Pontificia Universidad Católica de Chile
Facultad de Ciencias Biológicas
Programa de Doctorado en Ciencias Biológicas
Mención Ecología

TESIS DOCTORAL:

LIVING IN THE FAST LANE: FORAGING ECOLOGY OF THE ANTARCTIC FUR SEAL (Arctocephalus gazella) AT THE EDGE OF THEIR BREEDING DISTRIBUTION

Por

RENATO FRANCISCO BORRÁS CHÁVEZ

Diciembre 2020

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DISTRIBUTION

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Por

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LIVING IN THE FAST LANE: FORAGING ECOLOGY OF

THE ANTARCTIC FUR SEAL *(ARCTOCEPHALUS GAZELLA)*

AT THE EDGE OF THEIR BREEDING DISTRIBUTION

DEDICATORIA

No hay nadie en el mundo que haya celebrado más mis logros académicos que mi familia, y nadie tan presente en el arduo camino que implica la obtención de este grado que mi madre y padre. La presente tesis está dedicada a: Miguel Borrás Geisse y Sandra Chávez Ordenes. Quien soy hoy, es fiel reflejo de su incondicional amor y apoyo.

También dedico esta tesis a mi sobrino, Miguel Borrás Cerda. Por el sacrificio que implicó para mí alejarme tantos meses de tu lado en tus primeros años, tiempo congelado en los parajes Antárticos que nunca recuperaré…

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AFS: Antarctic Fur Seal

ANOVA: Analysis of Variance

BCI: Body Condition Index

CC: Calibration Coefficient

DF: Dive Frequency

e.g.: Exampli gratia (for example)

ENSO: El Niño Southern Oscillation

ES: Early Season

FA: Fatty Acid

i.e.: id est (this is)

IACUC: Institutional Animal Care and Use Committee

QFASA: Quantitative Fatty Acid Analysis

L: Lactating

LMM: Linear Mixed Effect Model

LS: Late Season

GLMM: Generalized Linear Mixed Model

HCA: Hierarchical Cluster Analysis

NL: Non-Lactating

MCMC: Markov Chain Monte Carlo

MDS: Multidimensional Scaling Analysis

ML: Machine Learning

MS: Middle Season

MMD: Mean Maximum Depth

MPPD: Median Pup Parturition Day

MUFA: Monounsaturated Fatty Acids

NOAA: National Oceanic and Atmospheric Administration

OFT: Optimal foraging theory

P: Perinatal

PC: Principal Component

PCA: Principal Component Analysis

PDI: Post Dive Interval

PERMANOVA: Permutational Multivariance Analysis of Variance

PSA-LTER: Palmer Station Antarctica LTER Program

REML: Restricted Maximum Likelihood Estimation

RFA: Random Forest Analysis

SIMPER: Similarity Percentages Routine

SAM: Southern Annular Mode

TDR: Time Depth Recorder

TID: Time Invested Diving

US-AMLR: United State Antarctic Marine Living Resources

USA: United State of America

WAP: Western Antarctic Peninsula

RESUMEN

Estudiar la conducta de forrajeo de las especies, es crucial para entender la relación entre la adquisición de energía de los individuos y su consecuente éxito reproductivo. En época reproductiva, las estrategias de forrajeo en mamíferos marinos dependen principalmente de dos factores; (1) La lactancia y los requerimientos energéticos de las crías a lo largo de la temporada de crianza y (2) la variabilidad del ambiente en el que se desenvuelven, la que afectará la disponibilidad y abundancia de las presas. Para lidiar con estos factores, los mamíferos marinos modifican su conducta en múltiples escalas y/o, de ser posible, modifican sus presas objetivo. Las consecuencias de estas modificaciones conductuales de cada individuo podrían gatillar diferencias en la sobrevivencia de las crías lo que en el largo plazo mostrará cambios a escala poblacional.

El lobo fino Antártico, *Arctocephalus gazella* es un gran modelo para estudiar ecología conductual de forrajeo. Investigaciones previas, han cuantificado las respuestas conductuales ante la variabilidad ambiental en múltiples y diversas colonias, permitiendo la comparación entre colonias con diferentes características. La plasticidad conductual es la mayor ventaja que posee la especie ante la incertidumbre que aporta el cambio climático sobre sus especies presa. Sin embargo, no comprenderemos en su totalidad cuan plástica puede ser la especie sin estudiar la conducta de aquellas colonias que se reproducen al borde de la distribución de la especie y que operan ya con limitadas posibilidades para modificar su conducta. Estudiar cómo sobrellevan los gastos energéticos propios de la crianza (i.e. lactancia) y la respuesta ante la variabilidad ambiental adicional aportada por fenómenos oceanográficos sobre áreas ya altamente heterogéneas, nos permitirá predecir cómo responderá la especie a la futura intensificación de los fenómenos atmosféricos producto del cambio climático.

A través del uso de instrumentos electrónicos denominados "temperature depth recorders" instalados en hembras de lobo fino Antártico durante tres temporadas reproductivas, combinamos datos de conducta, estimadores de dieta, y herramientas de inteligencia artificial para estimar las estrategias de forrajeo utilizadas al límite sur de la distribución geográfica de la especie. Cuantificamos la conducta asociadas a factores intrínsecos de los individuos (el costo de la lactancia) y las estrategias relacionadas al incremento en la variabilidad ambiental sobre una colonia que ya operan en ambientes altamente heterogéneos.

En el estudio de mamíferos marinos, conocemos mucho sobre el costo metabólico de la lactancia, pero no sabemos mucho sobre sus implicancias conductuales. En el primer capítulo, cuantificamos simultáneamente la conducta de individuos lactantes y no lactantes mediante la instalación, por primera vez en otáridos, de instrumentos sobre hembras sin crías. Las hembras lactantes mostraron una reducción del tiempo en costa y en la duración de los viajes de forrajeo además de un aumento en el tiempo invertido buceando. Estos cambios sugieren un claro esfuerzo adicional para compensar las limitaciones asociadas a la crianza. En el segundo capítulo, empleamos herramientas de inteligencia artificial para el reconocimiento de buceos asociados a cada presa capturada. Esto se logró mediante la validación de un algoritmo de toma de decisiones con información cuantitativa de la presa consumida obtenida a partir de análisis de ácidos grasos extraídos de muestras de leche, que representan la proporción de una u otra presa capturada en el viaje inmediatamente previo a la obtención de la muestra. Con esto, calculamos la proporción de tiempo invertido buceando y la frecuencia de buceos asociadas a la capturar de una u otra presa en cada viaje de alimentación. El modelo predice la presa capturada con un 76.2% de precisión y, junto a esto, se describió, por primera vez, la manera en la que las hembras lactantes bucean para adquirir krill o peces.

Finalmente, el capítulo tres determina las estrategias de forrajeo utilizadas por las hembras de esta colonia y las diferencias en la conducta de forrajeo de los animales entre las temporadas. Esto se realizó mediante dos estimadores de dieta (análisis fecales y ácidos grasos), evaluación de la conducta espacial, y la implementación de la herramienta predictiva diseñada en el capítulo dos sobre el set de datos completo. Contrario a la temporada 2015/16, las temporadas 2014/15 y 2016/17, presentaron anomalías en la disponibilidad de la presa que repercutieron en la conducta de los animales. 2014/15 se caracterizó por un inusual inicio de temporada muy frío en la costa, y la temporada 2016/17, fue influenciada por un evento extremo de El Niño Oscilación del Sur repercutiendo en las condiciones de hielo de invierno producto de un fuerte Modo Anular del Sur, influyendo sobre las condiciones de la presa durante el invierno y, consecuentemente, el estado de la presa en el verano austral 2016/17. Además, ambas temporadas, 2014/15 y 2015/16, registraron una significativa reducción de la densidad de krill comparado con 2015/16. En las temporadas de baja disponibilidad de krill (2014/15, 2016/17),

observamos como las conductas obedecen a las fluctuaciones de esta presa, cambiando a un mayor consumo de peces respecto al 2015/16. Esto se observó en 1.- un mayor porcentaje de ácidos grasos asociados a peces en las temporadas adversas y, 2.- Un mayor uso de estrategias que tendían a la captura de peces sobre krill en 2014/15 y 2016/17. Esto incluso se observó, en etapas de la temporada donde, según la literatura, la dieta se compone casi exclusivamente de krill. No se observaron cambios en las conductas de buceo entre las diferentes temporadas, presumiblemente por las limitantes energéticas asociadas a la crianza y la lactancia en ambientes extremos, siendo el cambio en la elección de presa la única alternativa para lidiar con la variabilidad adicional provocada por estos eventos atmosféricos sobre un ambiente ya altamente heterogéneo.

La tasa metabólica de campo de esta colonia es similar a la de hembras reproductivas en otras localidades pero que se encuentran bajo altos niveles de estrés debido a la disponibilidad y distribución de la presa. Al muestrear individuos no lactantes, hemos establecido que el límite sur de la distribución reproductiva de la especie no está dado por el medio en el que se desenvuelven, sino por las restricciones inherentes a la lactancia. Las colonias reproductivas de borde aún pueden responder ante estrés adicional impuesto por eventos atmosféricos y por esto, la especie podría estar preparadas para enfrentar la incertidumbre del cambio climático en localidades más al norte. Sin embargo, estudios ya sugieren complejos escenarios futuros para ambos grupos taxonómicos que constituyen las presas más importantes de esta colonia (krill y mictófidos), y que podrían reforzar el papel de una regulación "bottom-up" sobre la especie. Esto resalta la sensibilidad con la que deben operar las hembras al límite sur de su distribución geográfica reproductiva y lo limitadas que están de modificar su conducta ante cambios en la disponibilidad de presa. Por esto, la continuidad de los monitoreos de estas colonias, y la inclusión de aproximaciones de genética del paisaje, podrían entregar información invaluable para comprender el potencial de respuesta que este y otros depredadores tendrán frente al incierto futuro de la región.

ABSTRACT

Studying foraging behavior is essential to understand the relationship between individual energy acquisition and reproductive success. During the breeding season, foraging strategies of marine mammals are shaped mainly by two factors: (1) lactation constraints and the energetic requirements of their offspring and (2) the environmental variability that would determinate both prey availability and distribution. To cope with these factors, marine mammals need to modify behavior at multiple scales or, if possible, the prey targeted. The consequence of these modifications at an individual level may trigger differences in offspring survivorship and hence, result in changes at a population scale.

The Antarctic fur seal *Arctocephalus gazella,* is a great model to study foraging behavior. Previous studies have quantified the behavioral responses to environmental variability at multiple and diverse colonies, allowing comparison between colonies with different characteristics. The behavioral plasticity is the biggest advantage of this species under the uncertainty brought by climate change. However, we would not understand the full extent of how plastic the species is without studying behavior in colonies breeding at the edge of their distribution, where there is little room to modify behavior. Studying how they cope with the energy constraints associated with breeding (lactation) or the additional environmental variability provided by oceanographic events in already highly heterogeneous environments may also help us to predict how the species will respond to the intensification of climatic phenomena due to climate change.

Using Temperature Depth recorders in Antarctic fur seals we combined behavioral data, diet estimators, and machine learning tools to estimate the foraging strategies used at the southernmost breeding distribution of the species. We quantified the behavior associated to

intrinsic factors (the behavioral cost of lactation) and the behavioral strategies implemented to cope with additional variability in an already highly heterogeneous habitat.

In marine mammals, there is abundant information regarding the metabolic cost of lactation but little about their behavioral implications. In the first chapter, we quantify, simultaneously behavior of lactating and non-lactating individuals by instrumenting, for the first time in otariids, non-breeding females. The reduction of time spent onshore and on their foraging trips to sea and the increase in the time spent diving of lactation females suggest a clear additional effort to cope with the constraints of breeding at this location. In the second chapter, we used machine learning tools to recognized diving behavior associated with each specific prey captured. This was done by validating a decision-making algorithm with quantitative diet information obtained from fatty acid extracted from milk, which represents the prey proportions consumed in the previous trip to sea. We then calculate the time invested diving when targeting each prey and the frequency of dives associated to each prey on each foraging trip. The model predicted with 72.6% accuracy the prey targeted on each dive and with this, we were also able to fully described the behavior of lactating females when capturing krill or fish. Finally, Chapter 3 determined the foraging strategies used by this colony and the differences in behavior found between seasons. This was done by the use of two diet estimators (scats and fatty acids), evaluating spatial behavior, and by the implementation of the algorithm designed in Chapter 2 over the full data set. As opposed to 2015/16, seasons 2014/15 was influenced by an unusual cold beginning of the breeding seasons, and 2016/17 by two extreme events: the 2015-16 El Niño Southern Oscillation event and consequently, an unusually strong Southern Annular Mode, with both events influencing prey conditions and modifying the status of prey in the austral summer of 2016/17. In seasons where krill show reduced density which had an impact on krill availability (2014/15 and 2016/17), we observed a higher consumption of fish compared to 2015/16. This was detected by (1) A higher percentage of fatty acids associated with fish consumption in complex years and (2) a higher use of strategies that capture more fish than krill in 2014/15 and 2016/17. This was even observed on periods of the season which, according to the literature, diet should have been composed almost exclusively on krill. We did not observe changes in diving behavior presumably due to the constraints of breeding at their physiological limits, been the shifting of prey the only remaining alternative for this colony.

