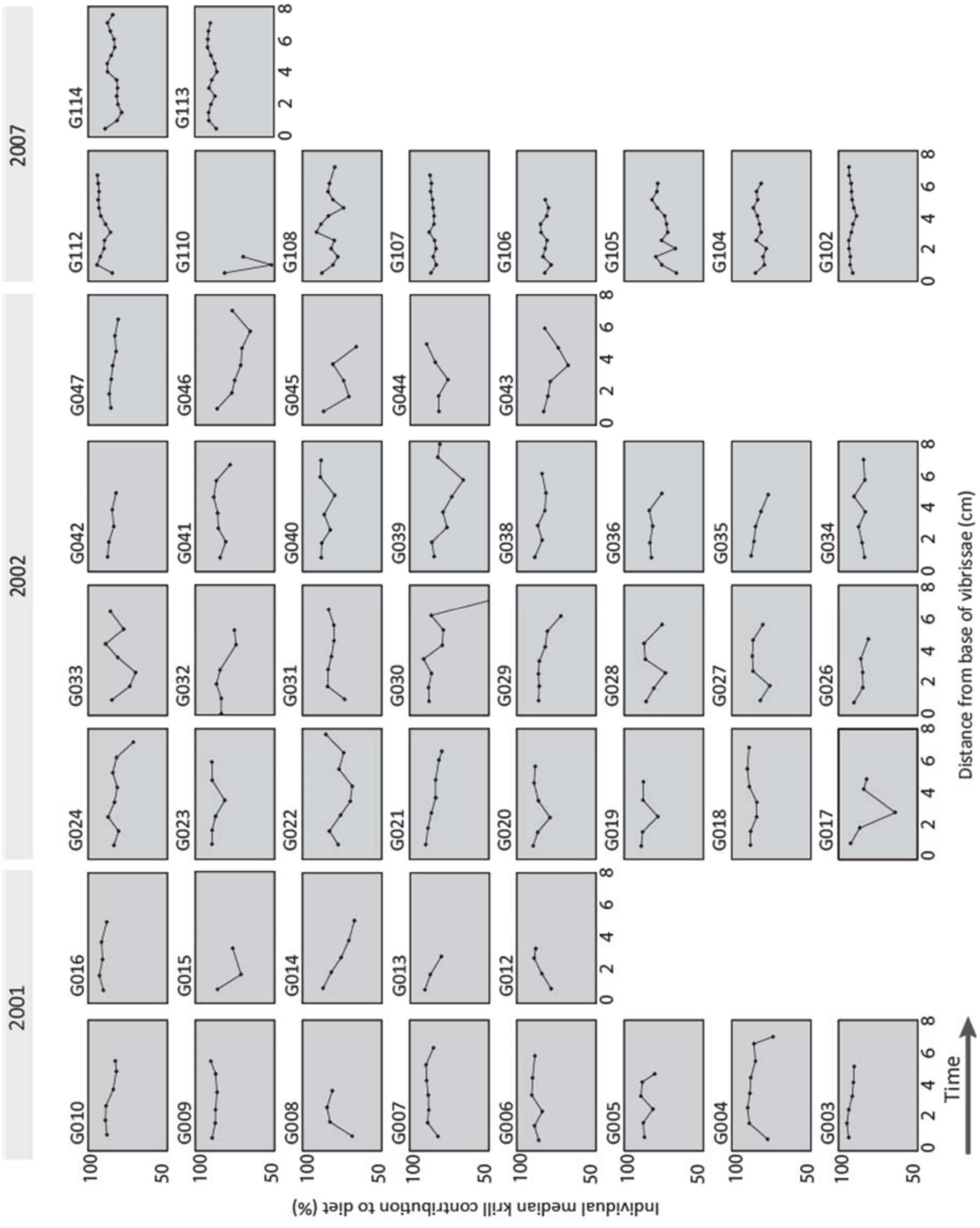


Figure 2.5. Temporal variation in the median contribution (percentage) of Antarctic krill *Euphausia superba* to the diet of individual crabeater seals from the western Antarctica Peninsula. Vibrissae samples provide a continuum in the diet history of the individual, from the proximal sample (closer to the base) representing the most recent diet information contained in the vibrissae, to the distal sample (farther away from the base) providing the oldest diet information in the sample. Individual IDs are provided in the top left corner of each panel.



Chapter 3 ENVIRONMENTAL EFFECTS ON THE FORAGING BEHAVIOR OF ADULT FEMALE SOUTHERN ELEPHANT SEALS FROM THE WESTERN ANTARCTICA PENINSULA: PELAGIC VERSUS SHELF FORAGERS

Luis Alfredo Hückstädt

Introduction

The at-sea distribution of marine top predators is linked to the distribution and abundance of prey, which in turn is determined by oceanographic features that physically force the aggregation of prey, creating areas where foraging efficiency is maximized (Costa et al. 1989, Campagna et al. 2000, Boyd et al. 2001). Thus, the physical properties of the water column are fundamental to understand not only the ecology of marine top predators, but also how these organisms may be affected by annual and long-term changes in ocean climate (Boyd 1999, Simmons et al. 2007). Marine top predators are anticipated to exhibit changes in their foraging behavior and movement patterns and at-sea distribution (Trathan et al. 2007) as a response to climatic change, primarily as a consequence of changes in prey distribution (Croxall 1992) rather than direct changes in the physical environment.

Female southern elephant seals (*Mirounga leonina*) have been traditionally considered predators that forage over wide pelagic areas of the Southern Ocean (McConnell et al. 1992, Field et al. 2001, Bradshaw et al. 2004, Biuw et al. 2007), although individuals venturing into the continental shelf waters of the Antarctic Peninsula have been reported (McConnell et al. 1992, McConnell & Fedak 1996). However, most of the research that has been carried out on this species has been focused on animals captured in Sub-Antarctic Islands or the South American continent (McConnell et al. 1992, Campagna et al. 2000, Field et al. 2001, McIntyre et al. 2011a), which either have to transit hundreds to thousands of kilometers to reach Antarctic waters, or do not forage on Antarctic waters.

Based on these studies, it has been described that the foraging behavior of the species is often associated with oceanographic features such as mesoscale eddies, Antarctic Polar Front (APF), continental shelf margin, sea ice concentration and thermocline (Hindell et al. 1991a, McConnell et al. 1992, Bradshaw et al. 2004, Campagna et al. 2007), and even specific water masses in the Southern Ocean (Field et al. 2001, Biuw et al. 2007). Further, new studies have found a relationship between the thermal structure of the water column and the diving behavior of elephant seals (McIntyre et al. 2011a). However, elephant seals colonies are also found on the Antarctic continent (Laws 1994), and animals from these sites can be expected to display a different foraging behavior than that of Sub-Antarctic seals, since their transit is significantly reduced to their Antarctic foraging grounds (Costa et al. 2010).

Recent advances in bio-logging technology have allowed us to significantly expand our understanding of the biology of several species of cryptic marine predators, gathering information on a wide diversity of aspects that include patterns of habitat usage, migratory routes, foraging and reproductive hot-spots, navigation, areas of potential interaction with human activities, areas of special interest for conservation and management purposes, etc. (Costa et al. 2010, Block et al. 2011).

The amount and type of new biological and environmental information that is now available has, in turn, forced the scientific community to explore adequate statistical techniques to robustly model the relation of between the patterns of habitat usage of these species and the environment they inhabit (Redfern et al. 2006, Aarts et al. 2008). For instance, among the advances achieved in the field of bio-logging is the capability of measuring environmental data directly in the areas that are utilized by these species, incorporating environmental information not only from surface, but also from the structure of the water column (Boehlert et al. 2001, Fedak 2004, Simmons et al. 2009), taking into account the conditions at the depth where foraging actually takes place which, for some species, can be well beyond 1,000 m.

Hence, these advances in technology have allowed us to move past the classical use of surface environmental variables derived from satellites, or static features such as bathymetric topography, toward a more elaborate approach that incorporates data measured in depth obtained from both the instruments themselves (Biuw et al. 2007, Dragon et al. 2010, McIntyre et al. 2011a).

In this Chapter, I investigate the foraging behavior of adult female elephant seals from the western Antarctica Peninsula (wAP) in relation with the *in situ* oceanographic conditions that they experience during their ca. 8-months post-molt migration at sea. The specific objectives of my study are (1) to develop a robust foraging habitat model of the female southern elephant seals incorporating data on both at-sea movement and diving behavior of the individuals, (2) evaluate the performance of models incorporating subsurface water column structure versus surface conditions, and (3) determine the environmental variables that influence the foraging behavior of animals foraging on Antarctic shelf waters.

Materials and methods

Animal handling and instruments deployment

Animal captures were conducted under National Marine Fisheries Service permit No. 87-1851-00. All animal procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at University of California Santa Cruz. Adult female southern elephant seals (n = 57) were captured and instrumented during the late molting season (January–February) at Cape Shirreff, Livingston Island (62°39’S, 60°46’W), South Shetland Islands (Fig. 3.1), between 2005 and 2009. Animals were immobilized with tiletamine HCl/zolazepam HCl (Telazol®, Fort Dodge Animal Health) administered intramuscularly (1.0 mg/100 kg), and immobilization was maintained with intravenous injections of Ketamine (100 mg/ml, Ketaset; Fort Dodge Animal Health). Females were weighed (Measurement Systems International, capacity 1,000 ± 1 kg) and body length was measured.

Southern elephant seals were instrumented with Conductivity – Temperature - Depth (CTD) Satellite Relay Data Loggers (SRDL) (Sea Mammal Research Unit, University of St Andrews), attached to the head of the animals using 5-minute Quick Set^{TM} epoxy (Loctite, USA). Data on at-sea locations of the elephant seals were collected and transmitted constantly via the Argos system (Toulouse, France). The CTD-SRDLs were programmed to collect and process on board information on the diving behavior of the seal, temperature and salinity (conductivity) of the water column (Fedak et al. 2001).

The tracking data for the animals in my study showed the existence of at least two foraging strategies (Chapter 1, Costa et al. 2010): shelf and pelagic foraging. Due to the anticipated differences between these systems, I used a simplistic bathymetric approach to assign individual seals to either group (i.e. shelf foragers or pelagic) before further analyses. Briefly, I defined a buffer zone of 100 km from the continental shelf break (1000 m isobath), and classified individuals as shelf foragers if they spent >50% of their time at sea between the coastline and the limit of this buffer zone. Conversely, if the individual spent <50% of its time within this area, it was classified as pelagic. This approach identified the majority of individuals in my sample (85%) as shelf foragers, while the remaining 15% was classified as shelf foragers, similar to the figures obtained in Chapter 1.

To investigate if there were any differences in the size of the animals between groups I used Linear Mixed Model (LMMs) with Individuals as random effect, using the *nlme* package in R (Pinheiro et al. 2011).

Tracking data

I pre-filtered the Argos location data using a forward/backward speed filter (McConnell et al. 1992) to remove aberrant positions as suggested by (Patterson et al. 2010), and later analyzed those data using a State-Space Model (SSM) (Jonsen et al. 2005) to generate a feasible track for each animal. State-Space Models allow the estimation of positions from the Argos location data, by measuring the errors associated with each location class, as provided by the Argos System, and from dynamics of the movement process (Jonsen et al. 2005, McConnell et al. 2010, Patterson et al. 2010). This methodology allows for statistically robust predictions that embrace the inherent uncertainty in the position of the animal. For this study, I configured the SSM to obtain a position estimate every 120 minutes. Obtained locations were then utilized to calculate maximum distance from the colony (km), transit rate (km h^{-1}), and total travelled distance (km), as well as to interpolate locations of the dives and CTD casts.

Diving data

The SRDL-CTD tags transmit diving (as well as CTD) data via the Argos system. Each diving profile consists of four inflection points in depth (point of the largest change in depth) and their corresponding time, including the maximum depth (Fedak et al. 2001). I pre-filtered these data to remove erroneous or incomplete dive profiles, likely the results of interrupted uplinks between the instrument and the satellites, by using a simple filter that removed dives with non-incremental times for the inflection points. I then applied a secondary filter; based on a conservative maximum speed an animal could dive to reach the maximum depth in 50% of the dive duration. For this second filter, I used a threshold speed of 4 m s^{-1}, a conservative value considering the mean speed of 2.1 m s^{-1} reported by (Hindell & Lea 1998) for female southern elephant seals.

I used LMMs to evaluate if there were diel variations in the diving behavior (dive depth or dive duration) of either shelf or pelagic foragers. Additionally, I used Generalized Additive Models (GAMs) to evaluate if the day of the year could have an effect on diving behavior of elephant seals, using the package *mgcv* in R (Wood 2012)

Several studies have explored the use of a wide variety of tracking and diving metrics to predict the location of foraging areas or zones of foraging success of elephant seals (Crocker et al. 1997, Biuw et al. 2007, Thums et al. 2008a, Robinson et al. 2010, Thums et al. 2011). In particular, the presence of drift dives, in both species of the genus *Mirounga*, has proven a successful method to identify areas where the animals are being improving the body condition (or not) at sea. However, for this dataset I was not able to identify the presence of drift dives, because most elephant seals from the wAP are foraging to the benthos of the continental shelf (<1,000 m depth), preventing the adequate classification of dives and while may carry out drift or processing dives they cannot be differentiated from benthic foraging dives as they are both flat bottomed dives.

In order to incorporate the vertical dimension in my analyses, I used instead the residual First Bottom Time (*rFBT*) (Bailleul et al. 2008), an extension of the First-Passage Time technique, a scale-dependent measure of search effort derived from two dimensional movement data (Fauchald & Tveraa 2003), which incorporates the vertical dimension in a diving predator.

Briefly, the *rFBT* incorporates the variability in the bottom time of a dive, defined as the time spent within 80% of the maximum dive depth of a dive, allowing the identification of areas where the animal spends longer (or shorter) time than average at the bottom of the dive (Bailleul et al. 2008), providing a putative measure of foraging effort. These data were calculated using a custom written algorithm in MATLAB, and were later standardized to a scale ranging between -1 to 1 for each individual. By doing this, I eliminated the possibility that one (or more) individual(s) with large variances would have a disproportionate influence than other animals in the analysis, which could result in the misinterpretation of environmental data and a localized biased towards that (those) individuals.

To investigate the spatial patterns in the standardized *rFBT* of southern elephant seals, I utilized the Hot Spot Analysis toolbox in ArcGIS v10, which calculates the Getis-Ord Fi* statistic for each dive location in my dataset, allowing the statistical identification of clusters of high (hotspots) or low (coldspots) values of *rFBT*.

Environmental data

The SRDL-CTD tag only collected CTD data from the deepest dive every 2 hours, so in order to assign CTD data to each dive in my analysis, I identified the closest CTD cast in time for each dive within a maximum of 0.5 d, and the corresponding temperature and salinity profiles were assigned to that particular dive. A time window of 0.5 d seems appropriate for these analysis considering that: 1) the spatial analysis in this study operates at the mesoscale level (tens to hundreds of km, see results for *rFBT*); 2) a time period of 0.5d is less than the expected temporal scale at which the water column responds to external forcing factors (Steele 1985), such as wind, internal waves, sea ice formation, etc., and 3) elephant seals cover an average distance of no more than 50 km during in 0.5 d, so changes in the oceanographic conditions that the animals experience can be considered small relative to the scale of their movements.