The field metabolic rate of this colony is similar to what it is observed in females of other locations under highly stressful scenarios of prey availability and distribution. By sampling non-lactating females, we have established that the southern limit of the species distribution is not given by the conditions of the environment but most likely, by the constraints of lactation. Females breeding at the edge are still capable of responding to additional stress caused by certain atmospheric events and the species seems to be well prepared to face the uncertainty of climate

change. However, studies already suggest a complex future for the most important preys of the species that may strengthen the role of bottom-up regulation over the species and limit the only possible strategy been used for this colony: compensate between preys with little room to work harder. This highlights, how sensitive Antarctic fur seals are to change even at their southernmost breeding distribution and the behavioral limitations of the individuals to respond to prey availability. For this, continuous monitoring of these colonies and the inclusion of landscape genetic approaches could provide invaluable information on the capacity of predators to respond to the future uncertainty linked to this region.

INTRODUCTION

Studying foraging behavior is essential to comprehend the relationship between energy acquisition and the consecutive reproductive outcome of an individual. This is why foraging behavior is considered to be the bridge between physiology and population ecology (Scantlebury *et al.*, 2014), because any factor that may change the foraging habitat of an individual will affect first behavior than population patterns (Morris *et al.*, 2009), making behavior a key element of an individual's fitness (Bolnick *et al.*, 2003; 2011).

Animals need to make optimal decisions on where and how they acquire food to maximize energy intake (Stephens and Krebs, 1986) and those decisions will depend on extrinsic and intrinsic factors (Festa-Bianchet, 1988; Werner and Hall, 1988; Lowe, 1996; Costa and Gales, 2003; Orr *et al.*, 2012). The study of how these factors shape foraging behavior, strategies, and decisions has been the core subject of what we know as Optimal Foraging Theory (OFT; MacArthur and Pianka, 1966; Stephens and Krebs, 1986; among many others).

Factors shaping foraging behavior

Extrinsic factors

Extrinsic factors are referred to every event that may affect the habitat of a species in which foraging takes place. At early stages, OFT models assumed a fixed environmental variability of which individuals would have enough information regarding their habitat to make decisions based on a set of optimal values of certain characteristics that would maximize the energy intake (Stephen and Krebs, 1986). However, some of these optimal values, such as optimal prey size (Richardson and Verbeek, 1986), prey searching time, and/or prey handling time (Meire and Ervynck, 1986), change with the environment in which individuals live, and do not necessarily apply equally to all areas. This result, at an evolutionary scale, in some species with a high degree of intraspecific variation of behavior shaped by the variety of habitats in which they are found (Cayford and Goss-Custard, 1990).

In addition, OFT models often condition foraging to the instantaneous rate of energy intake related to the expected intake rate in the surrounding environment (Pyke, 1977; Owen-Smith *et al.*, 2010). This ignores the decision-making process of highly cognitive species (e.g, mammals) that are capable of learning from past experiences and consequently, modify foraging behavior in response to these experiences (Bateson and Kacelnik, 1998). Actually, only recently, long term behavioral memory has been incorporated in modeling optimal foraging behavior (Gautestad, 2011; Gautestad and Mysterud, 2010a; 2010b; Fagan *et al.*, 2013; Mery and Burns, 2010, Polansky, 2013; Oliveira-Santos, 2016; Bracis and Mueller, 2017; Tsalyuk *et al.*, 2019). Although the habitat conditions could solely define the strategies used to obtain the energy

needed (Arnold, 1981; Dill, 1983; Harding *et al.*, 2007) decision-making process and intrinsic factors would also play a role in shaping the foraging strategies implemented by an organism.

Intrinsic factors

Intrinsic factors are mainly associated to the life history of each species (e.g., age, sex, mass; Houston and Shine, 1993; Vales *et al.*, 2015), the physiological constraints of individuals (Costa *et al.*, 2004; Naya *et al.*, 2008) and their reproductive events (Gittleman and Thompson, 1988). For instance, under the same habitat characteristics, a pregnant individual would require a greater amount of energy to cope with the additional metabolic costs that pregnancy implies compared to a non-pregnant female. This additional energy demand will necessarily require modifications of behavior to obtain more or energy-richer food (Clutton-Brock *et al.*, 1989; Shero *et al.*, 2018). Although this may sound obvious, in marine mammals such as otariids, little is known about the behavioral adjustments needed under high energy demanding reproductive events such as pregnancy (Shero *et al.*, 2018) or even more energy-expensive events such as lactation (Oftedal *et al.*, 1987).

Free-range energetics and the metabolic cost of lactation have been studied in a wide range of mammals. Rodents, for instance, will show a higher resting metabolic rate when lactating than during other reproductive events (Garton *et al.*, 1994; Harder *et al.*, 1996). This additional energetic requirement forces them to increase their energy intake during lactation 2.57 times compared to non-lactating periods (Zhu *et al.*, 2015). Lactating primates spend more time feeding than non-reproductive females (Watt, 1988). In some pinnipeds such as elephant seals (*Mirounga angustirostri*) and grey seals (*Halichoerus grypus*), lactation can account for ~60-

75% of the mother´s energetic expenditure (Fedak and Anderson, 1982; Costa and Gentry, 1986) and on fur seals, it can account for 31% (Arnould, 1997), in some cases increasing their food intake by 3.6 times the baseline energy requirements (Williams *et al.*, 2007). Whether terrestrial or marine, this high energy demand is mostly compensated by an increase in energy intake rather than changes in metabolic rate (Millar, 1975; Oftedal, 1984; Costa and Trillmich, 1988, Poppitt *et al.*, 1994; Harder *et al.*, 1996; Zhu *et al.*, 2015) which will result in behavioral changes (Arnould *et al.*, 1996).

Literature is extensive in the advantage associated to species that are plastic in their behavior, especially in colonies living in highly heterogeneous environments (Harding *et al.*, 2007; Woo *et al.*, 2008; Villegas-Amtmann *et al.*, 2011; Abrahms *et al.*, 2018; Kienle *et al.*, 2020, among many others) but in marine mammals, current studies usually present the combined effect that both intrinsic and extrinsic factors have in shaping foraging behavior, falling short in disaggregating the role that can, for instance, play only lactation.

Measuring foraging behavior in marine mammals

Marine mammals can travel long distances from their colonies and can be found in remote locations where human access is limited. Today, the rapid expansion of technology has helped us dealing with the complexity of understanding movement at sea, especially if a direct observation is not possible (Turchin, 1998; Cooke, 2004; Costa *et al.*, 2010a). This relatively new branch of ecological science is called "Bio-Logging" and is defined as the use of miniaturized electronic instruments attached to animals to register and transmit data related to

movement, behavior, physiology, and/or the environment associated to an animal (Bograd *et al.*, 2010; Borras-Chavez, 2018). When biologging is used together with diet estimators (e.g. Banks *et al.*, 2014), the combination of these tools allows us to fully comprehend behavior and physiology on a wide variety of marine species.

Austin *et al.* (2006) suggested that foraging behavior in marine mammals can be divided into four components: vertical movement, horizontal displacement, habitat use, and prey capture. Understanding these four components allow to estimate the usage of habitat, which reflects the quality and resource availability in a particular area but also the energy that an individual invests while obtaining resources (Davoren *et al.*, 2003; Laidre *et al.*, 2004; Austin *et al.*, 2006). Individuals can modify behavior based on prey availability and distribution (Boyd *et al.*, 1994) by using multiple strategies that maximize the energy consumed as a function of the changes occurring in their habitat. Some examples of these modifications are related to improving foraging efficiency such as the time invested in deeper dives (Burns *et al.*, 2008) or the extension of the time at the bottom of each dive (Mori *et al.*, 2007). Others will vary the time of the day they dive based on their prey vertical migration patterns (Croxall *et al.*, 1985) or show seasonal variability (Georges *et al.*, 2000). These modifications show how plastic marine mammal foraging behavior can be but also how capable they are to modify the multiple components of behavior at sea.

Otariids foraging behavior

Otariids are central place foragers (Orians and Pearson, 1979) and, as such, they perform multiple trips to sea while lactating to supply the energy needed by their offspring (Bonner, 1984; Oftedal *et al.*, 1987; Trillmich, 1996). This "attendance strategy" (Trillmich, 1996) is one of the most extreme adaptations to lactation (Sharp *et al.*, 2005) which, as opposed to other marine mammals, allows females to store only a limited amount of blubber before parturition. The rest of the energy needed during lactation is only replenished by the energy obtained during their foraging trips (Trillmich, 1996; Sharp *et al.*, 2005).

The duration of these trips depends on the species and is limited by intrinsic factors such as the age of the pup and the amount of milk demanded, (Beauplet *et al.*, 2003), female age status (Lea *et al.*, 2009), and the female reproductive condition (e.g. pregnant vs non-pregnant: Shero *et al.*, 2018). It is also defined by extrinsic factors such as population size (Staniland *et al.*, 2011), the use of different foraging areas (Staniland *et al.*, 2007; Goebel *et al.*, 2000), and the resource availability and seasonality (Gentry and Holt, 1986). The multiple foraging strategies that can be found between and within species to cope with energy constraints highlight the relevance of studying both inter and intraspecific foraging variation (Werth, 2000; Hocking *et al.*, 2017; Kienle *et al.*, 2019).

In central place foragers, anything affecting the time spent while traveling, searching food, or the availability and distribution of prey itself, will consequently affect the energy acquired and the late delivery of this energy to their offspring (Costa, 2008). As opposed to some pinnipeds or seabirds that have evolved life history patterns to cope with seasonal and/or interannual

resources variation, otariids are sensitive to change (Costa, 1991; 1993; 2008). Changes on climatic or oceanographic conditions may drive changes in behavior. Increasing oceanographic variability (Boyd 1999; Lea *et al.*, 2006) or different prey distribution and/or abundance (Costa *et al.*, 1989; Boyd *et al.*, 1994; Lea *et al.*, 2006; Ichii *et al.*, 2007; Staniland *et al.*, 2010) will force individuals to obtain better or more energy by spending more time searching, eating or hunting forcing animals to change their foraging behavior under new habitat conditions.

The Antarctic fur seal. An extensively studied Otariid

Foraging behavior has been extensively studied in the Antarctic fur seals (*Arctocephalus gazella*, (AFS; Peters, 1875). Today, we know that, if the foraging habitat changes from one year to another, the predictive capability of individuals could be negatively affected in the following year (Bonadonna *et al.*, 2001; Arthur *et al.*, 2015). This problem is accentuated in AFS since the prey diversity is very low, AFS mostly feeds on krill and a few fish species (see appendix A for further information on AFS feeding behavior) and therefore, the decisions of changing foraging strategies are narrowed only to a few options. Consequently, increasing oceanographic variability (Boyd, 1999; Lea *et al.*, 2006) or differences in prey distribution and/or abundance (Boyd *et al.*, 1994; Ichii *et al.*, 2007; Staniland *et al.*, 2010), will force individuals to obtain more energy (or reduce the energy used), and to condition foraging variables such as trip duration, niche utilization and/or diving behavior.

Living at the edge

The southernmost breeding colonies of AFS are found in the Western Antarctic Peninsula (WAP) at Cape Shirreff, Livingston Island, where breeding takes place during the austral summer (December to March). Here, foraging behavior changes throughout the breeding season going from an almost exclusive consumption of krill to a significant increase of fish consumption towards the end of the breeding season (Osman *et al.*, 2004; Polito and Goebel 2010). This may be related to the consumption of energy richer prey (Staniland *et al.*, 2007; Ichii *et al.*, 2007; Biuw *et al.*, 2009) or the natural occurrence of fish toward the second half of the breeding seasons (Santora, 2013). The specific reasons why these changes in foraging strategies occurred are especially important to decipher at Cape Shirreff since females are breeding at their maximum physiological capacity (Costa *et al.*, 2000) and climate change may have an important effect on prey availability at this region.

In addition, the WAP is characterized by a highly climatic heterogeneity that has been increasing during the last 50 years. Together, the intensification of atmospheric events such as the El Niño Southern Oscillation (ENSO; Lee *et al.*, 2010; Rahaman *et al.*, 2019), the rapid increase of oceanic temperature (Clarke *et al.*, 2007), the unusual decrease of sea ice extent, and the increase in precipitation (Bracegirdle *et al.*, 2008; Böning *et al.*, 2008; Stammerjohn *et al.*, 2012; Turner *et al.*, 2017; Stuecker *et al.*, 2017) have increased the regional heterogeneity even more. This has a direct effect on AFS prey availability (Siegel and Loeb, 1995; Atkinson *et al.*, 2004; Atkinson *et al.,* 2019), and onshore conditions and have incorporated an unprecedented degree of annual uncertainty to these colonies compared to other AFS breeding colonies around Antarctica. Therefore, studying how these colonies cope with such a degree of variability in contrasting years and what are the behavioral adjustments needed is of paramount importance.

This information will also provide insights on how well adapted the species is to cope with future climate changes scenarios (Costa *et al.*, 2010b; Bozinovic and Pörtner, 2015).

This thesis addresses key knowledge gaps in the understanding of otariids foraging behavior and the coupling between prey capture and behavior when females face atmospheric events that modify prey abundance and/or availability while breeding in already highly heterogeneous environments.

Project outline, research objective, and hypotheses

The general objective of this thesis is to quantify behavioral plasticity in colonies living in highly heterogeneous environments by determining the foraging strategies of Antarctic fur seals at their southernmost breeding location when coping with physiological and environmental constraints.

This cannot be done if we do not previously identify what behavioral modifications are necessary to cope with lactation itself. This energetically expensive reproductive event may be driving most of the changes in behavior compared to non-breeding females at the edge of their distribution. To the best of our knowledge, research on diving behavior on non-lactating otariids is not existent (Ponganis, 2015) and only spatial descriptions and attendance patterns have been quantified. Simultaneous comparison of behavior between lactating and non-lactating individuals is necessary to separate changes associated with environmental variability from those driven by lactation. Therefore, the first chapter of this thesis addresses the question **How does lactation constraints modify foraging behavior in AFS?**

Also, AFS consume krill and, in less proportion fish species (myctophids). Although diet has been extensively studied in the past, the coupling between prey species and behavior has only been inferred from spatial and diving behavior and capture attempts have been defined from diving data but never associated to each prey species targeted. By using a new diet estimation approach to calculate prey proportion, the second chapter validates the diving strategies used by AFS when targeting krill or fish, generating a predictive algorithm to validate prey capture from diving behavior. This chapter responds to the questions: **What are the diving strategies used when capturing krill or fish? Can diving behavior obtain from time-depth recorders be used to predict species-specific prey targeted?**

Finally, the third chapter explores how animals modify their foraging strategies in response to changes in prey availability driven by the influence of additional oceanographic events in already highly heterogeneous environments. For this, it was necessary to identify if the years evaluated were indeed different. We explore environmental variability for the years the study was conducted by measuring: 1.- female´s status upon arrival, 2.- offspring conditions after birth and their subsequent development during the breeding period, 3.- climatic conditions within the breeding areas, and 4. prey characteristics obtained from diet analysis and 5.- published literature on abundance, distribution and availability of krill during these years. We also knew that an ENSO event and a Southern Annular Mode (SAM) were occurring while this data was obtained. We evaluate differences in feeding behavior (diet), spatial behavior and the use of different foraging strategies of these colonies in contrasting years calculating the behavior linked to each prey captured (using the algorithm developed in chapter 2) and characterizing the foraging strategies used that may help them deal with variability in an already complex

environment. Chapter 3 covers the question, **what are the adjustments in behavior to cope with environmental variability in already highly heterogeneous environments?**

Hypotheses

1.- Lactation is driving most of the changes observed in behavior in this colony. Lactating individuals will increase their effort by modifying diving variables (reducing the time invested diving) and reducing their resting time as opposed to non-lactating animals. Lactating females will perform shorter foraging trips than non-lactating females since trip duration is limited by the nature of the area which imposes a challenging scenario for the offspring's survival, forcing mothers to increase attendance events during the breeding season.

2.- Diving variables can be used to predict species-specific capture attempts and therefore, described diving behavior associated to each prey captured by female´s Antarctic fur seals. As a result, when diving, females will use more time (diving time) to capture fish than krill and will increase the speed at the vertical component of the dive (ascent or descent rate) when capturing fish compared to krill.

3.- The heterogeneous conditions of the area leave little room for modifications of diving behavior. Energy-rich prey will be targeted more often in years when conditions are not optimal. Respective modifications in spatial behavior and niche utilization throughout the seasons would respond to the prey targeted. Animals will target more fish in rough years than in normal years when adult krill is abundant, increasing strategies that involve the visit of more oceanic areas where they are more likely to find fish species.

GENERAL METHODOLOGY

The three chapters of this thesis obey the same methodology for the study site, animal capturing/handling protocols and instrument configuration, and data filtering. Therefore, we create a general methodology section. Specific additional methodological descriptions and/or modifications are included in each chapter.

Study site and logistics

The study was conducted as part of a long-term AFS monitoring program at Cape Shirreff, Livingston Island of the South Shetland Islands, Antarctica (62°28' S, 60°46' W, Figure 1) leaded by the United States Antarctic Marine Living Resources (US-AMLR) of the National Oceanic and Atmospheric Administration (NOAA). Although declining, demographic studies performed in the SSI suggest that 80% of AFS pup production in this region occurred at Cape Shirreff. Therefore, this colony is the biggest breeding colony of the SSI. Furthermore, the colony corresponds to the southernmost breeding colony of the species (Hucke and Gaete, 2004), with individuals that have shown the highest field metabolic rate found for the species

(Costa *et al.*, 2000) with values similar to individuals in other locations facing complex scenarios such as strong ENSO events, even in years with abundant prey (Costa, 2008). Lately, colonies at this location have been also subject to high environmental variability driven by abrupt changes of temperature due to global change (Clarke *et al.*, 2007; Schofield *et al.*, 2010). These factors together make this colony a suited model to evaluate AFS colonies living at the edge of their distribution.

Figure 1. Cape Shirreff, Livingston Island. The South Shetland Islands, Antarctica (62°28' S, 60°46' W).

We conducted this research within the breeding seasons of 2014-15, 2015-16, and 2016-17 (hereby named based on the first year of the season: 2014, 2015, and 2016 respectively). This contemplated an unusually warm 2016 spring characterized by the lowest sea ice extent observed in the satellite record since 1979 (Stuecker *et al.*, 2017; Turner *et al.*, 2017) and an extreme ENSO event (2015-2016, Bodart *et al.*, 2019). This directly affect krill conditions of the austral summer of 2017 (i.e. our 2016 breeding season, Atkinson *et al.,* 2019) as previously reported with similar atmospheric events (Costa *et al.*, 1989; Siegel and Loeb, 1995; Loeb *et al.*, 1997; Atkinson *et al.*, 2004). Further details are found in chapter 3.

Animal characteristics

Because the US-AMLR Program has been monitoring this colony for more than 20 years, we were able to consider only known age, fully mature reproductive females in this study. This allowed us to control for behavioral differences related to age and size. We captured a total of 46 females for this study. We failed to recover instruments from three animals (two non-lactating and one lactating female), and we could not recover the information from three additional instruments of lactating animals due to severe damage leaving a total of 15 lactating females in 2014, 14 lactating and 2 non-lactating females in 2015, and 12 lactating and 3 non-lactating females in 2016. The instruments registered all trips until females lost their offspring (hereby "pup"). Therefore, the dates of instrument recovery differ among females but occurred mostly between mid-February and the beginning of March. For Chapters 1 and 2 we used only the information collected by the instruments of the trips that answer the research questions

addressed on each chapter. Further detailed information on which foraging trips were used per chapter can be found within their respective methodologies.

Capture protocol

The capture protocol was the same for all animals used in all chapters of this thesis. Three types of captures were performed:

- Perinatal captures: Upon arrival of the pregnant females (end of November to mid-December), harems are formed with one male and multiple, mostly pregnant, females. Once females give birth, they were capture using hoop nets. We sedated them with an intravenous midazolam injection (0.1-0.15 mg/kg) and anesthetized them with isoflurane gas and oxygen using a portable field vaporizer (Gales and Mattlin, 1998; McDonald *et al.*, 2009). Once anesthetized, we attached VHF radio transmitters (55mm x 22mm x 10mm and 23g, Advanced Telemetry Systems, Isanti, MN) and Time-Depth Recorders (TDR; manufacture by Wildlife Computers, USA. Instrument detailed description are given below) to their fur with 5-minutes Epoxy (dorsal to the midline). While anesthetized, we measured the weight, length, and girth of each female. In addition, two 20 ml tubes of milk samples were obtained milking the females manually. An intravenous oxytocin injection (0.25 mL, 10 UI mL^{-1}) helped the production and later acquisition of milk samples. Fatty acid extracted from milk samples and other details on diet data collected are given in chapters 2 and 3. We kept females in wooden boxes for recovery after anesthesia to protect them from male harassment. While waiting for the

female to recover, we captured, sexed, and measured morphometric parameters (mass, and total length) of their offspring (hereby called pups). All times were recorded: time of capture, time of the anesthesia on/off, recovery time, and pup-mother reunion time upon the release of the females. A team would remain hidden in the area to verify that females respond well to post-capture recovery and no pup abandonment occurred. No females died nor abandon their pup in this study.

- Instrument retouch or recovery: Daily visual observation of all females and pups on land allowed us to estimate the conditions of the instruments and to evaluate in the field if animals need to be re-captured for re-installation of their instrument (retouch) or if the instrument needed to be recovered. Instrument retouch occurred only when instruments were at risk of falling off and getting lost since the data can only be retrieved manually. Therefore, we only obtained mid-season female data of a reduced number of females since authorization for repeated captures were limited by our capture permit. The recovery of the instrument occurred when 1.- female pups died, 2.- When retouch was not possible (in case of very bad conditions of the instrument or when changes in female behavior were noticed due to the captures) and 3.- When the breeding season was over. Both capture protocols (retouch and recovery) were the same as the one described for perinatal captures, obtaining the same number of samples and measurements.

Antarctic fur seals capture and handling protocols were approved by the Institutional Animal Care and Use Committee (IACUC) of the US code: IACUC#SWPI 2014-03R and the Scientific Ethical Committee of Environmental and Animal Care of the Pontificia Universidad Católica de Chile (Code 150617016).

Instrument configuration and data processing

The TDRs recorded temperature (°C), time (seconds), and depth (meters) every second when instruments were wet. Two TDR models were used: MK9 and MK10. MK9 register time depth, temperature and light, and MK10 provided additionally, a geolocation of the animal every 30 minutes (detailed information of instrument´s configuration can be found in chapters 1 and 3). After instrument recovery, we filtered all raw diving data in MatLab 9.0 (MathWork, Inc. 2016) using the IKNOS toolbox (software developed by Y. Tremblay, unpublished data). This algorithm allows for a zero-offset correction at the surface and identifies dives based on a user-defined minimum depth (4 m) and dive duration (6 seconds). This analysis accounts for instrument errors at the surface when detecting minimum depth.

Day and night diving differences

The time of the day when foraging took place was determined assigning foraging dives to "Day" or "Night" based on the sun angle at the time of foraging and the interpolated location of the dive, using the function sun_position in Matlab (Reda and Andreas, 2004).

Diving effort

In central place foragers, there are multiple ways to measure effort while foraging. Animals increase their foraging activities by working harder (e.g. deeper dives, increasing the dive frequency, reducing the time resting or all the above). We determined changes in foraging effort by analyzing differences in (1) trip duration and haul-out time (the time spent ashore between foraging trips), (2) dive frequency and (3) the mean of dive performances (see below).

1.-Trip duration and haul-out time were calculated by using VHF data, confirmed with daily visual observations, and validated with TDR data after the recovery of instruments.

2.- Dive frequency (dives/hr) was calculated per foraging trip based on the time-depth data collected by the TDRs. All dives within each trip were counted and the mean frequency per hour was computed.

3.- Seven dive variables, obtained from the TDR data, were analyzed to quantify the dive phase of each animal (i.e. maximum dive depth (m), dive duration (s), bottom time (s), descent time (s), descent rate (m/s), ascent time (s), ascent rate (m/s)). These variables were used depending on the objective of each chapter.

CHAPTER 1. TIME AND BEHAVIORAL CONSTRAINTS OF LACTATION IN HIGHLY HETEROGENOUS ENVIRONMENTS

ABSTRACT

The energetic costs of lactation have been studied in many species of mammals, but little is known about the behavioral and time adjustments needed to cope with this event. The goal of this chapter was to determine, for the first time, foraging behavior of non-lactating female otariids and contrast it with lactating females to estimate the behavioral constraints of lactation. We simultaneously measured foraging behavior of lactating and non-lactating Antarctic fur seal females (*Arctocephalus gazella*) at their southernmost breeding distribution. Non-lactating females exhibited highly variable duration of their trips, performing long, average or short trips to sea but always spending longer times hauling out between trips. In contrast, lactating females exhibited shorter trips sustained consistently during the study period spending half the time hauling-out compared to non-lactating females. Minor but significant differences were found in most of the diving variables between groups with lactating females accumulating a higher proportion of time invested diving than non-lactating animals. The combination of shorter dives but an extended diving period per trip may allow them to increase energy intake per unit of time. The constraint of rearing a pup caused lactating females to reduce their resting time available onshore without increasing the duration of their trips. This increases the overall number of trips over the entire lactating period increasing the frequency of offspring provisioning. The reduction of time onshore, reduction of trip duration, and the modifications on dive performance suggest a clear additional effort of lactating females to compensate for the constraints of rearing a pup which has not been observed previously due to the lack of diving information on non-lactating individuals. Future studies should also consider the inclusion of non-lactating females, given that lactation may have a strong synergistic effect with other aspects that shape foraging behavior.

Keywords: Antarctica, Diving behavior, Foraging ecology, Breeding, Otariids, Lactation.