The SRDL-CTD tags present instrument-specific offsets for temperature and salinity, which made it necessary to correct these data before analysis using the method described by (Roquet et al. 2011). Since elephant seals can reach depth in excess of 2,000 m (Costa et al. 2010), I calculated potential temperature (θ), which was used for all analyses, as well as potential density of the water (ρ_θ, kg m^{-3}). Temperature and salinity data were used to calculate a number of oceanographic variables to be included later in the models:

a) Mixed Layer Depth, *MLD* (m). The depth at which the absolute temperature gradient with the surface becomes greater than 0.05°C.

b) Brunt-Väisälä frequency, N^2 (s^{-1}). Calculated using the package *SeaWater* (Phil Morgan, CSIRO) in MATLAB. This parameter is an indicator of the stability of the water column.

c) Maximum temperature (θ) below 200 m, *Tmax200* (°C). Depth of maximum temperature below 200 m

d) Depth of maximum temperature (θ) below 200m, *TmaxD200* (m)

e) Sea Surface Temperature, *SST* (°C). Calculated as the average temperature in the first 10 meters of the water column.

f) Sea Surface Salinity, *SSS*. Calculated as the average salinity in the first 10 meters of the water column.

g) Sea Surface Density, *SSD*. Average density (ρ) in the first 10 meters of the water column. Density was calculated using the package *SeaWater* (Phil

Morgan, CSIRO) in MATLAB.

h) Temperature at the bottom of the dive (T_{bot}).

i) Salinity at the bottom of the dive (S_{bot}).

j) Density at the bottom of the dive (D_{bot}).

k) Water Mass at the bottom of the dive. To calculate the percentage of each water mass, I defined a polygon in the two dimensional space defined by temperature and salinity (T-S), where each one of its vertices corresponded to the centroid of the specific T-S ranges for each water mass in the wAP, as defined by Klinck et al. (2004). If the T-S values at the bottom of the dive fell within the limits of this polygon, then I calculated the inverse Euclidean distance between the dive T-S values, and each one of the vertices of this polygon (water masses), as follows:

$$\%WM-x=\frac{1/D\ TS_{dive}\ WM-x}{1/D\ TS_{WM-a}+1/D\ TS_{WM-b}+1/D\ TS_{WM-c}+1/D\ TS_{WM-d}}$$

where,

%WM-x: Percentage of water mass *x* corresponding to the dive

TS: Temperature, Salinity value

D: Euclidean distance

$WM_{(a,\ b,\ c,\ d)}$: Centroid *TS* values for each one of the water masses present in the wAP, as defined by (Klinck et al. 2004).

Due to sea ice coverage and other restrictions to satellite imaginary in polar latitudes, most of the satellite derived products commonly used in these types of studies were not available for areas around the Antarctic continent. However, satellite data on sea ice concentration were available; whereas other variables could be obtained for those animals identified as pelagic that were not associated with areas where sea ice was present (see *Results*):

a) Daily sea ice concentration (%) (AMSR-E, 6.52 km resolution, National Snow and Ice Data Center, Boulder, CO).

b) Distance to ice edge, defined as the 10% daily sea ice concentration contour.

c) Bathymetric depth (m), obtained from the ETOPO 1-min dataset (Amante & Eakins 2009).

d) Bathymetric slope (°), calculated using the function *gradient* in ArcGIS 10 based on the ETOPO 1-min dataset.

e) Bathymetric roughness, calculated as the standard deviation of the bathymetry within 3 neighboring cells using *block statistics* in ArcGIS 10.

f) Distance to the continental shelf break, defined as the 1000 m isobath, as calculated using the ETOPO 1-min dataset.

g) Absolute Sea Surface Height, SSH (AVISO 0.25° resolution).

h) Zonal (x) and meridional (y) components of geostrophic currents (AVISO 0.25° resolution).

Data on SSH and geostrophic currents were obtained using the Xtractomatic tool (Pacific Fisheries Environmental Laboratory, NOAA) in MATLAB 2010a (Mathworks, Natick, MA, USA).

Statistical models

I used Non-Parametric Multiplicative Regression (NPMR) to model the relationships between the environmental variables and the *rFBT* using the software Hyperniche v2.20 (McCune 2006). Non-parametric statistics are advantageous for building habitat modeling since they do not rely on assumptions about the data fitting any particular distribution, a common situation with most ecological variables. NPMRs model nonlinear relationships while automatically considering interactions among predictors, without making the assumption that the structure of the model is fixed (McCune 2006, Lintz et al. 2011).

Before fitting the models, I grouped the environmental variables under the following categories: a) Water Column (MLD, Tmax200, Tmax200D, Dbot, WM), b) Surface Oceanography (SST, SSS, SSD, SSH, geoM, geoZ), c) Ice conditions (Ice, dist2ice), and d) Bathymetry (bathymetry, slope, dist2shelf). Given the high dimensionality of this dataset, I opted for a modeling approach based on conceptual models defined *a priori*, which considered the natural relationships between the pre-defined groups (Table 3.2), instead of the traditional hierarchical approach.

Due to computational limitations, I selected a random subsample of 20,000 dives to run the models. The NPMR models were fitted using a Gaussian weighting function with a local mean estimator (lm-NPMR), and using *rFBT* as the response variable. This modeling approach centers the Gaussian weighting function, whose form is determined by its standard deviation or tolerance (*s*), on the target point in an *n*-dimensional environmental space, where *n* is the number of covariates included in the model (Pinheiro et al. 2011, Dragon et al. 2012, Wood 2012). The goodness of fit for the models is expressed as a cross-validated R^2 (xR^2).

Results

A total of 57 adult female elephant seals were captured between 2005 and 2009 at Cape Shirreff, Livingston Island, and were instrumented with SMRU SRDL-CTD tags. Due to early malfunctioning of some instruments, I eliminated those tracks shorter than two months from further analyses, ending up with a total of 53 elephant seal tracks for this study.

SRDL-CTD tags collected data for 247.6 ± 69.5 d, with a mean of 4.7 ± 1.0 locations per day. On average, the tags collected and transmitted data for 6189 ± 2717 dives per individual, while data corresponding to 567 ± 244 CTD casts per individual were transmitted.

Tracking data

Adult female elephant seals from the wAP covered maximum distances from the tagging colony of 3,427 ± 3,047 km, while total traveled distance averaged 21,831 ± 16,168 km (including incomplete tracks, see Fig. 3.1), with transit rates of 3.9 ± 1.3 km h^{-1}. Most animals (85%) concentrated their foraging activity along the shelf break (500 m isobaths) and on shelf waters of the wAP and Bellingshausen Sea, while only 15% foraged pelagically off the continental shelf (Chapter 1, Costa et al. 2010). I found no differences in body mass between these two groups (LMM, $F = 0.22$, $p = 0.64$, Individual as random effect).

There was a wide diversity in the areas utilized by elephant seals, both in pelagic waters as well as along the wAP (Chapter 1, Fig. 3.1). Pelagic foragers showed a wide diversity in their patterns of habitat utilization, with animals foraging along the Polar Front, in association with the ice edge off the Amundsen and Ross Seas, or in association with seamounts (Fig. 3.1). Animals identified as shelf foragers were the most diverse in terms of patterns of habitat utilization, ranging from foraging at the shelf break north of the South Shetland Islands, to individuals reaching the shelf break in the Amundsen Sea. Shelf foragers also showed a significant use of coastal waters along the shelf, particularly animals venturing inside bays and fjords around Marguerite Bay and the Bellingshausen Sea (Fig. 3.1).

Diving data

After filtering the data, a total of 323,815 dives were retained for analysis. Adult female elephant seals dived to an average depth of 363 ± 174 m. The maximum dive depth recorded during this study was 2,377 m; however, the resolution of SRDL-CTD tags decreases below 2,000 m, and depth values are reported to within 32 m, which results in a maximum dive depth ranging between 2,361 – 2,393 m. The average dive duration was 27.8 ± 10.9 min, with the longest individual dive lasting 95.3 min. I did not find differences in diving depths according to the foraging habitat (LMM, $F = 0.55, p = 0.46$, Individual as random effect), but shelf animals dove for longer than pelagic animals (LMM, $F = 5.01, p = 0.03$, Individual as random effect). On the other hand, both pelagic and shelf foragers presented a clear diel pattern in their diving depth, with seals reaching deeper depths during the day than during night dives (LMM, Pelagic animals: $F = 17277.1, p < .0001$, Shelf animals: $F = 16292.5, p < .0001$; Individual as random).

There was an effect of day of the year on both dive depth, and dive duration (Table 3.1, Fig. 3.2), for both pelagic and shelf foragers. Adult female elephant seals from the wAP increase their diving depth as the year progressed, until about day 240 of the year (late August), when the trend was inverted and elephant seals started to dive to shallower depths while returning to the breeding colonies (Fig. 3.2). My analysis showed that the dive duration increased consistently reaching a maximum at about day 150 of the year (end of May), when the models for both groups show a decrease in the duration of their dives. A secondary increase can be observed later in the year, coinciding with the peak in diving depths at about day 240, followed by a decrease in dive duration (Fig. 3.2).

Residual First Bottom Time (rFBT)

The average spatial scale of the most intense searching behavior of elephant seals (i.e. maximum variance) was 116 ± 165 km for all individuals. There was, however, a significant difference in spatial scales between the defined foraging groups (Kruskal-Wallis, $H = 8.2$, $p = 0.004$), with a scale of 102 ± 141 km for pelagic seals, and 116 ± 165 km for shelf foragers. To avoid misinterpretations based on individual effects, I standardized the *rFBT* data for each individual on a scale of -1 to 1.

The spatial patterns observed in the *rFBT* of adult female southern elephant seals depict a different picture between pelagic and shelf foragers. The low proportion of individuals in the pelagic foragers group (15%) and the high variability observed in areas utilized by these individuals complicates the interpretation of the data for these seals (Fig. 3.3). This group shows, in general, a widespread combination of areas where their foraging behavior intensified, and areas where foraging was reduced, without a common pattern being evident.

Shelf foragers, as well, show several areas of intense foraging (positive *rFBTs*) both along the shelf break, as well as in waters well inside the continental shelf of both wAP and Bellingshausen Sea (Fig. 3.3). Some areas of particular intense foraging were Marguerite Bay, the area around Alexander Island and the Wilkins Ice Shelf, as well at the shelf break at the boundary between the Bellingshausen and Amundsen Seas, and in front of the Amundsen Sea itself (Fig. 3.3). Some other areas of important foraging activity for the elephant seals were the waters around the South Shetland Island, including the Brandsfield Strait, the shelf break in the area extending between Anvers and Adelaide Island, and inner shelf waters south of Alexander Island.

Southern elephant seals foraging and environmental variables

I ran a total of 16 NPMR models (8 per foraging strategy), based on the theoretical models described previously (Tables 3.3 and 3.4). In general, NPMRs models performed poorly when trying to describe the relationship between environmental variables and elephant seals foraging, without distinction of the foraging strategies.

The best model for the pelagic foragers group corresponded to Bathymetry + WC ($xR^2 = 0.0912$, Table 3.3). However, this model could only explain 9.1% of the variability in the dataset (Table 3.3), which significantly limits the interpretation of the results. The next two models that followed in order of importance were Surface + Ice ($xR^2 = 0.08$) and Surface ($xR^2 = 0.0794$). An even lower performance was found for the models of shelf foragers. The best model for this group corresponded to Water

Column (WC) with a rather low $xR^2 = 0.0489$ (Table 3.4), followed by the Bathymetry + Ice model ($xR^2 = 0.0372$) and finally the Bathymetry model ($xR^2 = 0.0299$, Table 3.4).

The most important variables affecting the foraging behavior of pelagic elephant seals were the maximum temperature below 200 m, bathymetric slope, distance to shelf break, sea surface temperature, sea surface height and ice concentration (Fig. 3.4). Among the more interesting relationships, pelagic foragers had a positive association of their foraging behavior with Tmax200 of about 1°C, and the *rFBT* decreased with higher temperatures below 200 m. As well, the models showed a general decreasing trend in the relationship between *rFBT* and distance to the shelf, but this pattern is interrupted by three peaks, at 200, 1000 and 1500 km (in order of importance). Finally, this group showed a response to surface conditions: sea surface temperature, sea surface height and ice concentration (Fig. 3.4), with the *rFBT* showing a decrease at 6°C at the surface, as well as an increase with sea surface heights of -0.03 m and 0.07 m, and an increase with sea ice coverage in the 0 – 25% interval.

The results for shelf foragers showed some interesting patterns as well (Fig. 3.5). Shelf elephant seals showed a general decrease in their foraging with increasing Tmax200, although a clear secondary peak can be observed at about 1.2°C; whereas this group showed an association with the sea ice edge, and shelf waters about 50 km from the break (Fig. 3.5).

Discussion

Adult female elephant seals from the wAP showed a wide diversity in individual foraging strategies and patterns of habitat utilization, a character shared with conspecifics from different study colonies across the Southern Ocean and South America (McConnell et al. 1992, McConnell et al. 2002, Bradshaw et al. 2004, Campagna et al. 2007, Biuw et al. 2009, Chapter 1). Yet, individuals included in my study are unusual among female southern elephant seals, since a large majority of them (85%) forage on the continental shelf of the wAP, Bellingshausen and Amundsen Seas (Costa et al. 2010, Chapter 1, this Chapter). Contrary to the general pattern observed in the species, shelf foragers in my dataset were not limited to the shelf break. Indeed, several individuals in my sample ventured into coastal bays and fjords, utilizing the entire width of the continental shelf. On the other hand, only 15% of the animals in my study foraged off shelf waters, a strategy that has been more commonly reported for the species (Hindell et al. 1991b, McConnell & Fedak 1996, Bradshaw et al. 2004, McIntyre et al. 2011b).

These data contradict the widely held notion that female elephant seals are primarily part of the northern slope and oceanic waters food web, where copepods, mesopelagic fish and squid occupy the mid-trophic levels, and extend their range into the southern/coastal food web, where the Antarctic krill, *Euphausia superba*, is considered the dominant mid-trophic species (Kock & Shimadzu 1994). To my knowledge, there is no evidence to suggest that Antarctic krill is included in the diet of elephant seals (Green & Williams 1986, Bradshaw et al. 2003), yet we cannot rule out that possibility. Regardless, if we consider the high metabolic requirements of elephant seals fur to their large body size and endothermic lifestyle, it is anticipated that they might be playing a significant role in the trophodynamics of these coastal ecosystems, constituting an important competitor for biological productivity in these systems, which has not be accounted for to date.

On the other hand, this natural separation between shelf and pelagic foragers presents interesting challenges when trying to understand the effect that the environment has on the foraging behavior of elephant seals. For instance, we can expect that animals foraging on the continental shelf will be influenced by bathymetric features and sea ice concentration (but see *Foraging habitat models*).

Diving behavior

Both species of the genus *Mirounga*, the southern and northern (*M. angustirostris*) elephant seal, are considered particularly proficient divers. Spending >90% of their time at sea underwater, elephant seals have been reported to dive to average depths of about 600 m for 20 minutes, although they are capable of reaching depths well over 1,800 m, whereas dives can last for almost 2 h for both species (Le Boeuf et al. 1988, Hindell et al. 1991a, McConnell et al. 1992, Biuw et al. 2007, Hassrick et al. 2010).

I did not find any differences in body size or diving depth between the pelagic and shelf foragers. The shelf of the Antarctic continent is unusually deep, as a consequence of the isostatic depression due to the large mass of the Antarctic ice sheets (Knox 2007), resulting in a shelf break that can be situated between 500 and 1,000 m deep. Further, the wAP continental shelf is characterized by the presence of several deep (> 500 m) troughs and canyons across the width of the shelf (Padman et al. 2010). Thus, the bathymetry of the continental shelf is not likely to limit the diving behavior of those animals that utilize this system to forage, other than in the case of very deep dives (>1,000 m).