INTRODUCTION

Lactation is the most expensive reproductive event in both terrestrial (Gittleman and Thompson, 1988; Clutton-Brock *et al.*, 1989; Poppitt *et al.*, 1993; Naya *et al.*, 2008) and marine mammals (Fedak and Anderson, 1982; Costa *et al.*, 1986; Oftedal *et al.*, 1987; Arnould, 1997; Boyd, 1998; Williams *et al.*, 2007). To better understand the behavioral cost of lactation, comparative studies focused on both lactating and non-lactating individuals are necessary, but only a few studies have been able to do so mainly in terrestrial mammals. Usually, cost-effective strategies will focus on obtaining more or better food. Lactating females will therefore regulate the foraging effort by incrementing the time spent eating (Watts, 1988; Zhu *et al.*, 2015) or the energy storage when food is available for later use (Macbe *et al.*, 2013). Others will focus on higher quality food items, the use of fat reserves, or changes in behavior (Gittleman and Thompson, 1988; Costa, 1999; Williams *et al.*, 2007; Shero *et al.*, 2018). Income breeders, such as otariids, obtain the energy necessary for milk production during lactation and must, therefore, intrinsically, modify their behavior (Bonner, 1984; Costa and Gentry, 1986; Oftedal *et al.*, 1987). These modifications in behavior are poorly understood since studies of diving behavior of non-lactating female otariids are lacking (Ponganis, 2015).

Otariids are central place foragers (Orians and Pearson, 1979) and, as such, they perform multiple trips to sea while lactating to supply the energy needed by their offspring. While at sea, they will perform bouts of multiple dives interspersed with brief inter-dive surface time intervals (Rosen *et al.*, 2017). One of the most studied otariids is the Antarctic fur a seal (*Arctocephalus gazella*, (Peters, 1875)) in which foraging behavior varies depending on the habitat and individual characteristics. The utilization of different foraging areas (Staniland *et al.*, 2007; Goebel *et al.*, 2000), female age status (Lea *et al.*,2009), and/or population size (Staniland *et al.*, 2011) will shape behavioral variables such as trip duration, niche utilization and/or diving behavior. Under complex scenarios such as increasing oceanographic variability (Boyd, 1999; Lea *et al.*, 2006) or different prey distribution and/or abundance (Boyd *et al.*, 1994; Boyd, 1999; Lea *et al.*, 2006; Ichii *et al.*, 2007; Staniland *et al.*, 2010) lactating females will modify their foraging trip duration or the time spent ashore having little capability of increasing their diving effort (Boyd, 1999; Costa *et al.*, 2000; Costa, 2008). In other words, the duration of the trips would be limited by the availability and abundance of the prey (Boyd, 1999; Lea *et al.*, 2002) and haul-out time (time ashore) by the rate of energy that is transferred to the offspring (Gentry, 1998; Boyd, 1999) but under no circumstances would animals modify their diving effort if they are operating at their maximum capacity (Costa *et al.*, 1989; Boyd, 1999; Costa *et al.*, 2000; Costa, 2008).

 These studies have only considered lactating females when comparing multiple scenarios; therefore, changes in behavior associated exclusively with lactation are hard to identify. Boyd 1999 hypothesized that females would adjust the time spent ashore and trip duration to maximize the delivery of food to their offspring. For instance, when they face limitations in prey availability, they would reduce their time ashore and increase trip duration (sustaining a

threshold energy intake). In contrast, in years when prey was abundant, animals would show shorter trips to sea. We argue that the short trips observed in abundant prey scenarios, could also be associated with the constraints of milk production and not solely to prey availability. The use of only lactating females could have underestimated the additional effort that lactation may impose on foraging decisions. Further, diving effort could be masked by the fact that only lactating animals are monitored in these studies, especially considering that modifications in diving effort have been seen recently in other pinniped species under similar demanding reproductive events such as pregnancy (Shero *et al.*, 2018).

In this chapter, we simultaneously recorded non-lactating females' foraging, diving, and haul-out behavior with lactating females' behavior to further understand the constraints and energetics of reproduction and lactation. We tested the hypothesis that non-lactating individuals would have longer trips to sea and longer times hauling-out than lactating females due to the absence of restrictions associated with lactation. In addition, we hypothesized that given the same foraging environment; lactating animals would show additional effort by increasing their diving activities as a result of the added energetic costs of lactation.

MATERIALS AND METHODS

We captured and instrumented 15 lactating (from here on designated "L") and seven non-lactating ("NL"; n=7) females following the protocol described in the general methodology. We use the same protocol to recover the instruments. A body condition index (BCI) was calculated on each animal dividing the total mass by the body total length (Mass/Length). To answer the question of this chapter, we used the information from females captured in the austral summers of 2015-16 and 2016-17 (hereby 2015 and 2016 respectively). We pooled the data from both seasons accounting for the differences associated with each season in the construction of the mixed models (see statistical section). Non-lactating females did not carry instruments the entire breeding season since the risk of losing instruments was too high in these animals due to less constraint on their behavior on land and the unpredictability of animals departing from the area. Therefore, we limit the analysis only to those foraging trips that allowed simultaneous comparison, and the selection of the trips to be incorporated in this section were based on the timeframe that non-lactating animals carried instruments. TDRs were configurated and data processed as described in the general methodology.

Overall spatial foraging locations and the most common preys targeted by this colony (feeding behavior) are discussed in detail on section 4 of Appendix A and also Chapters 2 and 3 but altogether, data suggested that, within the time frame of this study, prey targeted was very similar between seasons with three prey species found: one crustacean: krill (*Euphausia superba*) and two myctophid fishes: (*Electrona antarctica* and *Gymnoscopelus nicholsi*).

We estimated differences between L and NL females in the time of the day that foraging took place as described in the general methodology. After, we compared dive frequency as a function of the interaction between groups (L/NL) with BCI has a covariate and the foraging time (Day/Night) as fixed factor, using a linear mixed-effect model (LMM). Female's identity was used as a random factor.

Foraging effort

We determined changes in foraging effort by observing differences in (1) trip duration, (2) dive frequency, (3) mean of dive performance variables (see below), and (4) bout behavior (while diving, AFSs perform "dive bouts"- groups of dives interspaced with surface time intervals) between L and NL females. In addition, to determine differences in effort by reducing the time spent resting (on land or at sea), we investigated changes in (5) Haul-out (time ashore between foraging trips) and time between bouts at the surface (post-dive intervals; PDI). One, two, and partially three were calculated as described in the general methodology. Additional methods are described below.

(3) In addition to the diving variables, we also calculated the mean accumulated diving time per trip between groups. Furthermore, following Bestley *et al.* (2015) we determined if dive duration was longer or shorter than expected for a given depth. This was obtained from the residuals of the linear relationship between the maximum depth (m) and dive duration (sec) (see statistical analysis section). Longer dives than expected may indicate relatively higher effort for that group.

(4) Bout behavior: Because overall frequency (dives/hr) and overall diving variables per foraging trip may be masking differences that can be observed within bouts when different bout configurations are implemented (Boyd *et al*., 1994), we decided to explore bout behavior by calculating mean dive frequency, mean dive duration per bout and bout duration the former since longer/shorter bouts in one group with respect to the other would also reflect a higher/lower diving effort. The dive bout analysis was performed utilizing a custom-written code in R (Beltran, unpublished) and following Boyd and Croxall, (1992) definition of a dive bout. For the program to identify a dive bout, we set the following parameters: a) a minimum number of 5 dives and b) a minimum PDI (surface time between dives) of 10 minutes (i.e. a PDI of < 10 minutes will consider the following dive as part of the same dive bout). These parameters were chosen after a visual exploration of the data following Boyd *et al.* (1994).

(5) Resting/Recovering time was calculated by evaluating: (a) haul-out time between foraging trips and (b) Post dive interval time (PDI). This was calculated as the mean PDI time per trip per female with the custom-written code in R (Beltran, unpublished) mentioned above.

Statistical analysis

To test for differences between groups (L and NL) on each variable of all five groups (trip duration, dive frequency, diving variables, bout behavior, and resting/recovery time) depending on how data of each variable was distributed, we fitted LMM or Generalized linear mixed model (GLMM) using the R packages 'NLME' (Pinheiro *et al.*, 2017) and 'lme4' (Bates *et al.*, 2015). We constructed a full model for each variable based on biological information. We entered "group" (L or NL) as a fixed factor using BCI as a covariate in all models fitted. Also, we incorporated "season" has a fixed variable to account for differences derived from each season. For the diving variables, we considered that dives are influenced by the diurnal/nocturnal migratory patterns of both preys targeted; krill or fish (Croxall *et al.*, 1985; Collins *et al.*, 2008; Borras-Chavez *et al.*, in prep), and therefore, added whether each dive was performed during the day or night (fix factor). Finally, we used each female identity as the random factor to account for individual behavioral variability in all models. Other variables that may account for individual variability such as age remain constant as we only used known-aged females of similar size, therefore excluding age from the model. We selected the best model for each variable according to Zuur *et al.* (2009) using the AIC criterion (MuMin R package, Barton, 2010) comparing our initial model with others in which factors and/or interactions between factors were removed (Table 1 shows the final structure of each model used for each variable).

We test homoscedasticity and normality by visual inspection (q-q plots and histograms) (Zuur *et al.*, 2007). The variables that did not meet the basic assumptions of normality were transformed to a logarithmic scale (Ln) and tested again. Data of the variable descent time, maximum depth, mean dive depth per bout were gamma distributed and therefore a GLMM was fitted.

Table 1 Final models used for each foraging variable. Each model is presented as follows: Fix factors + (Random Factor). The type of model used depends on the distribution of each data set. We transformed all data that did not meet assumptions.

Foraging Variable	Model Structure*	Data Transformation	Model Type
Trip duration (days)	Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Log Transformed	LMM
Haul-out duration (days)	Group + BCI + Group*BCI + (Female ID)	Log Transformed	LMM
Dive rate (dives/h)	Group + BCI + Season + (Female ID)	Not transformed	LMM
Ascent rate (m/sec)	Group + BCI + Season + Group*BCI + D/N + (Female ID)	Square root Transformed	LMM
Descent rate (m/sec)	Group + BCI + Season + Group*BCI + D/N + (Female ID)	Not transformed	LMM
Ascent time (sec)	Group + BCI + Season + Group*BCI + Group*Season + D/N + (Female ID)	Log Transformed	LMM
Descent time (sec)	Group + BCI + Season + D/N + (Female ID)	Not transformed	GLMM
Bottom time (sec)	Group + BCI + Season + Group*BCI + Group*Season + D/N + (Female ID)	Not transformed	LMM
Maximum depth (m)	Group + BCI + Season + Group*BCI + Group*Season + D/N + (Female ID)	Not transformed	GLMM
Dive duration (sec)	Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Not transformed	LMM
Mean percentage of diving time per trip	Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Not transformed	LMM
Number of dives per bout	Group + BCI + Season + (Female ID)	Not transformed	LMM
Mean dive duration (min) per Bout	Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Not transformed	LMM
Mean dive depth per bout (m)	Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Not transformed	GLMM
Bout duration (min)	Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Log Transformed	LMM
Post dive time Intervals (PDI, in min)	Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Log Transformed	LMM

* The model presented was selected after using AIC criterion as suggested by Zuur *et al.* (2009) and starting from a complete model that incorporated all single variables and possible interactions backward. Group= Lactating or Non-Lactating females. Season= 2015-2016. D/N= Day or Night dive. BCI: Body Condition Index. LMM: Linear Mixed Model. GLMM= Generalized linear mixed model.

In addition, we calculated dive residuals by fitting a LMM between dive duration (s) and maximum depth (m, fixed factor) using the identity of each female as the random intercept since the duration-depth relationship may vary across females. Then, to determine if there were differences between groups, we tested the Pearson residuals obtained from the previously described LMM, as a response variable against group as a fixed effect with BCI as covariant and female ID as the random factor again using a LMM.

To check if there was a significant contribution of each variable to each model, we obtained p-values of all fixed factors and interactions by using the "car" R package (Fox and Weisberg, 2019) using a Type III Wald chi-square test. The significance threshold in all tests was set with a 95% confidence interval. Marginal means and confidence intervals are shown in the original scale of each variable and all data log-transformed for the model were back-transformed to be incorporated in the result section. Finally, trip duration data were tested for equality of variances (homoscedasticity) between L and NL females using a Fligner-Killen test. All statistical tests were performed in R (Team, Rcore 2017), the final LMMs were fitted via restricted maximum-likelihood estimation (REML) and GLMM by maximum likelihood.

RESULTS

We obtained diving records from 15 lactating females (76 trips and 87,734 dives total) and 5 out of the 7 non-lactating females that were instrumented (27 trips and 24,825 dives). Table 2 present the morphometric data of all females used for the calculation of the BCI after the initial capture.

All females exhibited a slight tendency of diving more during the night regardless of whether they were lactating (53% of the dives occurred at night) or not (54% of NL dives were at night). As night time during the summer is only ~5 hours long, both groups exhibited a higher frequency of dives per hour during the night than during daylight with no differences attributed to the group they belong; L or NL (Figure 2, $X^2(1)= 0.4183$, $P= 0.1957$).

Table 2. Mean morphometric information of Antarctic fur seal *(Arctocephalus gazella)* from both groups: Non-Lactating (NL, n=5) and Lactating females (L, n=15).

Female ID	Group	Mass (kg)	Body Length (cm)	Body Condition Index (BCI)*
342	NL	52.6	131.0	0.40
A03	NL	43.6	134	0.33
326	NL	53.8	139	0.39
494	NL	45	133	0.34
4970	NL	39.2	128.5	0.31
476	L	57	132	0.43
1827	L	50.2	128	0.39
2383	L	52.8	127	0.42
5227	L	46.4	123	0.38
A34	L	51	124	0.41
A40	L	59.4	137	0.43
6894	L	46.8	124	0.38
A01	L	57.4	131	0.44
A22	L	59.8	140	0.43
A44	L	49.2	131	0.38
A49	L	54.8	137	0.40
A51	L	48	135	0.36
A52	L	55.2	134	0.41
A59	L	47.6	130	0.37
481	L	54.8	131	0.42

*Body condition index (BCI) was calculated dividing the mass of each individual by the total body length.
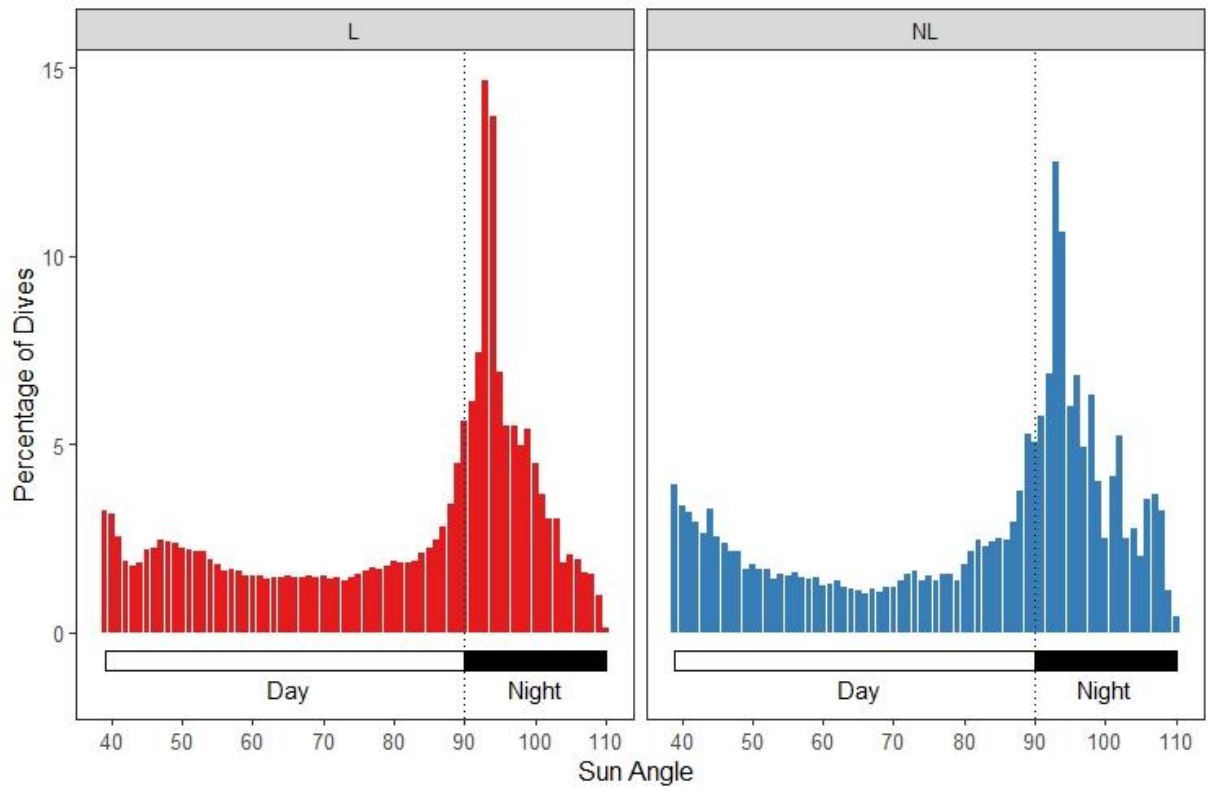
Figure 2. Diurnal/Nocturnal proportional frequency of dives performed by lactating and non-lactating females. Lactating (L, red) and non-lactating (NL, blue) Antarctic fur seal (Arctocephalus gazella) female dive frequency. The dotted line indicates the separation between day and night based on the sun angle (x axis) at the location and time where the study was conducted. No differences were found between groups (95% CI, $P = 0.1957$).

Trip duration and haul-out time

Mean trip duration is significantly different between groups ($X^2(1)= 13.5$, $P= 0.0002$, Figure 3A) but this significance was driven by females in 2016 (Table 3). In 2015 L and NL females presented similar trip duration, averaging ~3.5 days at sea. When testing equal variance between groups, differences were also found (Figure 3b; $X^2(1)= 13.064$, $P < 0.0003$). Individual NL females exhibited the shortest (less than a day long) and the longest trips to sea (e.g. female ID

326: 11.43 days with the three trips completed over six days) but most of them, showed both long and short trips (female ID 4970 show from very short trips; 0.3 days to longer than five days) explaining the greater variance observed in NL females (Figure 3b). In contrast, L females showed a very similar trip duration between individuals throughout the study period despite the season (~3 days, Table 3), with the longest trip being 5.9 days. Haul-out time varied significantly between groups ($X^2(1)= 4.3$, $P= 0.03$, Figure 4, Table 3). NL females spent more than double the time on land than L females (Table 3). The relationship between trip duration and time spent onshore after each trip shows that, regardless of trip duration, L females spent less time ashore, compared to NL females during the entire period monitored (Figure 5).
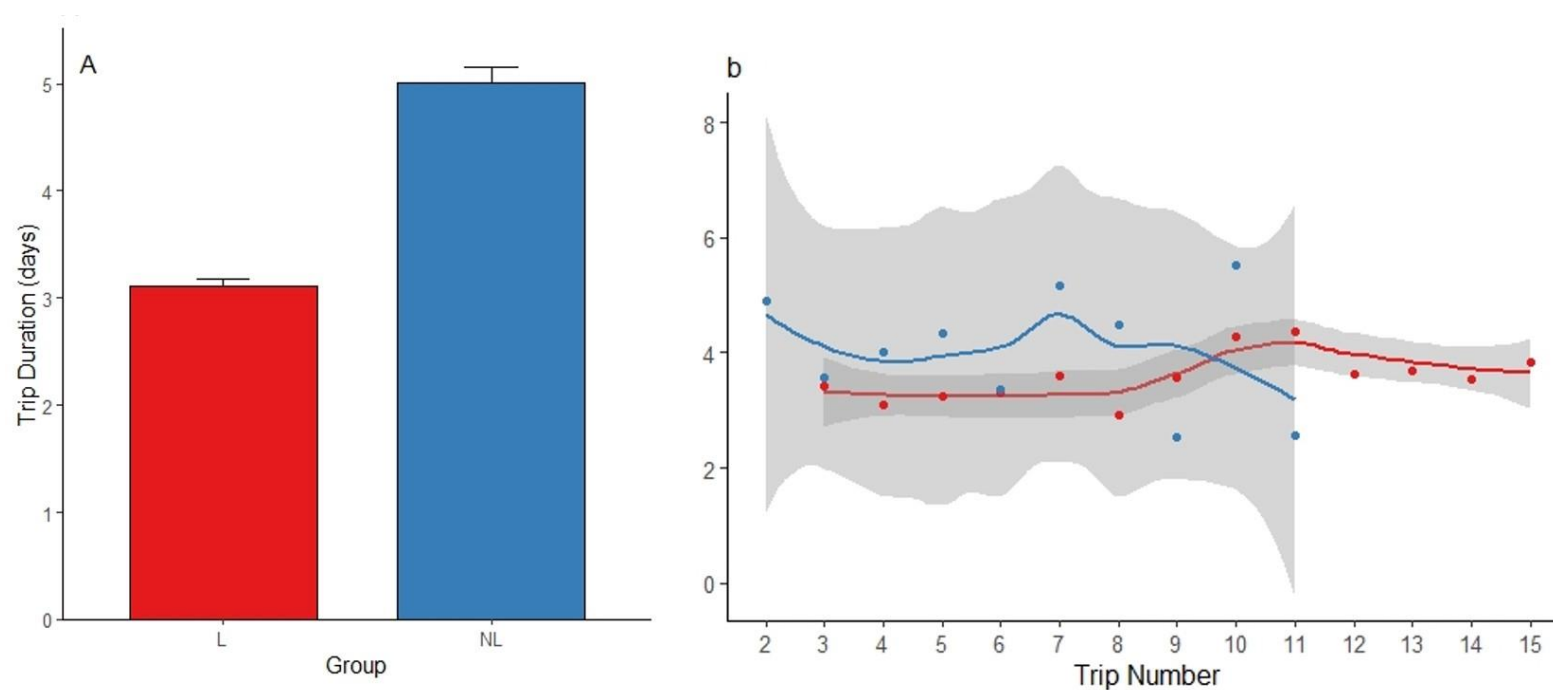
Figure 3. Trip Duration of lactating and non-lactating Antarctic fur seal females. (a) Overall trip duration in days (mean ± SE) of both lactating (L, red) and non-lactating (NL, blue) Antarctic fur seal females. (b) Trip duration (mean ± SE) per trip performed during the study period by L (red) and NL (blue) females. NL females had greater variance (grey area) in trip duration than L females (95% CI P < 0.001).

Table 3. Model means with 95% confidence intervals of all foraging variables for both Non-Lactating (NL, n=5) and Lactating females (L, n=15). Means and intervals were back-transformed and recovered in the original scale.

Season:	2015		2016		P values
Foraging Variables	L	NL	L	NL	
Trip duration (days)[b]	3.7 (2.9-4.6)	3.6 (2.4-5.4)	2.9 (2.5-3.4)	5.7 (4.1-7.9)	**0.0002**
Haul-out duration (days)[b]	1.4 (1.2-1.8)	3.4 (2.5-4.6)	1.6 (1.4-1.8)	3.7 (2.8-5.0)	**0.039**
Dive rate (dives/h)	16.6 (14.7-18.6)	14.1 (11.5-16.7)	17.2 (15.7-18.6)	14.6 (12.4-16.9)	0.215
Ascent rate (m/sec)[c]	1.0 (0.9-1.1)	1.1 (1.0-1.2)	0.9 (0.8-0.9)	0.9 (0.8-1.1)	0.37
Descent rate (m/sec)	1.2 (1.1-1.3)	1.2 (1.1-1.3)	1.2 (1.1-1.2)	1.2 (1.1-1.3)	0.34
Ascent time (sec)[b]	16.8 (15.5-18.3)	14.4 (12.6-16.5)	11.8 (11.1-12.6)	15.2 (13.2-17.4)	0.9
Descent time (sec)[a]	16.6 (15.4-17.9)	18.9 (16.9-21.5)	12.5 (11.9-13.1)	13.8 (12.7-15.0)	**0.02**
Bottom time (sec)	35.1 (30.4-39.8)	47.8 (40.8-54.8)	40.3 (36.8-43.9)	53.0 (45.9-60.1)	**0.005**
Maximum depth (m)[a]	25.1 (22.2-29.0)	22.4 (18.8-27.7)	18.1 (16.9-19.5)	23.7 (19.6-30.0)	**0.005***
Dive duration (sec)	75.1 (67.7-82.4)	83.2 (71.4-94.9)	68.0 (62.6-73.3)	91.4 (79.2-103.8)	**0.02**
Mean percentage of time diving per trip (%)	22.8 (18.8-26.8)	9.6 (3.2-16.1)	27.3 (24.4-30.1)	22.4 (16.9-27.8)	**0.005**

[a] Results from Generalized Linear Mixed model fit by maximum likelihood (Laplace approximation) performed with gamma distributed data