However, I did find that shelf animals performed significantly longer dives than pelagic animals. Southern elephant seals from Kerguelen Islands, in the Indian sector of the Southern Ocean, present an interesting comparison with animals in my study. Animals from this rookery present a similar partition, with seals foraging on the Kerguelen plateau (1,000 - 4,000 m deep), or in open oceanic waters. However, there were no differences in their diving depths or durations between animals that foraged on shelf or pelagic waters (Bailleul et al. 2007). Thus, since elephant seals from both groups identified in my study dived to similar depths, it is likely that the difference in dive duration was related to the variability in the seals' dive profiles, with pelagic animals performing relatively more V-shaped dives (Hindell et al. 1991a, Crocker et al. 1997), and therefore spending less time at the bottom of the dive. The longer duration of benthic dives compared to pelagic dives is a consistent pattern seen in other diving mammals (Costa & Gales 2000, Costa & Gales 2003, Costa et al. 2004, Villegas-Amtmann et al. 2011).

More interestingly, my data showed a peculiar pattern in the relationship between dive duration and day of the year for both pelagic and shelf elephant seals (Fig. 3.2). Elephant seals increase their diving capacity throughout their time at sea, as a consequence of the increase in body oxygen stores (Hassrick et al. 2010), which results in an increase of dive duration across their foraging trips (Hassrick et al. 2010, McIntyre et al. 2011a). The output obtained from the GAM model showed a constant increase in the duration of the dives, reaching a first peak at about day 150 of the year (late May), followed by a slight decrease and a subsequent increase to reach a second peak around day 230 of the year (mid-August). Adult female southern elephant seals from Macquarie Island showed a similar pattern in the changes in drift rates (i.e. foraging success), displaying a constant increase from the beginning of their post-molt trip to reach at maximum in May (coinciding with the first peak in dive duration that I found in my analysis), after which a slight decrease in drift rates was observed (Thums et al. 2008b), probably associated with the development of the fetus (lean tissue), affecting the drift rate (a direct consequence on the percentage on lipid tissues in the body).

The coincidental patterns observed in dive durations and drift rates might be a consequence of fetal development during the post molt trip. As in other pinnipeds, elephant seals display delayed implantation, which is thought to occur sometime around the annual molt of the seals on land (Jan- Feb). Since fetal development occurs during the 8 months long post-molt trip, there are no studies, to my knowledge, addressing fetal growth on elephant seals. However, the first reduction in dive duration occurs at the end of the third month after implantation. Studies on harp seals (*Phoca groenlandica*), a much smaller species of Arctic phocid, showed a linear increase in the length of fetuses during pregnancy (Stewart et al. 1989). Assuming that elephant seals' fetuses display the same pattern of development, this could imply that by the end of the third month the fetuses have reached a size that not only affects the ratio between lean and fat tissues and the mothers (and hence their drift rate), but also the physiology of the females, potentially triggering a reduction in their diving abilities. Further, these results contradict the vision of a positive effect of pregnancy on oxygen stores of adult females as a result of the increase in blood volume (LeBoeuf 1994) and instead point toward a more complicated effect of pregnancy on the diving abilities of elephant seals. Finally, the different methodological approach of using an additive model instead of a linear model, as in the studies by Hassrick et al. (2010) or McIntyre et al. (2011a), contradicts the idea of a constant linear increase in dive duration along the post-molt trip.

Residual First Bottom Time (rFBT)

Recent studies on foraging behavior of both species of elephant seals have been successful at identifying foraging areas by using an indirect measure of changes in animal's condition, the changes in drift rate (Biuw et al. 2007, Robinson et al. 2010, Thums et al. 2011). However, 85% of the animals in my study foraged over shelf waters (<1,000 m), which makes separating drift dives from benthic dives difficult, thereby reducing my ability to accurately identify areas of foraging success.

Many metrics have been proposed to identify putative foraging areas for both species of *Mirounga* (Robinson et al. 2010, Thums et al. 2011, Dragon et al. 2012), most of them based on analysis of tracking data. New efforts have been made to develop metrics that consider the diving behavior of these animals in the identification of foraging areas (Bailleul et al. 2008, Bailleul et al. 2010, Dragon et al. 2012). For my analyses, I used the *rFBT*, a scale dependent measure of search effort that incorporates the vertical dimension by looking at the variance in bottom time of the dive (Bailleul et al. 2008).Yet, there are limitations to the use of *rFBT* in identifying areas where seals have been successful at foraging, particularly as foraging effort (measured here as diving behavior) does not necessarily represents foraging success as seals may be actively searching for or pursing prey without actual prey capture (Bailleul et al. 2008, Bailleul et al. 2010, Dragon et al. 2012).

My analysis showed a great heterogeneity in the foraging patterns of elephant seals foraging both on pelagic or shelf waters (Fig. 3.2a). I could identify a wide diversity of places along the shelf of the wAP where elephants seals spent more time than expected at the bottom of their dives, both in association with the shelf break, as well as in inner shelf waters. This finding reinforces the idea that elephant seals must be considered an important component of the coastal food web of the wAP and Bellingshausen Sea (Fig. 3.2a). A similar complex pattern was observed for pelagic animals, for which it is not possible to identify a general foraging area of importance (Fig. 3.2b). This group of seals presented a large variability in the areas they visited that further complicates the interpretation of the results, particular considering the low number of individuals in my sample that ventured to forage in pelagic waters.

Foraging habitat models

The models generated in my study had, in general, very low predictive power to identify areas of positive *rFBT* based on environmental variables, as evident from their low xR^2 values.

Despite the aforementioned low performance, I extracted the predicted values to visually evaluate the shape of the relationships between the elephant seals foraging behavior and the environmental variables (Figs. 3. 4, 3.5). These relationships should be considered merely illustrative of the type of responses that the elephant seals display since the best models only explained about 5% of the variability observed. According to the top models, foraging by pelagic elephant seals is associated with

Circumpolar Deep Waters, as evident from the shape of relationship with Tmax200, and the increase in *rFBT* observed at about 1°C, which is indicative of this water mass (Fig. 3.4), a relationship that has been previously described for elephant seals foraging along the Polar Front (Biuw et al. 2007). Furthermore, there is a general decrease in foraging further away from the shelf break, but three distinctive peaks at 200, 1000 and 1500 km were observed, which roughly coincide with the ice edge, Polar Front and Antarctic divergence, where pelagic animals in my sample were observed to forage. The association with both boundaries of the Polar Front are also evident from the relationship with Sea Surface Height, which showed an increase at -0.03 (indicative of foraging at the Antarctic divergence), and 0.07 m (indicative of convergence, at the Polar Front) (Fig. 3.4).

The results for shelf foragers also showed the influence on CDW on elephant seals foraging (Fig. 3.5). Despite a general decrease in foraging with increasing temperature below 200 m, there is a bump in the relationship at about 1.2°C, which indicates a positive effect of this relatively warm water mass on the foraging of shelf foragers. The other relationships point toward the already describe shelf foraging patterns, such as the increase in *rFBT* at the ice edge, and at shelf waters 50 km from the break.

The low performance of NPMR models, although somehow disappointing, was not completely unexpected. I explored a variety of modeling approaches that included Linear Mixed Effect Models (LMMs), as well as Generalized Additive

Mixed Models (GAMMs) (results not shown here). The best model that I obtained when using these parametric approaches had a $R^2 = 0.06$ for the pelagic models (as opposed to the xR^2 of 0.09 of the NPMR model), which is again an indicative of poor performance of these models to predict the response variables, in my study the *rFBT*. Two mechanisms could explain this consistent low performance of different modeling approaches: (1) the foraging metric selected, the *rFBT*, might not a good indicator of foraging in elephant seals from the wAP, and (2) the elephant seals from the wAP display such a wide diversity of individual foraging strategies, that modeling a common pattern is unlikely.

Both species of elephant seals have been extensively studied throughout their ranges, and are likely to be the two of the best known species of marine top predators. The large effort involved in deploying satellite tags and dive recorders in a large number of individuals has offered a unique opportunity to gain an insight of the at-sea behavior of these deep diving predators, as well as to develop metrics of putative foraging zones (or success), using both two dimensional tracking data or incorporating diving behavior (Hindell et al. 1991a, Biuw et al. 2007, Robinson et al. 2010). The *rFBT* is one of the few foraging metrics that incorporates the diving behavior of the seal that I was able to use, given the peculiarities in my dataset. It has been shown that the *rFBT* metric corresponds very well with the results obtained from the calculation of changes in drift rates and other metrics of foraging behavior (Bailleul et al. 2008, Dragon et al. 2012), although these analyses have been conducted on southern elephant seals from Sub Antarctic islands that travel to the Antarctic continent to forage in association with the sea ice edge, or along the Polar Front area. Hence, I cannot rule out the possibility that, given the benthic foraging behavior display by animals in my dataset, this metric might not perform very well at identifying areas of intense foraging.

On the other hand, elephant seals from the wAP display a very unique behavior among elephant seals. My dataset consisted of tracking and diving information from animals that were captured on the Antarctic continental islands, with immediate access to their foraging grounds, as opposed to animals from other colonies that have to travel hundreds or thousands of kilometers to reach their foraging areas (Hindell et al. 1991a, McConnell & Fedak 1996, Biuw et al. 2007, Campagna et al. 2007, Bailleul et al. 2008, McIntyre et al. 2011b). Additionally, I found a large diversity in the individual foraging strategies for seals in this dataset (Chapter 1), in agreement with the complex pattern in habitat utilization observed in the tracking and diving data (Figs. 3.1, 3.3). For instance, one individual in my dataset spent its entire post molt trip (ca. 8 months) foraging within 300 km of its tagging location, at the shelf break just north of the South Shetland Islands; whereas I also had an individual in my study that travelled over 5,400 km to forage in association with the sea ice edge off the Ross Sea (Fig. 3.1). Despite the fact that these two individuals represented extreme cases in my dataset, it is evident that animals in both groups displayed high individual variability in the areas utilized to forage, which is likely to have an effect when trying to understand what environmental variables might define the foraging habitat for elephant seals from the wAP.

The identification of relationships between environmental variables and the distribution and foraging behavior of marine top predators has been widely explored in scientific literature, and strong evidence suggests a the association of foraging activities with both surface and water column oceanographic features in several species (Biuw et al. 2007, Tew Kai et al. 2009, Block et al. 2011, McIntyre et al. 2011b, Robinson et al. 2012). Nonetheless, I could not find a strong model with enough predictive power to explain the relationship between the foraging behavior of elephant seals from the wAP and their environment. Thus, I suggest that the high variability in the patterns on habitat usage of individual seals affects the performance of statistical models, decreasing the likelihood of identifying general patterns in the data as a consequence of the wide spectrum of variables and interactions among these that the elephant seals experience during their post-molt foraging trip.

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Table 3.1. Relationship between diving behavior of adult female elephant seals and track duration, analyzed using General Additive Models (GAMs)

Model	Estimate	SE	*t*	*P*	R^2
Dive duration ~ s(day of the year)	5200	0.31	5200	<2e-16	0.42
Dive depth ~ s(day of the year)	383.2	0.16	2325	<2e-16	0.28

Table 3.2. Conceptual environmental models and environmental variables included in each one.

Model	Variables
Water column structure	*MLD* , N^2, *Tmax200, Tmax200D, Dbot, WM*
Surface oceanography	*SST, SSH, geoM, geoZ*
Oceanography	*MLD*, N^2,*Tmax200, Tmax200D, Dbot, WM, SST, SSS, SSH, geoM, geoZ*
Ice	*Ice, dist2ice*
Surface conditions	*SST, SSS, SSH, SSD, geoM, geoZ, Ice, dist2ice*
Bathymetry	*Bathy, slope, dist2shelf*
Bathymetry + Ice	*Bathy , slope, dist2shelf, Ice, dist2ice*
Bathymetry + WC	*Bathy, slope, dist2shelf, MLD*, N^2, *Tmax200, Tmax200D, Dbot, WM*

Table 3.3. Top three NPMR models for pelagic foragers southern elephant seals. The best model, as selected based on its xR2 value corresponded to Bathymetry + WC, which only explained 9.1% of the variance in the data.

Pelagic					
Model	Ranking	xR^2	Variable	Tolerance	Sensitivity
Bathymetry + Water Column	1	0.0912	Tmax200	0.508	0.152
			slope	6.0	0.0046
			dist2shelf	112127.2	0.107
Surface + Ice	2	0.08	SST	0.68	1.698
			ice	15	0.057
Surface	3	0.0794	SST	0.68	1.345
			SSH	0.01	0.449

Table 3.4. Top three NPMR models for shelf foragers southern elephant seals. The best model, as selected based on its xR2 value corresponded to WC, which only explained 4.89% of the variance in the data.

Pelagic					
Model	Ranking	xR^2	Variable	Tolerance	Sensitivity
WC	1	0.0489	MLD	21.95	0.1344
			Tmax200	0.508	0.0683
Bathymetry + Ice	2	0.0372	dist2ice	63.714	3.055
			bathy	601.5	0.813
Bathymetry	3	0.0299	bathy	300.75	0.1761
			dist2shelf	81091.3	0.0932

Figure 3.1. Movement of adult female southern elephant seals from the western Antarctic Peninsula (2005 – 2009). Tracks shown in red correspond to animals that displayed pelagic foraging, while blue tracks correspond to animals that displayed shelf foraging

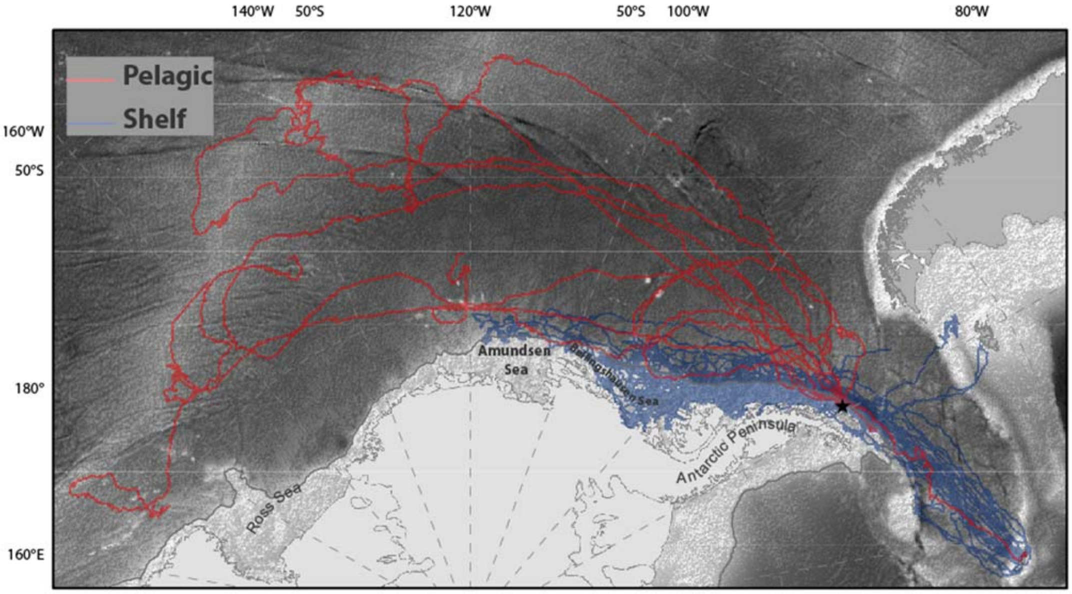


Figure 3.2. Relationship between dive depth (top panels), and dive duration(lower panels) for adult female southern elephant seals from the wAP. The left panels show the raw data, and the right panels show the output from the fitted GAMs model: *divedepth ~ s(dayof year)*; *diveduration ~ s(dayof year)*. Light gray indicate pelagic foragers. Dark gray indicate shelf foragers