[b] LMM fitted with log transformed data

[c] LMM fitted with square root transformed data

* only significant when interacting with BCI: Group*BCI p value
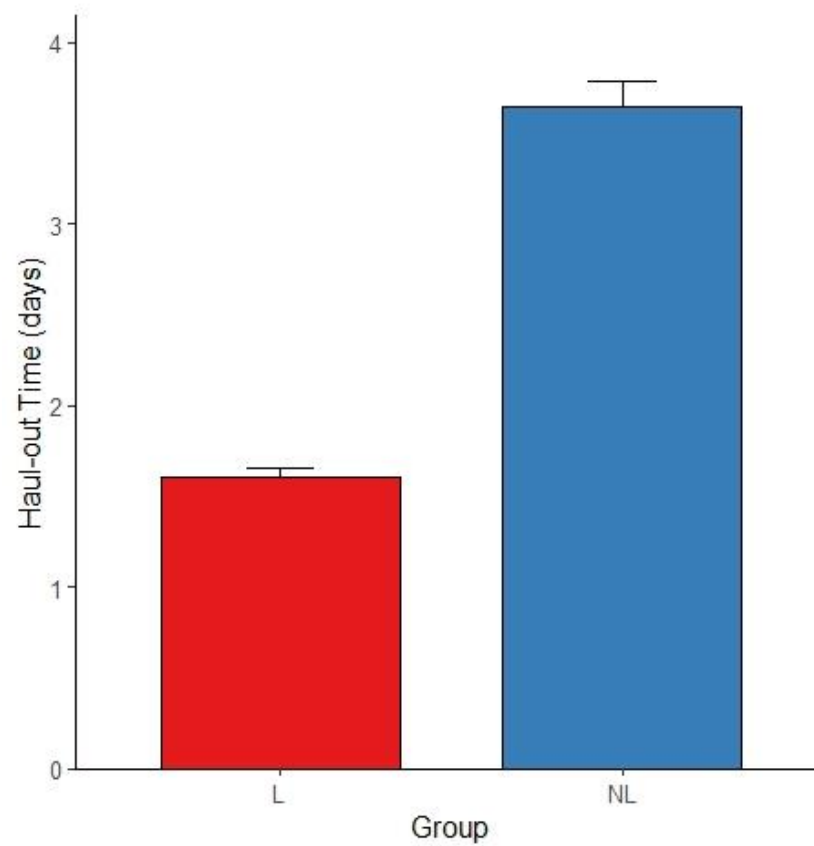
Figure 4. Haul-out time (days) of lactating and non-lactating Antarctic fur seal females. Non-lactating (NL, blue) females spent more time ashore than lactating (L, red) females (95% CI, P = 0.03). mean ± SE.
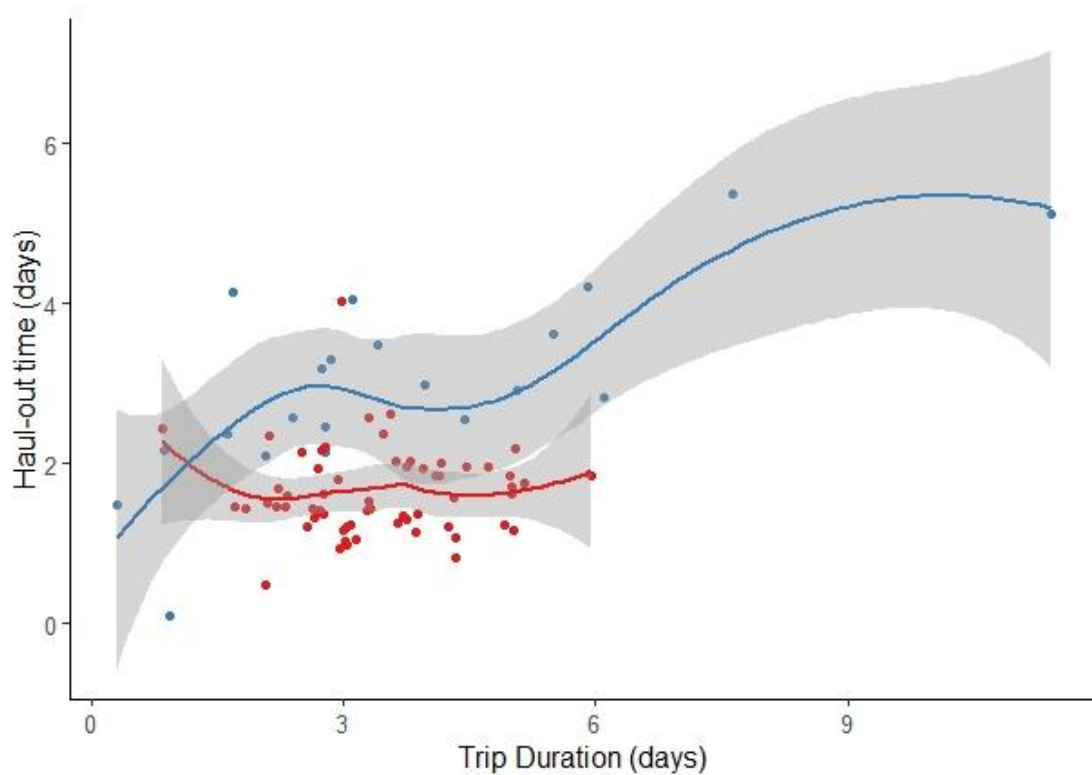
Figure 5. Haul-out time (days) vs trip duration (days) of lactating and non-lactating Antarctic fur seal females. Lactating (L, red) females show consistently less overall time spent onshore than non-lactating (NL, blue) Females. mean ± SE.

Diving behavior

No differences were found in the frequency of dives per hour ($X^2(1)$= 2.4 P= 0.12, Table 3) or the frequency of dives per bout between L and NL females ($X^2(1)$= 1.4, P= 0.24, Table 4). However, we did find differences in dive duration where L females performed shorter dives than NL females ($X^2(1)$= 5.6, P= 0.02). This may be explained by the shorter time spent by L females at the bottom phase of each dive ($X^2(1)$= 7.9, P= 0.05) in addition to a shorter descent time while lactating ($X^2(1)$= 5.3, P= 0.02). We found no differences between groups in the vertical speed of each dive (i.e. descent rate: $X^2(1)$= 0.9, P= 0.3 or ascent rate: $X^2(1)$= 0.8, P= 0.4), the ascent

time ($X^2(1)$= 0.02, P= 0.9) or how deep they would dive ($X^2(1)$= 0.3, P= 0.6, maximum depth

was only different when interacting with BCI and therefore, the differences were only driven by

the mass of the animals, (see Table 3). Although L females spent less mean time diving at a

single-dive level, the mean accumulative time spent diving per trip was ~10% higher in 2015

than NL females ($X^2(1)$= 8.0, P= 0.05) but showed similar values in 2016 (Figure 6, Table 3).

Table 4. Model means with 95% confidence intervals of bout variables for Non-Lactating and Lactating females. Non-Lactating (NL, n=5) and Lactating (L, n=15) females. Means and confidence intervals were back-transformed and recovered in the original scale.

Season:	2015		2016		P values
Foraging Variables	L	NL	L	NL	
Number of dives per bout	23.4 (19.2-27.6)	19.6 (14.1-25.2)	24.8 (21.7-27.8)	21.0 (15.5-26.6)	0.55
Mean dive duration (min) per Bout	1.3 (1.1-1.4)	1.1 (0.9-1.3)	1.3 (1.2-1.4)	1.8 (1.6-2.0)	**0.02***
Mean dive depth per bout (m)[a]	27.1 (24.3-30.5)	21.6 (18.6-25.7)	20.9 (19.7-22.3)	25.3 (21.7-30.5)	**0.028***
Bout duration (min)[b]	17.7 (15.2-20.5)	17.0 (13.6-21.2)	19.8 (17.7-22.0)	19.0 (15.3-23.6)	0.4
Post dive time intervals (PDI, in min)[b]	1.2 (1.0-1.3)	1.1 (0.9-1.4)	1.1 (1.0-1.2)	1.3 (1.0-1.6)	0.7

[a] Result from Generalized Linear Mixed model fit by maximum likelihood (Laplace approximation) data gamma distributed
[b] LMM fitted with log transformed data
* only significant when interacting with BCI: Group*BCI p value
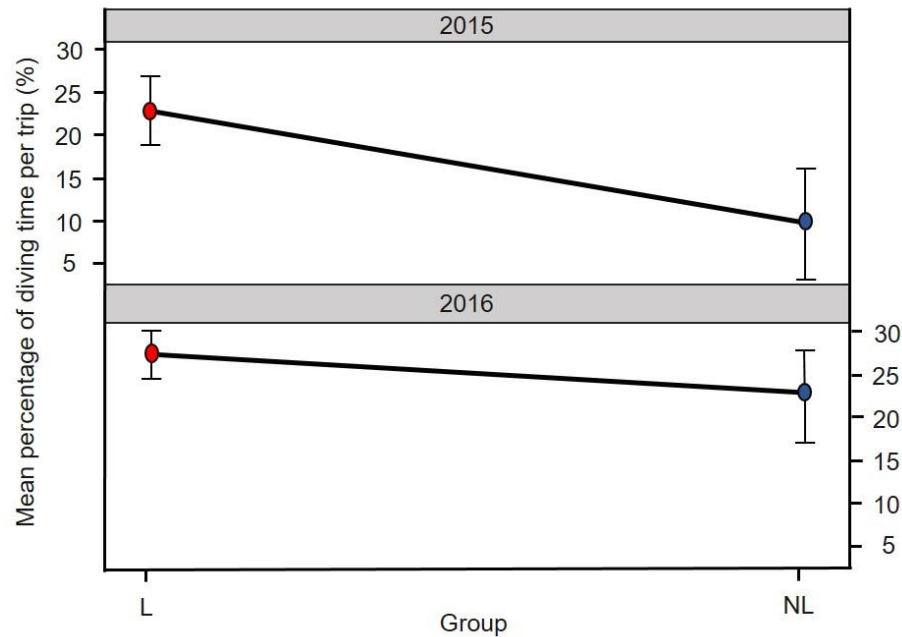
Figure 6. Mean percentage of diving time invested per trip of lactating and non-lactating Antarctic fur seal females. On average, Lactating (L, red) females spent twice the time diving than non-lactating (NL, blue) in 2015 but similar time invested in 2016 between both groups.

The residuals of the relationship between dive duration and maximum depth showed no differences between groups ($X^2(1)= 0.0017$, $P= 0.9668$). Based on the fitted model, the positive (higher effort) and negative (lower effort) residuals showed a similar pattern in all females of both groups despite the differences found in dive duration (Appendix B, Figure 1). Therefore, when evaluating the entire trip, we found no overall differences in effort driven by the way animals configure their dives.

Bout analysis and post-dive surface intervals

We found no significant differences in bout duration between groups ($X^2(1)= 0.7$, $P= 0.4$, Table 4). Likewise, there were no differences found for dive variables within bouts (dive frequency ($X^2(1)= 1.4$, $P= 0.24$, mean dive duration ($X^2(1)= 2.03$, $P= 0.2$ and mean dive depth ($X^2(1)= 0.003$, $P= 0.95$,Table 4). Differences were only present when mass was taken into account (interaction between BCI and Group, Table 4). Although the duration of the dives composing each bout did not differ between groups, the slight difference found in the mean dive duration between groups (Figure 7a) may account for an important accumulated difference in diving time between groups especially when animals perform long bouts (i.e. those lasting hours) as observed in the mean percentage of mean accumulated time diving per trip (Table 3). When comparing the time spent at the surface between dives (PDI), no differences were found by the reproductive condition of the animal ($X^2(1)= 0.2$, $P= 0.6$, Table 4) and the extension of each PDI time was only associated to the preceding bout performed (Figure 7b).
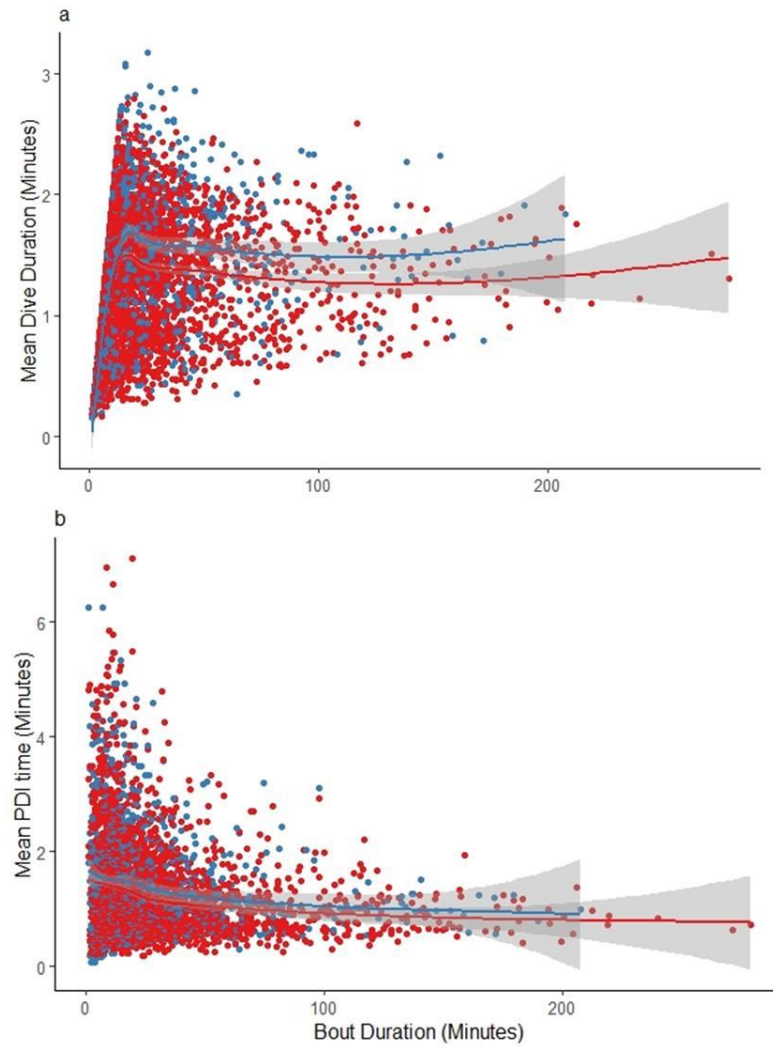
Figure 7. Bout behavior of Lactating and non-lactating Antarctic fur seals females. (a) Bout duration v/s mean dive duration within bouts in lactating (L, red) and not lactating (NL, blue) Antarctic fur seal females. Visually, for a given bout duration NL females showed a slightly longer mean dive duration than lactating females. This may result in a longer accumulative time spent diving for NL and L. (b) mean post-dive interval (PDI) v/s mean bout duration. Longer PDI times are observed when shorter bouts are performed in both groups. The variance of the PDI time is explained by the mean of the previous bout (bout duration, 95% CI, $P < 0.001$) but not by groups (95% CI, $P = 0.6$).