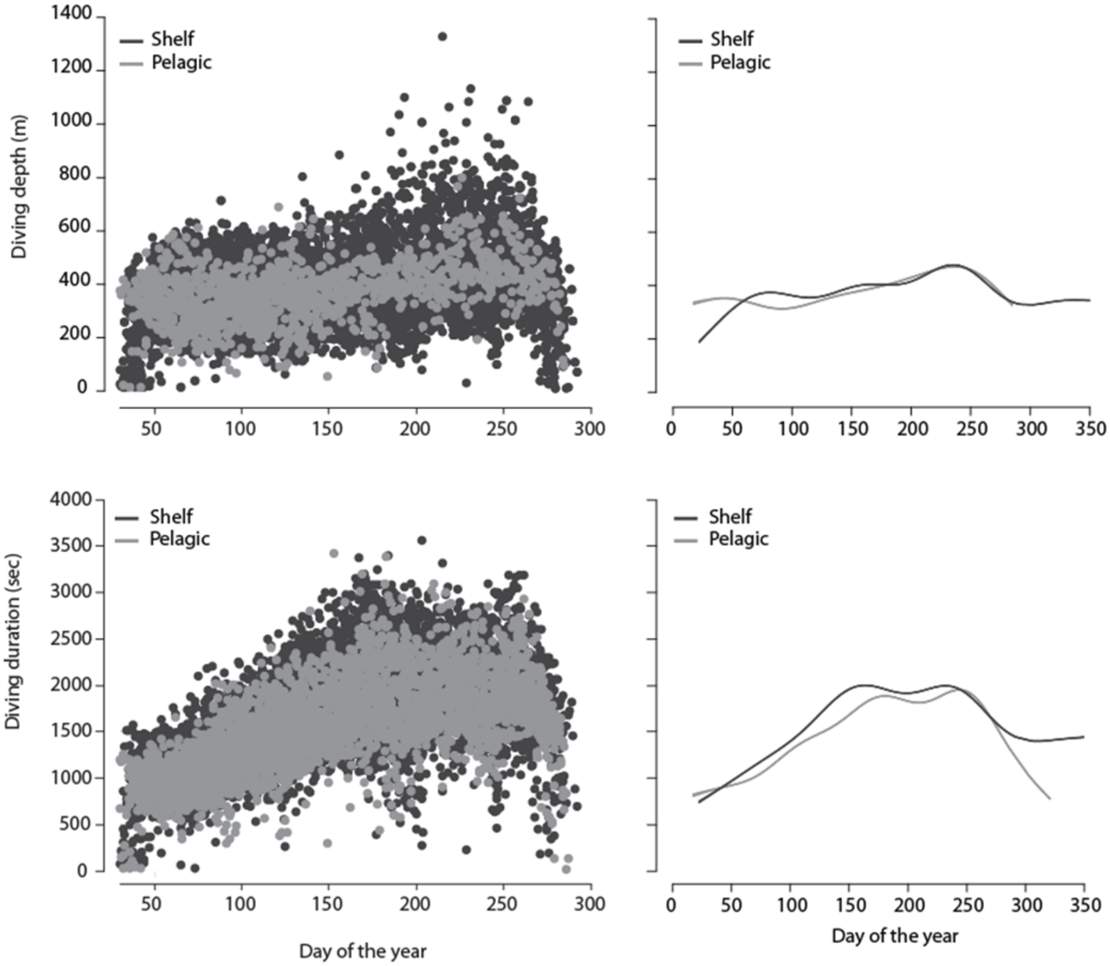


Figure 3.3. Foraging behavior of southern elephant seals. Top panel corresponds to pelagic foragers, bottom panel corresponds to shelf foragers. The color scale changes in foraging behavior: red indicates positive changes in *rFBT* (i.e. the seal increases the time at the bottom of the dive), blue colors indicate negative changes in *rFBT* (i.e. the seal decreases its time at the bottom of the dive

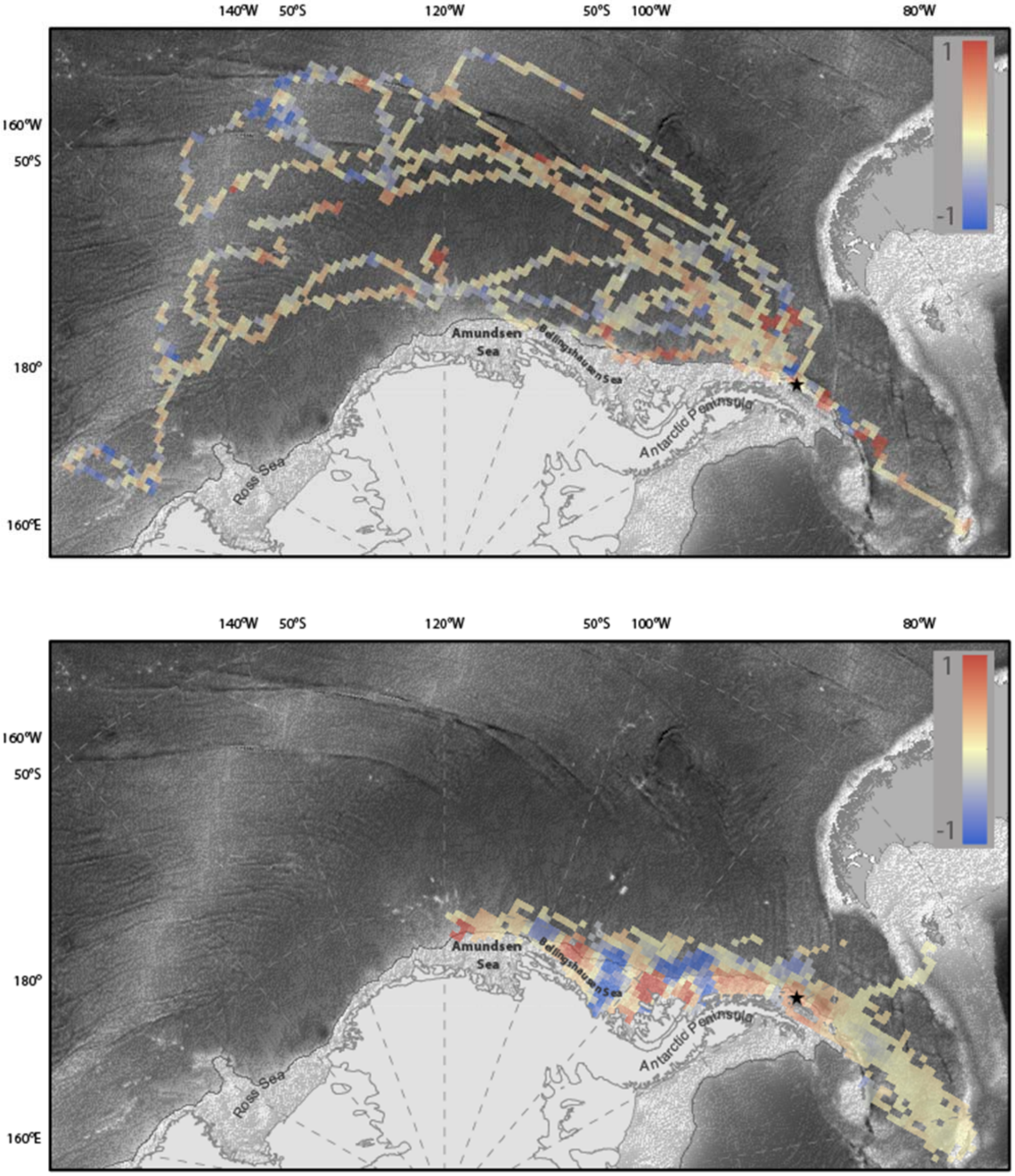


Figure 3.4. Relationships between elephant seal foraging behavior and environmental variables, as predicted from Non Parametric Multiplicative Regression Models. The figure shows the most important variables for seals identified as pelagic foragers

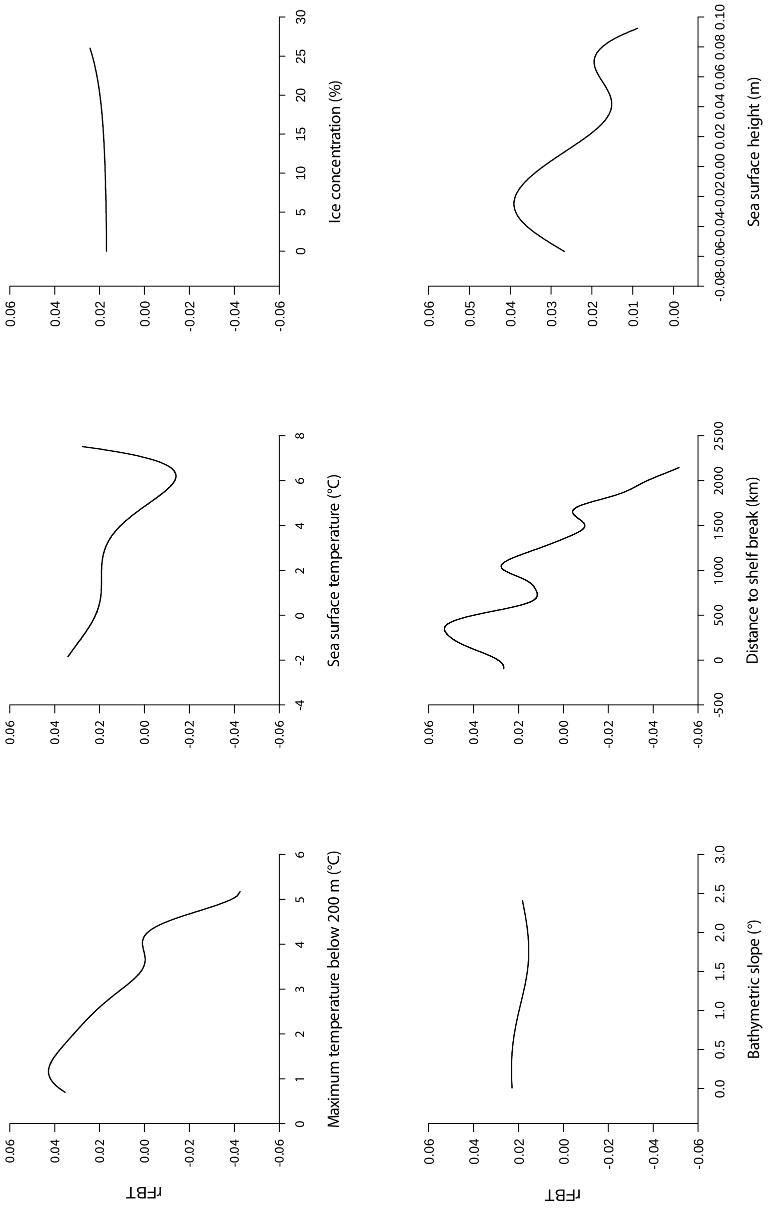
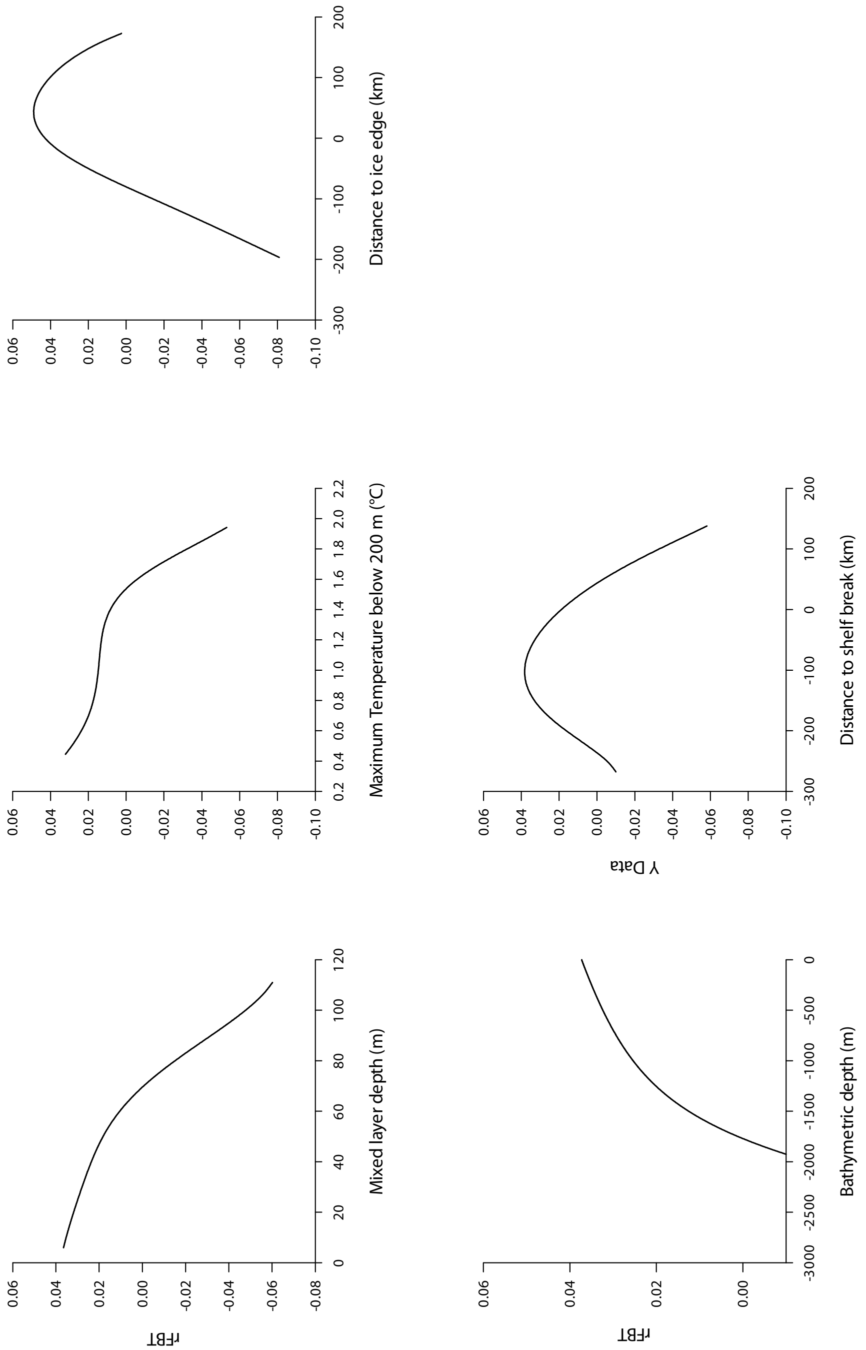


Figure 3.5. Relationships between elephant seal foraging behavior and environmental variables, as predicted from Non Parametric Multiplicative Regression Models. The figure shows the most important variables for seals identified as shelf foragers



Chapter 4 CRABEATER SEALS DISPLAY HABITAT PREFERENCE IN THE RAPIDLY CHANGING WESTERN ANTARCTIC PENINSULA

Luis Alfredo Hückstädt

Introduction

During the last decades, we have seen a significant increase in the use of bio-logging technologies to study different aspects of the biology of marine predators, including animal behavior, movement patterns, habitat utilization, feeding ecology, physiological processes, etc. (Block et al. 2002, Block 2005, Naito 2010). Likewise, new applications of such technologies include the use of different sensors in the instruments deployed on animals (e.g. temperature, salinity, light level, chlorophyll-*a*) to collect environmental data from a wide diversity of ocean environments occupied by the animals under study, thus providing information from areas that might be difficult, if not impossible, to reach by more traditional methods (e.g. oceanographic vessels, ARGO floats) (Boehlert et al. 2001, Boehme et al. 2008a, Boehme et al. 2008b, Costa et al. 2008, Costa et al. 2010).

In the case of studies of habitat definition and usage patterns for highly-mobile and cryptic species (as is the case of most marine top predators), tagging technology has significantly impacted the field since it offers a less biased account for the distribution of species (Skov et al. 2008), improving our ability to identify the areas of occurrence of animals and consequently allowing us to describe distribution patterns , to infer the use of different areas by the animals (e.g. migration corridors versus foraging areas), to make inferences about the behavior and condition of animals in the wild, as well as to obtain data about the environment that the animals are experiencing and relate this with the behavior of the animals (Biuw et al. 2007, Robinson et al. 2010). However, the use of these kinds of data to model the potential distributional range of different species has been less explored, regardless of the acknowledged potential that such data have to advance the field of habitat modeling (Aarts et al. 2008, Skov et al. 2008, Beyer et al. 2010, Jiguet et al. 2011).

On the other hand, despite the fact that diving marine top predators utilize a three dimensional environment, where foraging can be effectively separated from the surface by hundreds, or even thousands of meters (Biuw et al. 2007, Robinson et al. 2010, Hazen et al. 2011, Chapter 3), attempts to build habitat models have relied heavily on environmental conditions at the surface and/or static features such as bathymetry and coastline (Block et al. 2011, Friedlaender et al. 2011, Shillinger et al. 2011). This is explained, mostly, by our limited ability to effectively sample the water column at the appropriate temporal and spatial scales that the study species are effectively utilizing that particular layer in the water column.

Finally, another drawback of using telemetry in studies of habitat preference of marine predators is the fact that this type of data do not provide information on where the animals did not go (i.e. absence data), and our ability to obtain environmental data of these 'non-visited areas', particularly in the vertical dimension, is limited or non-existant (Aarts et al. 2008).

The aforementioned limitations have impacted our ability to address the issue of habitat preference for diving marine top predators, a critical issue when trying to understand and predict how these species respond to environmental variability. These studies are considered of particular relevance in areas such as the western Antarctica Peninsula (wAP), where one of the fastest rates of climatic change in the world is likely affecting the structure and dynamics of the entire ecosystem (Atkinson et al. 2004, Schofield et al. 2010).

Here, I present a habitat model for a conspicuous predator of the wAP, the crabeater seal (*Lobodon carcinophaga*), considered a highly specialized specialist predator of Antarctic krill (*Euphausia superba*), and likely the largest consumer of krill in the world. The characteristics of the species, such as its rather limited feeding niche (as implied from the highly specialized diet), relatively low mobility (Burns et al. 2004, Burns et al. 2008, Costa et al. 2010, Friedlaender et al. 2011), and high dependence on sea ice as substrate, make the crabeater seal a species of high interest in studies of impacts of climate change, since it is likely that this species will be highly impacted by the drastic environmental changes predicted for the area. The goal of my study was to develop a habitat model for the crabeater seal along the wAP using animal diving behavior and movement data (as obtained from satellite telemetry) combined with environmental properties of the water column obtained from animal-borne instruments and oceanographic models developed for the study area.

Materials and methods

Animal captures

Crabeater seals (n = 42) were captured in the wAP as part of three different cruises to the Crystal Sound/Lau Beouf fjord/Marguerite Bay area along the wAP on board the *ARSV Lawrence M. Gould* during the fall and/or winter seasons of 2001, 2002 (US Southern Ocean GLOBEC (GLOBal ocean ECosystems dynamics) research program (Hofmann et al. 2004) and 2007 (Costa et al. 2010). Tracking and diving data for the animals captures in 2001- 02 has been presented elsewhere (Burns et al. 2004, Burns et al. 2008, Costa et al. 2008, Friedlaender et al. 2011).

Animals were captured and sedated as described in Burns et al. (2004 and 2008) and Chapter 2, and instrumented with three different models of Sea Mammal Research Unit (SMRU) Satellite Relay Data Loggers (SRDL) (see Burns et al. 2004, Burns et al. 2008, Costa et al. 2010). In 2001 (n = 16), seals were instrumented with regular SMRU-SRDL tags which determine at-sea location and diving behavior. Animals in 2002 (n = 18) were instrumented with temperature-SRDL tags (tSRDL), which along with the location and diving data, also recorded temperature of the water column. Finally, animals in 2007 (n = 8) were instrumented with Conductivity-Temperature-Depth SRDL tags (CTD-SRDLs), which have the additional capability of measuring salinity of the water column. The behavioral (diving) and, when available, environmental data collected by these instruments are processed and compressed on board (see Fedak et al. 2001), and transmitted via the ARGOS satellite system.

Track analysis

Argos location data were conservatively pre-filtered using a forward/backward speed filter (20 km h^{-1}) to remove aberrant positions (Patterson et al. 2010), and later analyzed using a State Space Model (SSM) (Jonsen et al. 2005). SSMs allow the estimation of positions from the Argos location data, by measuring the errors associated with each location class, as provided by the Argos System, and from dynamics of the movement process (Jonsen et al. 2005, McConnell et al. 2010, Patterson et al. 2010). This methodology allows for statistically robust predictions that embrace the inherent uncertainty in the position data. For this study, I configured the model to obtain a position estimate every 4 hours. To determine the location of the dives, temperature (2002) and CTD casts (2007) I used linear interpolation based on the filtered tracks and time of each dive.

Patterns of habitat use and diving effort

I calculated the number of dives within 20 km^2 cells, and use these data to identify areas of importance for the foraging behavior of crabeater seals along the wAP, using the Hot Spot Analysis toolbox in ArcGIS v10, which calculates the Getis-Ord Fi* statistic for each 20 km^2 grid cell in my dataset, allowing the statistical identification of clusters of high (hotspots) or low (coldspots) values of dive locations. For comparison purposes, I ran the same hot spot identification analysis with the data from the simulated tracks/dives (see *Track and dive simulation*).

Track and dive simulation

A correlated random walk (CRW) is considered an appropriate model to describe animal movement since it introduces a correlation factor to the simpler random walk, which accounts for the tendency of animals to go forward (Bovet & Benhamou 1988). Moreover, modeling animal movement using CRW assumes that habitat use is rather homogeneous and that animal behavior is consistent with time (Kareiva & Shigesada 1983, Bergman et al. 2000, Byers 2001).

To incorporate pseudo- absences in my habitat model, I created a suite of 10,000 simulated tracks for every individual in our sample, using CRWs. For my simulations, I calculated the distributions for both step length (km) and turning angle for every individual seal based on their actual tracks, and used these parameters to simulate the tracks. I used the first real location for that individual as the initial point for all corresponding simulated tracks. Since the purpose of this part of the study was to model the habitat available to crabeater seals, I restricted the simulations so that they created positions at-sea only, by implementing a custom made land mask of the study area.

The second step was to create one simulated dive for each real dive in my data. Briefly, for every real dive conducted by a seal at time *i*, the algorithm randomly selected one simulated tracks from the 10,000 created for that individual, estimated the locations at time *i*, and placed a dive at that point in space and time. The parameter of interest for each simulated dive was diving depth (used later to extract environmental data at the bottom of the depth, see *Environmental Data*), which was randomly drawn from the distribution of actual diving depths for that individual seal. A new simulated track was then selected for diving time *i* + 1, and a new diving location and depth was assigned as previously described. This process was repeated until every real dive performed by the seal had a corresponding simulated dive. I did not explicitly restrict the depths of the simulated dives based on bathymetry, but if the diving depth was deeper than the bathymetry for that location, as defined in the ROMS model (see *Environmental Data*), that dive was not included in the analysis.

Since all simulated tracks had the first real location for that individual as point of origin, I added a time buffer, consisting of the first 5 dives for both the real and simulated tracks, which were eliminated from the analysis, thus preventing spatial overlap. As well, the algorithm only accepted simulated dives that were located at >4 km from the real dive at any specific time, again avoiding spatial overlap between real and simulated dives. This distance threshold (4 km) was selected since it corresponds to the size of the grid cells for the oceanographic model used to obtain the environmental data (see *Environmental data*).

Environmental data

For this study, I used a complimentary approach to obtain the environmental data for real and simulated dives from different sources.

(1) Ice data

Daily sea ice concentrations for 2001 and 2002 were obtained from the National Snow and Ice Data Center (NSIDC) dataset of Special Sensor Microwave/Imager (SSM/I) products. These data are provided on a 25 km grid. For 2007, daily sea ice concentrations were obtained from the NSIDC dataset of Advanced Microwave Scanning Radiometer-Earth Observing System (AMSR-E), with a resolution of 6.25 km. These datasets were also used to calculate the ice edge (see *Data analysis*).

(2) Bathymetric data

Data on sea floor depth were obtained primarily from the SO GLOBEC bathymetry dataset 75 m grid (http://www.whoi.edu/science/PO/so_globec/get_data.html). Apart from sea floor depth, these data were also used to calculate the slope (degrees) and a sea floor roughness (see *Data analysis*).

(3) Animal-borne instruments

Satellite tags deployed on crabeater seals in 2002 and 2007 also provided data on temperature (hereafter T_{cast}) for 2002, and temperature and salinity (hereafter TS_{cast}) for 2007. These data were quality controlled before analysis by comparing them against the monthly climatological casts provided by the World Ocean Atlas. For every 1 degree cell within the study area, I created a mean temperature and salinity profile with its corresponding standard deviation, by taking all data within a radius of 2.5 degrees from the center of that particular cell. The seal data were then compared against this 1-degree mean monthly cast, and values that differed by more than two standard deviations were flagged as suspicious and visually inspected before confirming its elimination from further analysis. Since dive and T_{cast} / TS_{cast} do not necessarily correspond in time, I matched each dive in the analysis with the closest T_{cast} /TS_{cast} in time.

The dive had to have occurred within 0.5 days of the T_{cast}/ TS_{cast}, otherwise the dive was not included in the analysis.

(4) *Oceanographic model*

Finally, oceanographic data (temperature, salinity and current velocity, *u* and *v*) were obtained for both real and simulated dives from a Regional Oceanographic Model System (ROMS) model developed for the study area (Dinniman & Klinck 2004, Dinniman et al. 2011). The model, with a spatial resolution of 4 km, was run for 2001, 2002, and 2007, obtaining an output file for every 48 hours period. I then extracted the environmental data for each dive (both real and simulated) from the closest output file in time, i.e. there is a maximum time lag of 48 hours between the dive and its corresponding environmental data obtained from the ROMS model. Large changes in environmental conditions in the wAP are not expected at such temporal scale, so the 2-day output from the ROMS model captures is appropriate for this analysis and captures the environmental variability.

Data analysis

A set of environmental variables was obtained for the construction of the habitat models:

(1) *Bathymetric variables*: I created grids of bathymetric depth (m), and bottom slope (degree) from the SO GLOBEC bathymetric dataset and the corresponding values were obtained for each dive. Continental shelf break, defined as the 1,000 m depth contour, was calculated for the study area and the minimum distance between this contour and the dive was calculated. To account for animals on- versus off-shelf, I assigned negative distances when the dive locations were located on the shelf, and positive when dives were located beyond the limit of the shelf break. All of these calculations were performed using the Spatial Analyst toolbox in ArcGIS v10.

(2) *Ice conditions*: Daily sea ice concentrations were obtained for each dive location as well as distance to ice edge (5% sea ice concentration contour) using a custom written algorithm in MATLAB.

(3) *Sea Surface Variables*: Sea Surface Temperature (SST) and Sea Surface Salinity (SSS) were calculated as the mean value for the first 5-m of the water column. These temperature values were either obtained from the animal tags, or from the ROMS model. Since the outputs from both the tags and the ROMS model provided data for a determined number depth layers of the water, I interpolated values at each meter of the water column using a piecewise cubic hermite interpolation in MATLAB.

(4) *Water column properties*: The reconstructed profiles of temperature and

salinity were used to derive the following oceanographic variables at depth: (a) Mixed Layer Depth (MLD), calculated as the depth at which the gradient in the temperature profile over 3 meter was greater than 0.05°C; (b) maximum temperature below 100 m ($Tmax_{100}$); (c) depth of $Tmax_{100}$,($Tmax_{100D}$) as obtained from the interpolated temperature cast; (d) water column stability, derived from the Brunt-Väisäla frequency (N^2) estimated at the diving depth; and (d) water mass at diving depth, which was estimated as follows:

$$\%WM - x = \frac{1/D\ TS_{dive}WM - x}{1/DTS_{WM-a} + 1/DTS_{WM-b} + 1/DTS_{WM-c} + 1/DTS_{WM-d}}$$

where,

%WM-x: Percentage of water mass *x* corresponding to the dive

TS: Temperature, Salinity value

D: Euclidean distance

$WM_{(a, b, c, d)}$: Centroid *TS* values for each one of the water masses present in the wAP, as defined by (Klinck et al. 2004).

Lastly, I obtained the current velocity vectors in its two components, *u* and *v*, for the diving depth. Current velocities were obtained exclusively from the ROMS model.

Habitat models

Habitat preference is governed by the different activities performed by the animal (Aarts et al. 2008), and as such the preferred ‘foraging habitat’ might be different from the ‘breeding habitat’ for the species of interest. For this study, I was interested in describing the preferred foraging habitat of crabeater seals along the wAP, and therefore I used the presence of dives as my response variable, since these vertical incursions of seals are intrinsically related to the process of searching, pursuing and catching prey.

As in Chapter 3, I used Non Parametric Multiplicative Regression (NPMR) models to investigate patterns of habitat preference of crabeater seals along the wAP, using the software Hyperniche v2.20 (McCune 2006, Lintz et al. 2011, Chapter 3). To fit the models, I followed the same approach as in Chapter 3, that is, constructing conceptual models *a priori* (Table 4.2). Due to the large size of the final dataset (306,874 real and simulated dives), I selected a random sample of 20,000 samples to run the models.

NPMR models were fitted using a Gaussian weighting function with a local mean estimator (lm-NPMR), using a binomial response (1: presence, 0: absence). The fundamentals of this modeling approach are provided in Chapter 3. There are, however, some differences when evaluating the models, due to the different nature of the variable response (binomial as opposed to quantitative). The goodness of the fit for the models is expressed as log likelihood ratios, which express model improvement over a naïve model that consists on the average frequency of occurrence of the species in the data (McCune 2006). The log likelihood ratio used in these analyses (log*B*) increases in direct relationship with the goodness of the fit.

Model evaluation was based on the Receiver Operating Characteristic (ROC) curve, a graphical method representing the relationship between the fraction of true positives (sensitivity) and the fraction of false positives at various threshold settings. The Area Under the Curve (AUC), corresponding to the area between the ROC curve and the 45° line, evaluates the ability of the model to correctly classify presence of, in this case, a dive. AUC values > 0.75 indicate that the model shows a useful amount of discrimination, performing better than random predicting the presence of a dive (Elith et al. 2006).