DISCUSSION

Lactation is the most energetically expensive reproductive event in mammalian life history (Gittleman and Thompson, 1988; Clutton-Brock *et al.*, 1989; Veloso and Bozinovic, 2000). As a result, females increase their energy intake 2 to 6-fold modifying their foraging behavior substantially (Sadleir, 1984; Perez and Mooney, 1986; Williams *et al.*, 2007; Thometz *et al.*, 2016). To best investigate these changes in behavior, studies must compare lactating and non-lactating individuals under similar conditions but the unconstrained, unpredictable behavior of non-lactating animals makes simultaneous comparisons difficult. We obtained, for the first time, diving record of free-ranging non-lactating female otariids simultaneously with lactating females, allowing us to understand to what extent animals adjust their behavior exclusively due to lactation. Our results show that, contrary to non-lactating females, lactating females showed more regular and structured attendance cycles. This is observed in a reduction of resting time and trip duration when females are lactating. In addition, we have enough evidence to suggest that animals also increase their effort while diving and that the condition of operating at their maximum capacity at this location, with little room to modify the way they dive (Costa *et al.*, 2000; Costa, 2008) is only given by the demand of energy imposed by lactation and not by the conditions of the area on which they operate.

Behavioral constraints of rearing a pup

In this species, short trips have been associated with abundant prey scenarios. An increase in trip duration linked to changes in prey availability/abundance or environmental variability (Boyd, 1999; Boyd *et al.*, 1994; Lea *et al.*, 2002a; Lea *et al.*, 2006; Ichii *et al.*,2007; Staniland *et al.*, 2010). However, in this study where prey is not limited, L animals of this study performed short trips regularly. In these cases, the reduction of trip duration may be explained by the energetic restrictions of lactation and/or offspring provisioning but not by prey availability. L females showed similar trip durations compared to those previously reported at this location (This study: ~3 days; Goebel *et al.*, 2000; 4.6 days; McDonald *et al.*, 2009: ~3 days) and also similar to other locations where krill is the main prey item (~4 days, Boyd *et al.*, 1999, see Table 4 in Lea *et al.*, 2002a for comparison between locations). Non-lactating females, however, show longer trips to sea than what was observed in lactating females of this and other studies, and greater behavioral flexibility (i.e. short and/or long trips to sea). Alternatively, the energetic demands of lactation could result in longer trips for L females to facilitate increase energy intake, but instead, the restrictions in provisioning take precedence over the decisions of how extensive a trip is (Boyd, 1998; Boyd, 1999; Trillmich and Weissing, 2006). In this case, shorter trips would provide the advantage of increasing the number of times delivering milk. This suggests that short trips in highly heterogeneous environments can also be associated to the limitations of rearing a pup and are not necessarily the result of an abundance of prey (Boyd, 1999) since we observed longer trips to see when animals are not lactating and short trips in L females when prey is abundant.

Further, under contrasting scenarios, lactating animals have shown little capacity to modify time ashore and its duration is limited to a very narrow range of variation (Boyd *et al.*, 1997; Gentry, 1998; Boyd, 1999). Authors suggested that the time spent ashore is driven by milk delivery per visit (i.e. provisioning hypothesis) independent of trip duration (Gentry, 1998; Boyd, 1999) and is reduced when associated to changes in prey availability/abundance (Boyd *et al.*, 1994; Lea *et al.*, 2002a; Lea *et al.*, 2006; Ichii *et al.*, 2007; Staniland *et al.*, 2010). This was also observed in our study, where lactating females spent significantly less time hauling-out than NL females despite the season confirming that lactating animals at this location cannot modify time ashore under any circumstance. Although very few long trips (> 5 days) were found in L females, the reduction of time spent ashore suggests that lactation is stress-inducing, similar to the stress caused by habitat changes. short times hauling-out combined with short trips is a strategy used for L animals to cope with the limitations of rearing a pup at this location even when prey is available.

Lactation and diving behavior

Changes in behavior while at -sea are necessary to cope with the additional energetic cost of lactation, especially since females spend only brief resting periods when they return to land. Marine mammals can modify the phases of a dive (transit and/or bottom time) to forage efficiently (Boyd *et al.*, 1995a; Crocker *et al.*, 2001; Watanabe *et al.*, 2006) but these changes can also be associated to the characteristics of the prey targeted. Diurnal/nocturnal diving patterns and the season in which each dive is performed were important factors explaining

differences in most of the diving variables. These differences are associated with differences in the prey vertical migratory patterns of both fish and krill (Croxall *et al.*, 1985; Collins *et al.*, 2008) as well as temporal variation in prey abundance at this (Polito and Goebel, 2010; Santora, 2013, chapter 2), and other locations (Boyd *et al.*, 1991; Georges and Guinet, 2000). By doing simultaneous measurements between groups in both years, and incorporating these two factors in our model, we accounted for the differences in behavior driven by the preys targeted, and therefore, we could attribute changes in diving behavior to an increase of foraging efficiency.

Trips used in this study were not obtained in the same period on both seasons. Those trips measured simultaneously between L and NL females in 2015, were obtained from mid-December through the end of January when krill is abundant in this area but fish is not found in great quantities, whereas, trips obtained in 2016 were obtained during the second half of the season (from the end of January through March) in which a higher abundance of fish is expected in the diet (Osman *et al.*, 2004; Polito and Goebel, 2010, Santora 2013; chapter 2). We control for these differences in the models by accounting for the variance explained by seasons. The changes found in the time budget were consistent across all diving variables (i.e. dive duration, bottom time, descent and ascent time). L females showed shorter times than NL females despite the season or the time of the day (day/night) dives were performed and therefore, despite the prey species that was been targeted. This suggests that L females reduced the time used within each dive which could means a more efficient way of capturing prey or be a fine-scale time limitation due to the constraints of lactation. Either way, it will also implicate additional effort of L females despite the season the dives were performed.

Interestingly, we found important differences between groups in the mean proportional diving time invested per trip that differ based on the season in which the dives were performed. In 2015 the time invested diving of L females was approximately twice higher than the time invested by NL females (Table 3). In contrast, the time invested in 2016 was only 5% higher in L females than NL females. We have found enough evidence to suggest that the way animals dive at this location, is mostly associated with the prey targeted (Chapter 2), which may explain the differences between seasons in the overall time budget within trips. If trips performed in 2015 target krill, the reduced energetic value of krill compared to the most abundant myctophids found in this region (*Euphausia superba*: 3.7-4.8 KJ g^{-1} depending on the krill stage, myctophids: ~6.0-8.5 KJ g^{-1}, Ichii *et al.*, 2007), would force to increase the foraging effort only to those who need it (L females). Furthermore, in 2016, where fish tend to be more abundant (Osman *et al.*, 2004; Polito and Goebel, 2010, chapter 3), and a reduction of krill availability was observed (Atkinson *et al*., 2019) L females spent similar diving time than in 2015 whilst NL females increase two-fold their mean dive time invested per trip compared to 2015. We hypothesized that there may be a preference to consume fish over krill among individuals even though krill is the most abundant prey registered in diet analysis of L females. NL females would dive on average less than 10% of the time in periods where only krill is likely to be found, and increase this to more than double the time when fish is found or krill is less abundant. Lactating females could be targeting krill in 2015 due to (1) the lack of other options during the first half of the breeding season (Santora, 2013) or (2) the energy per dive obtained from abundant krill (i.e. multiple krill captured per dive) when more energy is needed. To prove this, however, having instruments during the entire breeding season of NL females couple with simultaneous measures of energy budget is necessary.

Marine mammals can modify bout configuration in multiple ways that allow them to forage efficiently (Hastie *et al.*, 2007; Fahlman *et al.*, 2008; Gerlinsky *et al.*, 2013; Ramasco *et al.*, 2014). When additional effort is used, females can extend the duration of dives within each bout, increase the frequency of dives per bout, or both (Shero *et al.*, 2018). Although L females in our study did show some of the longest bouts of the study, neither mean dive duration, dive depth, or dive frequency within bouts were different between groups and the only differences found were explained by the interaction between group and BCI (therefore, "Mass") which is a condition also explained by the additional mass that lactation implies to breeding females.

Alternatively, differences could have been observed in the time resting at the surface between dives (PDI). This is especially important since diving metabolism is affected not only by how much time an animal spends diving (i.e. bout duration) but also by the recovery time necessary after each dive (Costa *et al.*, 2004; Hastie *et al.*, 2007; Fahlman *et al.*, 2008; Gerlinsky *et al.*, 2013). We should therefore expect that L females would spend more time at the surface especially when longer bouts were performed. Instead, for any given bout duration, L females spent equal PDI time (Figure 7b) than NL individuals. This may be explained by the duration of the dives in this species. Animals are diving constantly under their aerobic dive limits (ADL) and in this study, the average dive duration in both groups was always under 1.6 minutes (Table 3) which has been established as the ADL limit of the species (Costa *et al.*, 2004). Therefore, no additional time at the surface is needed since oxygen debt is not generated. We recognize the importance of measuring behavior and metabolism simultaneously (Neises *et al.*, 2017; McHuron *et al.*, 2019) to identify the relationship between behavior and the different metabolic cost of L and NL females foraging strategies. Future approaches should incorporate field

metabolic measurements of NL females to fully understand the true cost of lactation while at sea.

The foraging strategies found in L females and the reduced sample size of NL animals only reflect their behavior within a limited timeframe characterized by abundant prey but do not cover how consistent this maybe in time. We were not able to keep instruments in NL females for a longer period to compare it with L females (only within this study we lost two instruments and, fortunately, found two onshore that were removed by NL females rubbing their backs against the sand). Altogether, the challenges of working with females that do not return to breed and the elevated costs of losing instruments are the main reasons why this and other studies have been constrained to narrow temporal scales and smaller sample sizes. This may also explain why previous studies have not attempted to evaluate diving behavior in NL females or why they have not incorporated NL females as control groups in their experimental design. Future studies using a higher sample size of NL females would provide additional power to our conclusions and a better understanding of how NL female behavior changes in time. A higher sample size will also provide information on intraspecific variation (Kernaléguen *et al.*, 2015) in NL female´s foraging behavior. With this, the behavioral plasticity of NL females could be tested to see if they are constrained by their consistency while foraging at larger temporal scales and/or under different habitat conditions which has been described in multiple species (Harris *et al.*, 2014; Patrick *et al.*, 2014; McHuron *et al.*, 2018).

CONCLUSIONS

The behavior of non-lactating females is characterized by the independence given by the absence of breeding constraints. Behavior in lactating females is characterized by significantly short trips to sea and also a reduction in haul-out time, the last, described in previous studies when prey availability is not limited (Boyd, 1999; Lea *et al.*, 2006). We concluded that performing short trips to sea in L females is also a consequence of the limitations caused by the constraints of provisioning and, together with reducing the time spent ashore, the strategy maximizes the delivery of energy to their offspring. In addition, we found differences in diving effort at a single-dive scale where L females reduce their time budget per dive. However, these differences were not clear at a bout scale. Within each trip, L females spent significantly more time diving than NL females especially when krill is more abundant than fish. A strategy that combines a reduction of time per dive, and increases the diving time per trip would provide a more efficient way of increasing energy intake per trip which is also done by other marine mammals under energetically expensive reproductive events (Thometz *et al.*, 2016; Williams *et al.*, 2007; Shero *et al.*, 2018). The success of this foraging strategy in allocating time and energy during lactation influences the fitness of the pup and its mother (Rogowitz, 1996) which has an impact on both individual and population dynamics (Brose, 2010) especially, in individuals breeding at the edge of the species distribution