Lastly, predictive grids were generated using Hyperniche v2.20 for the top 5 variables identified in the best models, in order to address the performance of the best models when compared with the actual diving data of the crabeater seals. Individual predictive grids were made for each relevant variable, as identified from the top 4 models, using the environmental data obtained for the 153,437 simulated dives from the ROMS model. These grids were imported into ArcGIS v10, and multiplied by their respective sensitivities as obtained from the NPMR (which can be interpreted as a measure of the relative importance of the variables, McCune 2006). Finally, these grids were multiplied by each other to account for the interactions among them, using the multiplicative approach of a NPMR. For these calculations, I masked out any predictions made outside the shelf, as identified by the 1,000 m isobaths, since seals in my dataset did not ventured beyond the shelf break. Finally, the end predictions were compared against the habitat of crabeater seals as identified from the Hot Spot analysis performed in ArcGIS v10.

Results

Tracking and diving data

A total of 42 crabeater seals were tagged in the three years included in this study, which transmitted data between 4 and 189 days (Table 4.1). Although tracking and diving data for animals captured in 2001 and 2002 have been presented elsewhere (Burns et al. 2004, Burns et al. 2008), I re-analyzed these data for this study. Mean transit rate for crabeater seals in this study was 1.8 ± 0.6 km h^{-1} (Table 4.1) with a maximum of 3.4 km^{-1}. The mean total distance travelled was 2586.6 ± 1720.8 km; whereas the mean maximum distance travelled from the tagging location was 555.9 ± 425.3. Maximum distance travelled was significantly correlated with the duration of the individual record (linear regression; $R^2 = 0.82$, $p < 0.001$). Likewise, the range of the movements (how far animals displaced from the capture location) was also related to the duration of the record (linear regression; $R^2 = 0.54$, $p < 0.001$).

Transit rate was significantly different among years (ANOVA; $F_{(2,39)} = 3.64$, $p = 0.04$), as seals in 2002 had significantly higher transit rates than animals in 2001

(Holm-Sidak *post hoc* analysis; $t = 2.64$, $p = 0.035$). My analysis did not reveal yearly differences in the range of movements (distance to tagging locations), but I did find statistical differences in the total distance travelled among years (Kruskal-Wallis; $H = 7.42$, $p = 0.02$), as seals in 2001 travelled further than 2002 (Dunn's *post hoc* test). However, this difference in total distance travelled is likely to be related to the duration of tracking records, which was significantly longer in 2001 compared with the other two years in my study (Kruskal-Wallis; $H = 11.8$, $p = 0.003$; Dunn's *post hoc* analysis).

A total of 138,020 real dives were included in the analysis. Crabeater seals in my study dived to an average depth of 102.3 ± 94.0 m, reaching a maximum depth of 713 m, whereas the mean dive duration was 353.8 ± 195.3 sec (Fig. 4.2), with the longest dive lasting for a little over half an hour (1,890 sec). Dive depth was positively related to dive duration (linear regression; $R^2 = 0.52$, $p < 0.001$). There was a significant difference on diving depths among years (Kruskal – Wallis, $H = 20.02$, $p < 0.001$); animals in 2001 dived deeper than in other years (Dunn's *post-hoc* analysis), as well as significant differences in dive duration (Kruskal – Wallis, $H = 22.1$ $p < 0.001$), associated with the longer dives in 2001 compared with both 2002 and 2007 (Dunn's *post-hoc* analysis) (Fig. 4.2).

Patterns of habitat use

Crabeater seal from the wAP presented a coastal distribution, preferably occupying water of the inner continental shelf, and rarely venturing beyond the break of the continental shelf (1,000 m isobath, Fig. 4.1). Individuals in my study did not show a common pattern in their displacement trajectories after release, with animals heading North or South of their capture locations indistinctively. Most individuals' movements occurred between Anvers Island and Alexander Island, including Marguerite Bay, with a few exceptions of animals heading north of this area to reach the Brandsfield Strait and the South Shetland Islands, as well as few individuals heading offshore (likely, females with pups that drifted away on ice floes, Burns et al. 2004), or towards the Bellingshausen Sea (one individual in 2002) (Fig. 4.1).

The hot spot analysis revealed a high clustering pattern in the number of dives per 20 km^2 along coastal waters of the wAP, particularly at the Crystal Sound area, between Anvers Island and Adelaide Island (Fig. 4.3a). It is precisely Crystal Sound where we can see the most important concentration of dives by crabeater seals (i.e. hot spot), but this also corresponds to the area where most of the animals from 2002, the larger dataset in my study, were captured (Fig. 4.1). My analysis allowed the identification of a band of shelf waters that is heavily utilized by the crabeater seals, extending from Anvers Island on the north, to the northwest tip of Alexander Island, including Marguerite Bay (Fig. 4.3a). This band spreads from the coastline to about 110 km offshore north of Adelaide Island, and then extending south along mid-shelf waters, over the Marguerite trough, to reach the northern tip of Alexander Island (Fig. 4.3a). On the other hand, the hot spot analysis of the simulated dives provides a useful way to discriminate between random utilization of space (Fig. 4.3b) and preferred habitat utilization by crabeater seals (Fig. 4.3a).

Habitat models

I constructed 8 habitat models using NPMR based on the different a combination of the different environmental variables (Table 4.2). The best habitat model, as selected based on log*B* and AUC values, corresponded to Bathymetry + Water Column (WC), followed by the bathymetric and oceanographic models (Table 4.3, Fig. 4. 5). The most important variables for the top model, as identified by their sensitivities, corresponded to distance to shelf (*dist2shelf*), bathymetric slope (*slope*) and mixed layer depth (*MLD*). With an AUC of 0.79, this model discriminates between presence and absence of crabeater seal dives ca. 80% of the time. Other variables that were emphasized in other models that performed well (Oceanography) corresponded to maximum temperature below 100 m ($Tmax_{100}$) and sea surface temperature (SST) (Table 4.3). On the other hand, the lowest ranked models corresponded to Surface conditions and Ice (Table 4.3). In particular, the Ice model performed the worst among the set of models included in my study, predicting presence of crabeater seals only 60% of the time.

The best bathymetric predictors of crabeater seal presence along the wAP, as indicated by their sensitivity (Table 4.3) corresponded to the distance from the continental shelf break (*dist2shelf*) which ranged between 100 and 200 km, a bathymetric slope of about 5° (~10%), and shallow depths (<500 m deep) (Figs. 4.6, 4.7, Table 4.3). The best oceanographic predictors, on the other hand, showed a decrease in the presence of seals in water columns with a MLD of about 50 m, and an increase in more stratified water columns (increasing MLD). As well, there was a negative trend between crabeater seals presence and $Tmax_{100}$, suggesting that crabeater seals avoid zones of intrusions of warm, off-shelf Circumpolar Deep Water (CDW), as well as sea surface temperatures above the freezing point for sea water (> -0.5°C) (Figs. 4.6, 4.7).

The variables selected for the top 5 models, i.e. those models with AUC values > 0.75, were used to generate predictive grids of the distribution of crabeater seals using based on each variable (Fig. 4.5). The output obtained for the top model (Bathymetry + WC) corresponds very well with actual distribution of seals along the wAP (Fig. 4.8a), identifying areas around Crystal Sound, Marguerite Bay and the northwest tip of Alexander as areas of importance for the crabeater seals. The model also correctly outputs a rather coastal distribution for the seals, and a decrease in their probability of occurrence both north of Anvers Island, as well as south of Alexander Island. However, my model did not perform very well misidentifying the cold spot found at the mouth of the Marguerite trough (Fig. 4.8). The second best model

(Bathymetry) also renders good predictions of the distribution of seals, although the estimates obtained from this model are somehow lower than those from the top model. For instance, both the hot-spot identified inside Marguerite Bay, as the one off the northwest tip of Alexander Island are more intense in the predictive map obtained from the top model, compared with the second best model. The Oceanography model, finally, performed poorly in identifying the preferred habitat of crabeater seal in the wAP. This model assigned a very restricted range of occurrence for the seals, mainly in coastal waters north of Crystal Sound. However, it was successful at identifying the Marguerite trough cold spot (Fig. 4.8).

Discussion

The crabeater seal is considered a specialist predator of Antarctic krill along the Antarctic continent, which could account for >90% of its diet, although fish can also be included in the diet as well (Knox 1994, Zhao et al. 2004, Chapter 2). This high level of diet specialization, in combination with its high biomass (>15 million individuals, Erickson et al. 1990, Knox 1994), makes this species the largest consumer of Antarctic krill in the world. The high dependence of crabeater seal on sea ice for resting and breeding substrate, and its high level of diet specialization makes this species particularly susceptible to environmental changes, which are likely to impact predators through changes in prey distribution on the short term (Croxall

1992), as well as through direct changes in the physical environment (i.e. reduction of sea ice).

Here, I present a study that successfully combines data on animals' movement and diving data, with environmental data obtained from animal-borne instruments, remote sensing and oceanographic models, to construct habitat models for the crabeater seal in the wAP. My study demonstrates that bathymetric features and water column properties play a fundamental role in determining the habitat selected by this species. Crabeater seals are thus identified as shelf foragers that prefer shallow, mid-shelf zones with gentle slopes, the presence of a well stratified water column with a deeper mixed layer (> 60 m), and avoid areas of deep intrusions of warm waters.

Crabeater seal movement and diving pattern

The seals included in my study showed a restricted spatial range, mainly remaining within 560 km of their capture location (Table 4.1), although this limited usage of space is likely related to the duration of the tracking record, as these two variables were significantly related to each other. Nonetheless, few individuals in my study did make longer movements, reaching over 1,400 km from the capture locations (Table 4.1).

The hot spot analysis (Fig. 4.4a) revealed the locations of areas of importance for the crabeater seals. As expected, given the restrictions in spatial range and tracking record, we can see a large effect of the tagging location on the hot-spot identification, with a clear bias towards the Crystal Sounds area (north of Adelaide Island), where most of the captures in 2002 occurred. However, my analysis revealed the presence of a coastal band, extending from Anvers Island in the north, towards the northern tip of Alexander Island, to the south (Fig. 4.4), that is heavily utilized by crabeater seals across years. As well, waters within Marguerite Bay stand out as a hotspot for crabeater seals, whereas, conversely, the Marguerite trough was identified as the only coastal cold spot for crabeater seals diving along with coastal areas north of Anvers Island, rarely visited by individuals in my study (Fig. 4.4).

Few studies have studied the patterns of habitat utilization of crabeater seals. With the exception of the studies by Burns et al. (2004, 2008), most works have reported an association of the seals with the continental shelf break and marginal ice zones, over much deeper ocean depths than those used by animals in my study (Nordøy et al. 1995, McMahon et al. 2002, Bengtson & Cameron 2004, Southwell et al. 2005, Wall et al. 2007). These studies, however, have been conducted in drastically different environments in Eastern Antarctica or the Weddell Sea, where the edge of the sea ice usually coincides with the continental shelf break.

Along the wAP, sea ice season and extent have both been considerably reduced in the last decades (Stammerjohn et al. 2008). Further, in the vicinities of Marguerite Bay, a winter polynya persists as a result of the intrusion of deeper warm waters (Klinck et al. 2004), maintaining an area of open waters through the Antarctic winter well within the continental shelf. Since the aforementioned relationship between ice edge and shelf break does not occur in this study area, it makes sense that crabeater seals' diving did not occur in association with the shelf break, and instead was restricted to shelf waters with low sea ice coverage. Consequently, crabeater seals in my study displayed a more restricted spatial distribution compared to animals from other parts of the Antarctic continent.

Crabeater seals have been described as epipelagic predators that focus their foraging in the upper 50 m of the water column (Nordøy et al. 1995, Wall et al. 2007), although seasonal and regional differences in their diving behavior are recognized (Bengtson & Cameron 2004). Recent work on the species conducted along the wAP indicates that crabeater seals can dive deeper (maximum depth of 712 m) and longer (maximum dive duration of 32 min) (Burns et al. 2004, Burns et al. 2008, this work), thus extending both the maximum dive depth and duration reported for the species (Burns et al. 2004).

It has been suggested that diving to deeper depths is a response of crabeater seals to the natural vertical migration of krill, and not a consequence of switching to other prey during winter months (Burns et al. 2008). For instance, during fall and winter (when data for these study were collected), high biomass aggregations of krill in wAP waters are found between 100 – 250 m in the water column (Ashjian et al. 2004, Lawson et al. 2004, Lawson et al. 2008), coinciding with the deeper diving depths observed in this dataset.

Yet, we cannot rule out a shift in the diet of the crabeater seals to include more fish during the fall and winter (see Chapter 2), and both mechanisms would explain the increase in their diving depth through the fall and winter months. Regardless of the ultimate reason, my data confirmed the findings of (Burns et al. 2004, Burns et al. 2008) in the sense that crabeater seals are capable of performing deeper and longer dives during fall and winter months, and therefore they utilize a larger portion of the water column than previously reported for the species in summer months.

Habitat models

A combination of accurate position data, measurements of foraging behavior, and available oceanographic data, is the key to identifying how patterns of habitat utilization by large marine predators and to understanding how they may be affected by annual and long-term changes in ocean climate (Boyd 1999, Simmons et al. 2007). The wAP has been experiencing profound and accelerated rates of environmental change affecting both the atmosphere and ocean, and yet linking these environmental shift to changes in the ecosystem remains an unsolved issue that has proven difficult to approach (Atkinson et al. 2004, Schofield et al. 2010). Although my study is not the first attempt to model the habitat utilization of the species in the wAP (Burns et al. 2004, Burns et al. 2008, Friedlaender et al. 2011), it constitutes an important contribution in understanding the relationships between the crabeater seal and its environment and, since it includes pseudo-absence data for the first time, allowed me to address the issue of habitat selection (Aarts et al. 2008), a subject that was not incorporated past studies that analyzed presence data only.

Despite crabeater seals being a pagophilic species that depends on sea ice for reproduction, molting and resting (Nordøy et al. 1995, Bengtson & Cameron 2004, Southwell 2004), the Ice model performed the worst among the suit of models I constructed (log*B* = 173.38, AUC = 0.6, Table 4.3). Distance to ice edge (*dist2ice*) seemed to have a predictive effect on the presence of crabeater, as it is evident from the improvement in the Surface model when ice variables were incorporated, which resulted in a 25% improvement in log*B* and an 8% improvement in AUC (Surface + Ice model, log*B* = 681.71, AUC = 0.71; Surface model, log*B* = 545.41, AUC = 0.66, Table 4.3), however, it is surprising that the ice variables were not selected in the best performing models.

Nonetheless, the Ice model predicts a consistent increase in the probability of the occurrence of dives in the 0 to 250 km from the ice edge, and after the threshold the probability of dive occurrence decreases, while the presence of crabeater seals' dives increases with decreasing ice concentration, although the model only renders predictions for the 0 – 40% sea ice cover range. However, none of these variables performs well when trying to discriminate between the presence and absence of seals, and therefore these trends should be treated accordingly. It is likely that the low resolution (25 km) of sea ice concentration in 2001 and 2002 (when most of the individuals included in my study were tracked) affected the results of the models.

As expected from the analysis of the spatial distribution of the dives, the best models suggest that the distance to the shelf break, bathymetric slope and bathymetric are important predictors of crabeater seals presence in the wAP. The predictive outputs that I created for the top models (Fig. 4.8) matched the actual distribution of crabeater seals, with the exception of the model incorporating oceanographic variables alone.

Burns et al (2004) reported that crabeater seals in their study (all of which are also incorporated in my study) utilize a habitat that is characterized by shallow and discontinuous bathymetry, in agreement with the findings of my modeling approach. Yet, their study also found an effect of ice, with crabeater seals using areas with higher than average ice density. This seemingly contradiction with my results does not necessarily imply opposites results. Burns et al (2004) utilized environmental data only for areas where the seals were present, whereas in my models I incorporated pseudo-absences within a spatial domain (defined by the ROMS model) which can be heavily covered by sea ice during the fall and winter seasons. The results of my models do not indicate that seals are no associated with ice, but instead they point to the low predictive power that sea ice concentration has to resolve between areas where the seals were present versus areas that were not utilized by seals.

Additionally, my modeling approach was based on the presence of dives, as opposed to most of the studies on crabeater seals, that either are based on hauled out animals (Testa et al. 1991, McMahon et al. 2002, Southwell et al. 2004) or do not separate dive locations from haul-out locations (Nordøy et al. 1995, McMahon et al. 2002, Burns et al. 2004, Wall et al. 2007, Burns et al. 2008). Crabeater seals dives (and therefore foraging activities) are not bound to occur in areas covered by thick ice, as they need access to air to breathe which would explain the low predictive power of my models incorporating ice as variables. Further, crabeater seals are capable of extensive use of ice free water in winter (Burns et al. 2004).

The results of my models suggest that crabeater seals avoid areas with low SSTs, mixed layer of about 50 m in depth (similar to the average diving depth of the seals), as well as areas with warm $Tmax_{100}$ (Table 4.3, Figs. 4.6, 4.7). The monotonically increasing relationship between SSTs and presence of crabeater seals dives (Fig. 4.6) supports the idea that sea ice does not have a positive effect on seal's diving. Contrarily, crabeater seals do not dive in water with temperature around the freezing temperature of sea water (-1.8°C), since sea ice limits their access of air breathing predators to air.

To better understand these associations between the crabeater seals and their oceanographic environment, it is necessary to understand the typical hydrographic properties of the area under study.

My results indicate that crabeater seals actively prefer stratified water columns (Fig. 4.6), with mixed layer depths > 50 m. Studies on the winter distribution of Antarctic euphausiids in the wAP indicate vertical and horizontal segregation among the most abundant species (*E. superba*, *E. crystallorophias* and *Thysanoessa macrura*), although they generally concentrate between 100 and 300 m in the water column, preferring stratified water columns (Lawson et al. 2008, Wiebe et al. 2011). Hence, the association between crabeater seals and MLD described in my models is a consequence of the distribution of krill (their preferred prey).

A typical vertical profile of temperature for the study area can be characterized by the presence of Antarctic Surface Water (AASW, -1.5° to -1°C) or Winter Water (WW, -1.8° to -1.6°C) in the upper 100 m of the water column, and by the presence of Circumpolar Deep Water (CDW, >1°C), or modified CDW, sitting beneath these water masses below 200 m (Dinniman & Klinck 2004, Klinck et al. 2004, Costa et al. 2008). Along the wAP, the shelf break is dominated by the southern front of the Antarctic Circumpolar Current (ACC) (see Fig. 1), which episodically intrudes on the continental shelf, affecting the oceanographic properties and sea ice concentration (Dinniman & Klinck 2004, Klinck et al. 2004), bringing warmer, saltier and nutrient-rich water CDW upwards into the surface waters with the consequent impact on the biological productivity (Prezelin et al. 2000). These intrusions tend to occur at specific sites along the shelf break, associated with topography (e.g. Marguerite Trough, Dinniman & Klinck 2004, Klinck et al. 2004).

Contrary to the findings of (Friedlaender et al. 2011) for the species in 2002 (using the same dataset with a presence-only modeling approach), my models indicate that crabeater seals avoid these intrusions of CDW. Though it might seem contradictory (given the positive effect of these intrusions on biological productivity) aggregations of Antarctic krill are negatively associated with the location of CDW intrusions (Lawson et al. 2008). It then follows that crabeater seals should also avoid these intrusions as their preferred prey item is not found in large densities in those areas, which would then explain this negative relationship that my models indicate between the presence of crabeater seals and warmer temperatures (Fig. 4.6).

My study successfully established links between the presence of crabeater seals and bathymetric and oceanographic variables along the wAP by creating a suit of habitat models using Non Parametric Multiplicative Regression. The restricted habitat of crabeater seals in the wAP

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Table 4.1. Tracking and diving statistics for crabeater seals, *Lobodon carcinophaga* from the western Antarctic Peninsula

Year	N	Transit rate (km h^{-1})	Distance to capture location (km)	Total distance travelled (km)	Days transmitting (d)	Dive duration (sec)	Dive depth (m)
2001	16	1.6 ± 0.4	607.2 ± 384.3	3161.5 ± 1470.1	85.3 ± 38.3	337.1 ± 53.8	101.2 ± 25.5
2002	19	2.0 ± 0.6	507.3 ± 438.0	1805.5 ± 1492.5	40.2 ± 34.1	215.1 ± 80.8	57.0 ± 27.5
2007	8	1.7 ± 0.6	562.5 ± 515.1	3194.2 ± 2134.9	84.3 ± 54.0	229.8 ± 36.0	61.0 ± 7.6

Table 4.2. Conceptual environmental models and variables included for the crabeater seals habitat models, using Non-Parametric Multiplicative Regression (NPMR)

Model	Variables
Bathymetry	Bathymetric depth (m)
	Bathymetric slope (°)
	Distance to shelf break (km)
Bathymetry + Water Colum	Bathymetric depth (m)
	Bathymetric slope (°)
	Distance to shelf break (km)
	Mixed layer depth (m)
	Maximum temperature below 100m (°C)
	Depth of maximum temperature below 100m (m)
	Current velocity at dive depth (u-component)
	Current velocity at dive depth (v-component)
	Water mass
Bathymetry + Ice	Bathymetric depth (m)
	Bathymetric slope (°)
	Distance to shelf break (km)
	Ice concentration (%)
	Distance to ice edge (km)
Water Column	Mixed layer depth (m)
	Maximum temperature below 100m (°C)
	Depth of maximum temperature below 100m (m)
	Current velocity at dive depth (u-component)
	Current velocity at dive depth (v-component)
	Water mass
Ice	Ice concentration (%)
	Distance to ice edge (km)
Oceanography	Mixed layer depth (m)
	Maximum temperature below 100m (°C)
	Depth of maximum temperature below 100m (m)
	Current velocity at dive depth (u-component)
	Current velocity at dive depth (v-component)
	Water mass

Table 4.2. *Continuation*

	Sea Surface Temperature (°C)
	Sea Surface Salinity
	Surface current velocity (u-component)
	Surface current velocity (v-component)
Surface + Ice	Sea Surface Temperature (°C)
	Sea Surface Salinity
	Surface current velocity (u-component)
	Surface current velocity (v-component)
	Ice concentration (%)
	Distance to ice edge (km)
Surface	Sea Surface Temperature (°C)
	Sea Surface Salinity
	Surface current velocity (u-component)
	Surface current velocity (v-component)

Table 4.3. Binomial NPMR habitat models for crabeater seal (*Lobodon carcinophaga)* from the western Antarctic Peninsula. The best model, as selected based on its log*B* and AUC values corresponded to Bathymetry + WC, which explained 79% of the variance in the data

Model	Rank	log*B*	AUC	Variables	Tolerance	Sensitivity
Bathymetry + WC	1	1046.05	0.79	Dist2shelf	44101.62	1.8
				Slope	0.85	0.9
				MLD	22.6	0.23
Bathymetry	2	1042.56	0.76	Dist2shelf	44101.62	1.78
				Slope	0.85	1.1
				Bathy	1155.64	0.12
Bathymetry + Ice	2	1042.56	0.76	Dist2shelf	44101.62	1.6
				Slope	0.85	1.03
				Bathy	1155.64	0.06
Oceanography	4	988.72	0.76	Tmax100	0.25	1.40
				SST	0.23	1.13
				MLD	67.8	0.07
Surface + Ice	5	681.71	0.71	Dist2ice	69.9	0.75
				SST	0.23	0.73
				SSV	0.13	0.18
				SSU	0.12	0.16

Table 4.3. *Continuation*

Model	Rank	log$B$	AUC	Variables	Tolerance	Sensitivity
Water Column	6	608.05	0.69	Tmax100	0.25	1.03
				Tmax100D	100.15	0.55
				MLD	67.8	0.03
Surface	7	545.41	0.66	SST	0.23	1.03
				SSV	0.06	0.48
				SSU	0.06	0.4
Ice	8	173.38	0.6	Dist2ice	69.89	0.77
				Ice	20.0	0.11

Figure 4.1. Movement patterns of individual crabeater seals *Lobodon carcinophaga* from the western Antarctica Peninsula. Seals were captured in 2001 (*n* = 16, blue), 2002 (*n* = 19, green), and 2007 (*n* = 8, red). The figure shows the bathymetric depth (m) for the study area, circumscribed to the spatial extent of the ROMS model used to extract the environmental data for this study (Dinniman & Klinck 2004a, Dinniman et al. 2011). The gray line shows the 1,000 m isobath, which indicates the continental shelf break.

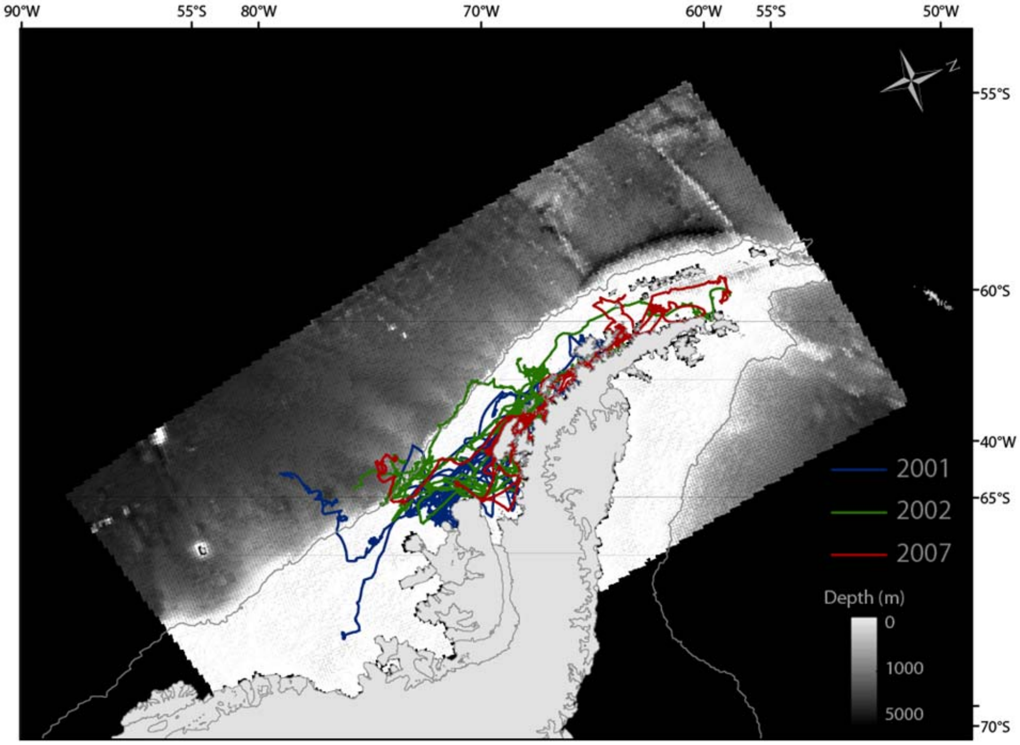

Figure 4.2. Differences in diving duration and diving depth of crabeater seals between 2001, 2002, and 2007. Seals in 2001 dove for longer and deeper than animals in 2002 and 2007 (Kruskal –Wallis test)

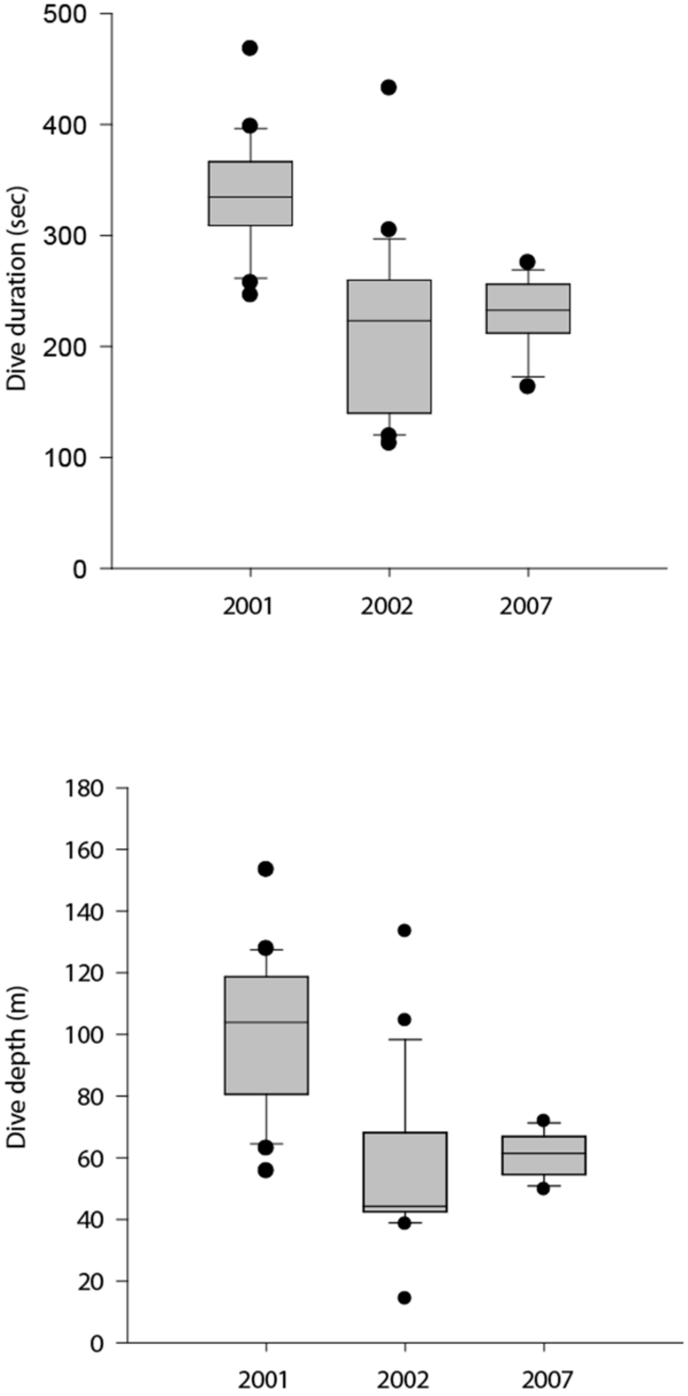

Figure 4.3. Example of a crabeater seal real track (dark blue) and a subsample of 20 simulated tracks created for that particular individual using Correlated Random Walks (CRW). The simulated tracks were generated based the distribution of turning angles and transit rates for that each particular individual

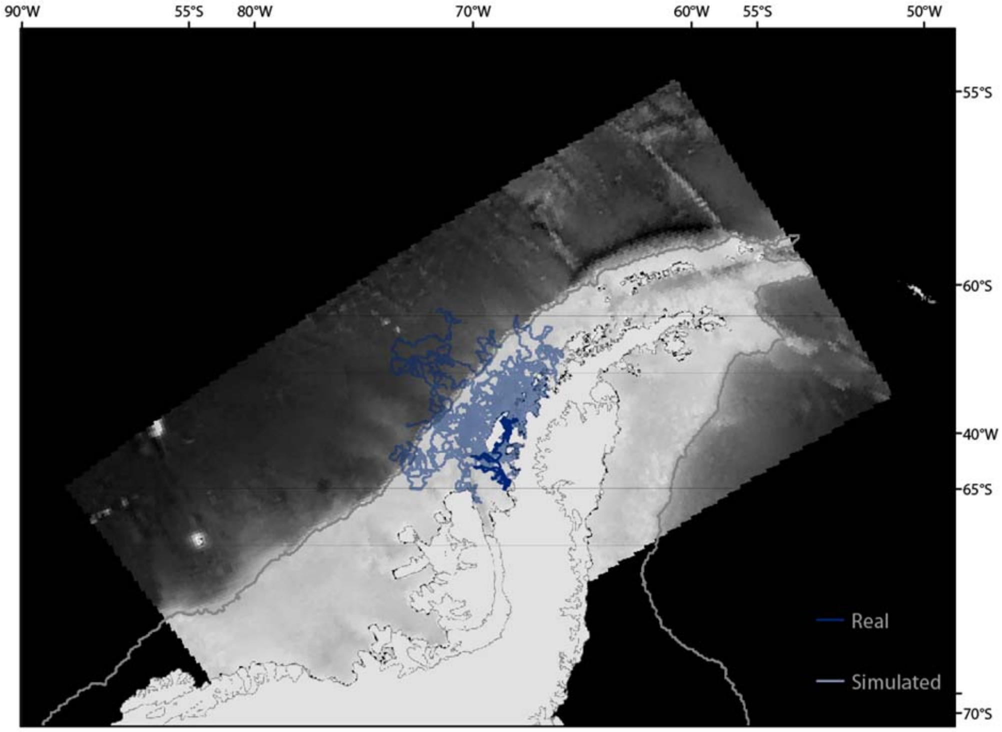

Figure 4.4. Hot spot analysis (Getis-Ord Fi* statistic) for the number of crabeater seal dives every 20 km^2. (a) Hot spot analysis for the real dives performed by crabeater seals in 2001, 2002 and 2007. (b) Hot spot analysis for the simulated dives performed. Simulated dives were created based on the dive depth distribution for each particular individual seal. Red colors indicate significant clustering of high density of dives (hot spots), while blue indicates low number of dives (cold spots).

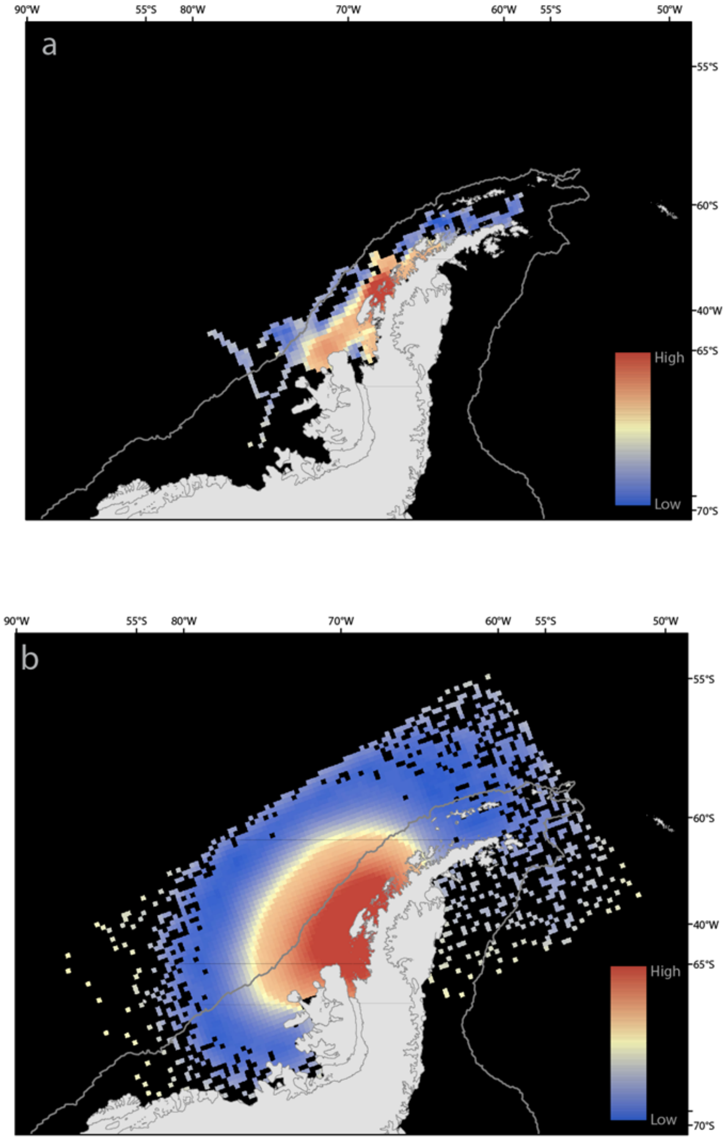

Figure 4.5. Receiver Operating Characteristic (ROC) curves for the eight habitat models constructed for crabeater seals from the western Antarctica Peninsula. Area Under the Curve (AUC) values of > 0.75 indicate that the model shows a useful amount of discrimination, performing better than random at predicting the presence of a dive

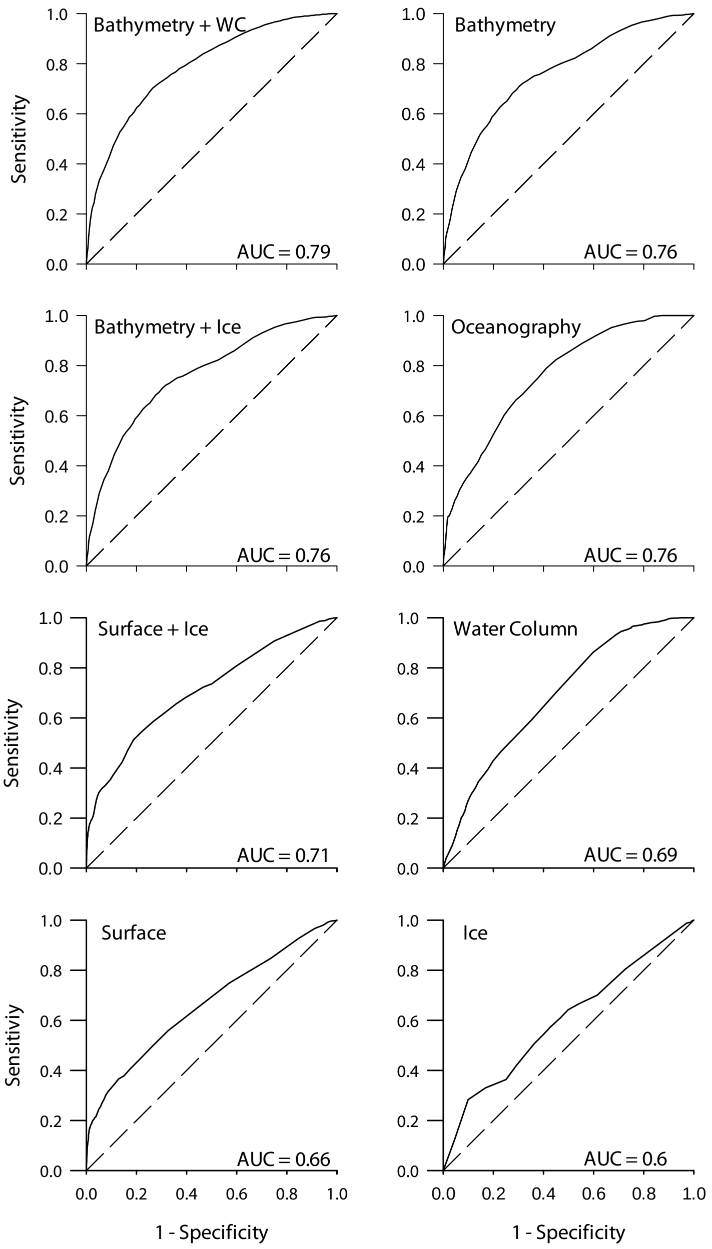

Figure 4.6. Relationships between environmental variables and the presence of dives by crabeater seals from the western Antarctica Peninsula, as modeled using Non Parametric Multiplicative Regression (NPMR) models. The variables included were selected as the most significant in the top four models, identified using log*B* and AUC values (see Materials and Methods for details)

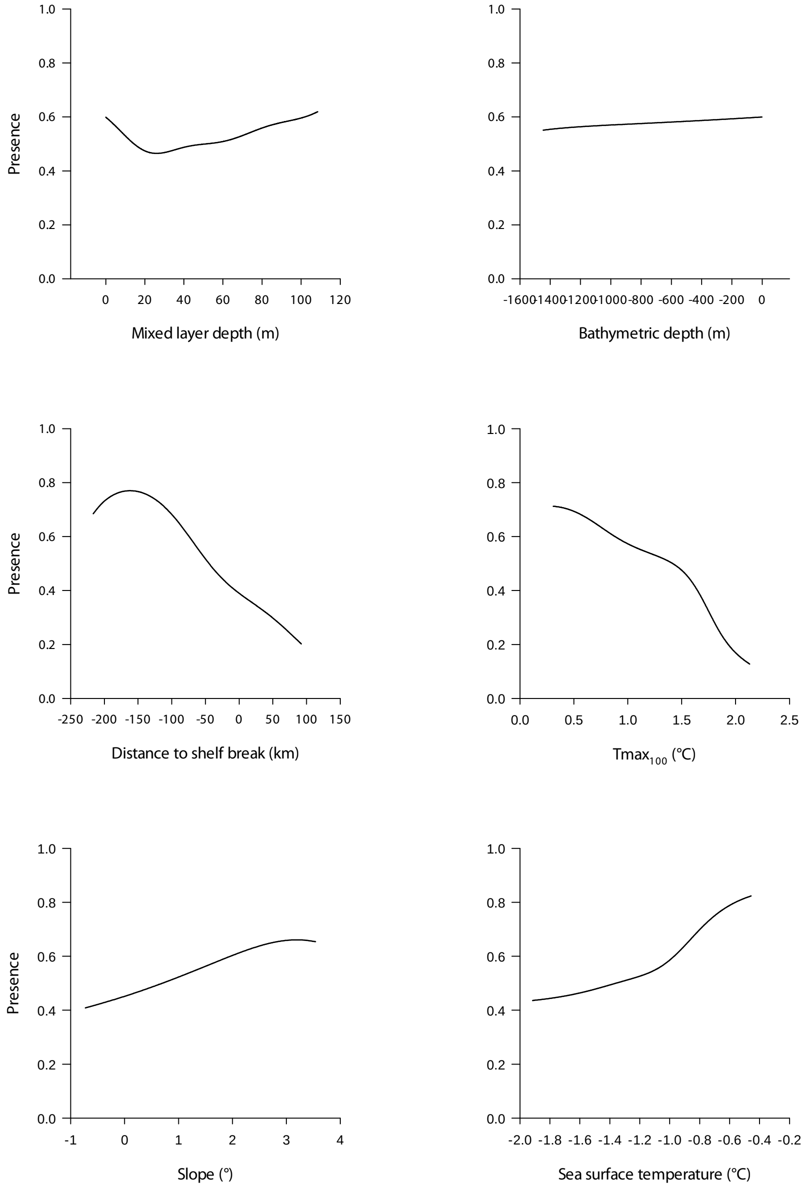

Figure 4.7. Non Parametric Multiplicative Regression (NPMR) response surfaces showing the relationship between the most significant environmental variables and the presence of dives by crabeater seals along the western Antarctica Peninsula. For the top model Bathymetry + WC

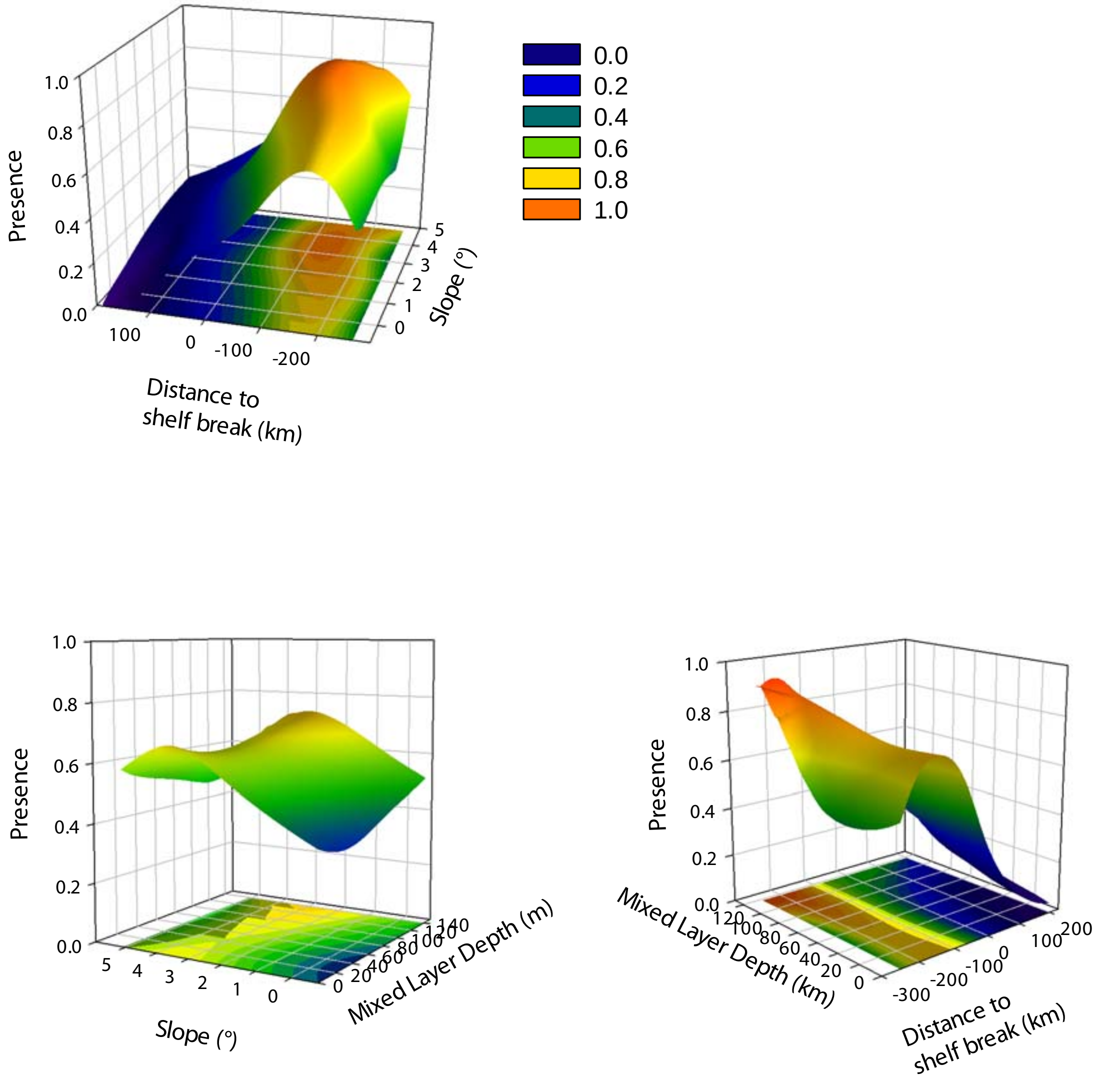

Figure 4.8. Predicted habitat of crabeater seals (*Lobodon carcinophaga*) along the western Antarctic Peninsula as obtained from Non Parametric Multiplicative Regression (NPMR). The figure shows the best three models, as identified from their log*B* and AUC values