CHAPTER 2. COUPLING DIET WITH BEHAVIOR IN HIGHLY HETEROGENEOUS ENVIRONMENTS. VALIDATING SPECIES-SPECIFIC PREY CAPTURE ATTEMPTS COMBINING MACHINE LEARNING TOOLS WITH QUANTITATIVE FATTY ACID ANALYSIS
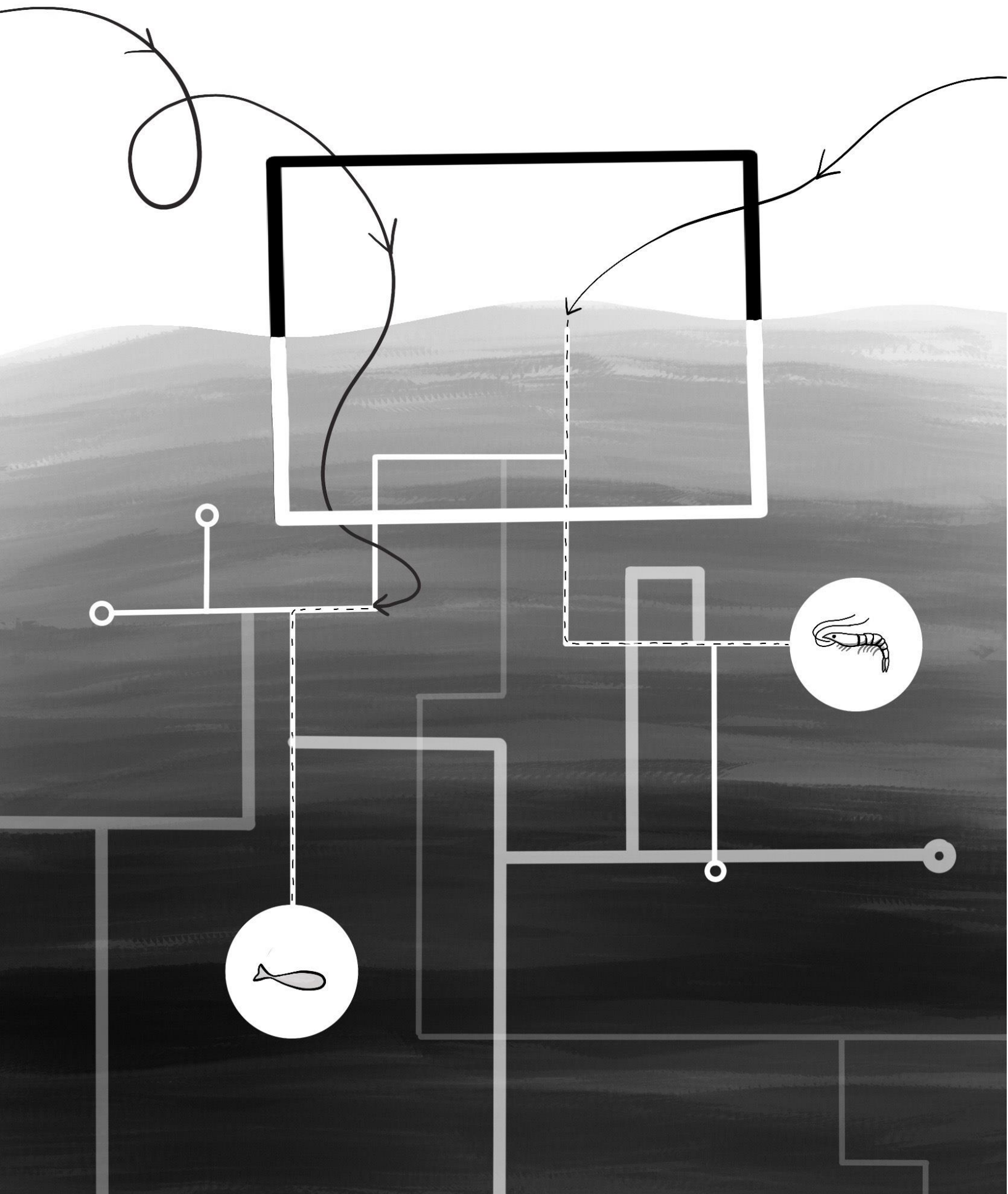
ABSTRACT

Our limited capacity to observe how feeding takes place in marine mammals challenges our ability to understand the relationship between marine predators and their prey. Bio-logging tools have opened a door to quantify behavior in areas with limited access and recent development in technology also have helped us to identify the exact moment when capture attempts are made. Most of these tools, however, fail to identify the prey species consumed, and those that can do so, have still limited memory capacity to be used in long-term data sets or they demand additional instruments to be carried by the animals. Furthermore, their use has been limited to recent years with no long-term monitoring of colonies with these instruments. Time Depth Recorders (TDRs) have been used for decades accounting for much of our knowledge in diving behavior of Antarctic pinnipeds including, the Antarctic fur seals (AFS). AFSs and quantification of fatty acids obtained from milk provide a unique opportunity to associate the proportion of each prey consumed with the diving behavior of the previous trip. We associated every single dive performed to each prey been targeted by validating diving behavior with milk fatty acids (FA) proportional data that represent the prey captured in the previous trip to sea immediately before the milk samples were taken. We generated and tested a predictive tool using a machine learning open-source approach. After training the algorithm, we tested it on trips associated with samples in which the proportional diet per prey was known. We calculated dive time spent capturing each prey as well as the frequency of dives associated to each prey.

 Our model showed a predictive accuracy of 76.2%. An average 93% proportion of krill diet was obtained by investing a ~77% of their diving time capturing krill and an average fish diet

proportion of 80% was obtained by investing a 69% of their diving time targeting fish. Likewise, the mean frequency of dives targeting krill (~71%) and targeting fish (~71%) when consuming each of them, confirmed that the multiple decision trees applied to behavioral data (Random forest analysis), can accurately be used as a predictive tool for diving behavior in the absence of dietary data. We finally fully described diving behavior when capturing the two most important preys of AFS. Overall, both krill and fish are captured in deeper water during the day than during the night. During the day, fish is captured in shallower waters than krill and demands less time to be captured. At night, both preys are found in shallower waters performing slightly longer dives capturing fish than krill. When capturing fish at night, animals chase their prey going upward to the surface increasing their ascending speed as opposed to capturing krill which mostly occurred downward from the surface down. Altogether, results are consistent with the vertical migration of both preys. This led us to obtain a more reliable estimation of the proportion of behavior capitalized to each prey per trip with no need of using additional instruments and instead, relying on cheaper, long-lasting, and highly autonomous instruments. It also provides a tool for retrospective data analysis in datasets already collected during decades on this species with a potential use in other otariid's species.

INTRODUCTION

Feeding behavior of Antarctic Fur Seals (AFS) during the breeding season is well known. Animals show variation in diet between colonies at different locations but also within each colony. In the WAP and South Georgia, krill is the most important resource during the entire breeding season of AFS. However, there is a relevant increase in fish consumption towards the second half of the breeding season. This transition has been described multiple times using different dietary proxies: feces analysis (hereby scats), fatty acids, and stable isotopes (Reid and Arnould, 1996; Iverson *et al*., 1997a; Brown *et al.*, 1999; Lea *et al.*, 2002b; Osman *et al.*, 2004; Polito and Goebel, 2010; Santora, 2013, section 4 of Appendix A). Despite the location, all studies agreed that mesopelagic fishes of the family Myctophidae are an important prey item for AFS, accounting in some cases for approximately 95% of the fish consumed (Lea *et al.*, 2002b; Cherel *et al.*, 1997; Klemmedson *et al.*, 2020). This responds to the availability of myctophids in Antarctica, which represent the second largest resource of Antarctic waters after krill (Sabourenkov, 1991) both in abundance and biomass (Cassaux *et al.*, 2003; Osman *et al.*, 2004; Polito and Goebel, 2010). Squid is also a very important prey item for certain colonies around the Southern Ocean (Rodhouse and White, 1995; Goldsworthy *et al.*, 1999; Green *et al.*, 1997) but at Livingston island, this prey seems to be incidentally consumed (Osman *et al.*, 2004; Polito

and Goebel, 2010). Krill and fish, therefore, are the two most important prey items for the Cape Shirreff breeding colony.

Methods carried out to estimate diet in AFS are mostly qualitative. Prey composition is estimated by identifying hard remains from feces (e.g. Osman *et al.*, 2004; Reid and Arnould 1996; Cherel *et al.*, 1997), regurgitation (Goldsworthy, 1992; Kirkman *et al.*, 2000), stable isotopes (Polito and Goebel, 2010), Fatty Acids (FAs) (Iverson *et al.*, 1997a), or a combination of them (Lea *et al.*, 2002b). Quantitative Fatty Acid analysis (QFASA) was the first tool designed to quantify proportions of prey consumed. Essentially, the technique is based on unique arrays of FA that are transferred largely unaltered up the food chain from prey to predator (Iverson *et al.*, 1997b). Together with a later data processing with multivariate analysis of the FA arrays, an estimated quantification of the FAs composing the tissue in question is obtained. Although the technique has been used successfully to quantify proportions of prey consumed for several marine mammals (Nordstrom *et al.*, 2008; Bourque *et al.*, 2020), its initial debate (Grahl-Nielsen and Mjaavatten, 1995; Iverson *et al.*, 1997b; Smith *et al.*, 1997; Grahl-Nielsen; 1999) and its slow evolution due to limitations such as the reduced ability to incorporate ecological mechanisms into the model (Neubauer and Jensen, 2015) or the complexity of dealing with predators consuming multiple species (Happel *et al.*, 2016), make QFASA harder to use. Alternatively, the use of Bayesian analytic tools developed for stable isotopes is recently proved to be effective using fatty acids data (Galloway *et al.*, 2015; Blanchard, 2011) and to be a reliable tool for FAs quantification in a variety of species to correctly estimate diet proportions at a species level (Guerrero and Rogers, in prep (a)). The implications of quantitative diet data on marine mammal's behavioral sciences have not been explored in depth since coupling studies of quantitative diet estimators and diving behavior data derived from instruments are scarce.

Detailed information in proportional diet data may imply a tremendous impact on the understanding of the tradeoffs between energy acquisition and diving effort in marine predators.

The coupling of foraging behavior and diet is crucial to better predict energetic models especially when metabolic measurements are hard to obtain. The quantification of FAs and their relationship with behavior is known within the spatial scope of foraging behavior (Banks *et al.*, 2014), but has never been associated to their at-depth foraging behavior (diving), on which assumptions of the prey targeted are made (Boyd *et al.*, 1995a; Croxall *et al.*, 1985; Fedak *et al.*, 2001; Freeman *et al.*, 2010). Today, new tools such as video cameras are helping to link actual prey capture with diving behavior (Volpov *et al.*, 2016) but longer monitoring periods demand a significant amount of video recording or instrument memory use and the technology to save this amount of data has not been created yet. Alternatively, accelerometers are the best new instrument to fully describe diving behavior and its link with capture events in detail. Their use is mostly related to activity budget estimation and energy expenditures (Battaile *et al.*, 2015; Jeannieard du Dot *et al.*, 2017) but with their high temporal resolution, it is also possible to measure short-scale behaviors such as feeding events (Carrol *et al.*, 2014; Kawabata *et al.*, 2014). However, to be linked with foraging success or prey-specific information, incorporation of an additional instrument, such as video cameras, are needed since these methods are unable to distinguish among prey types (Volpov *et al.*, 2016; Viviant *et al.*, 2014) and therefore, they cannot discriminate feeding activity by each prey capture (Bidder *et al.*, 2014; Pucci *et al.*, 2020). The only way of validating species-specific behavior is by incorporating diet estimators that can offer simultaneous match with diving behavior.

The use of modeling and machine learning (ML) approaches have been tested to predict behavior using accelerometer data (Brewster *et al.*, 2018; Ladds *et al.*, 2017). However, these approaches have been applied only using movement patterns such as headshaking behavior (Brewster *et al.*, 2018) or mouth opening events (Viviant *et al.*, 2014) to validate capture atempts. Although these are good approaches to quantify foraging success, these methods fail to corroborate models' outcomes with the species of prey consumed and do not recognized the differences in behavior that may be associate with the life history of each prey. Other less sophisticated instruments, such as Time Depth Recorders (TDRs) provide a good way of indirectly measure foraging success (e.g. Bonadonna *et al.*, 2000; Goebel *et al.*, 2000; Lea *et al.*, 2002a) and, although these instruments cannot measure prey capture directly either, they present other advantages such as the provision of reliable and stable long term data collection, they are relatively inexpensive compared to other sensors and have multiple alternatives to retrieve data. By analyzing the collected TDR data with ML methods such as the random forest analysis (Breiman *et al.*, 2001) using prior information that can validate the correct classification of behavior (i.e. quantitative diet data), the results of the analysis can associate single diving behavior to actual prey capture without the need of other instruments.

AFS is a great model to achieve this coupling since FA extracted from milk is a truthful representation of the diet consumed in the preceding trip to sea (Iverson *et al.*, 1997a; Arnould *et al.*, 1995). Furthermore, FAs present an advantage over other quantitative tools such as stable isotopes. With stable isotopes, only two variables are used for prey identification (i.e. nitrogen and carbon isotopes). In contrast, the multivariate approach given by working with multiple FAs, improves the resolution of a diet analysis. For this, in consumers feeding on different species within the same trophic level, it is more likely that prey will be identified at a species-

specific level using FA than stable isotopes. Guerrero and Rogers (in prep (b)) tested both approaches simultaneously; stable isotopes and FA analysis in the diet of three species: Leopard seals, Weddell seals, and Crabeater seals. They found that the full range of fish species consumed was identified when using FA analysis, but no distinction between some fish species was achieved using stable isotopes. Together, the level of accuracy reached by FA analysis in the identification of prey, and the fact that FAs from milk could represent the diet consumed in the preceding trip, makes FA analysis an excellent proxy to link prey-specific captured with diving data.

The objective of this chapter is to characterize in detail each dive associated with capturing fish or krill in Antarctic fur seals by validating behavior with FA quantitative estimations by the use of machine learning open access tools. This is the first study that validates free-range behavior with actual species-specific diet information which could reduce the uncertainty associated with prey capture when using only instruments helping to obtain a more realistic description of the habitat, identify the differences in behavior associated with each prey, and more accurately model the energy acquired by predators.

MATERIALS AND METHODS

To estimate diet, we used qualitative and quantitative proxies. A qualitative initial estimator was performed on the field (scat analysis) and helped to understand how diet changes throughout each field season. This allowed for instant decision making in the field regarding the duration of the instruments attached to females. We discuss further scats analysis in chapter 3, where the results are presented.

Fatty acid quantitative analysis

Milk collection

We obtained 61 milk samples from 34 females captured during three breeding seasons (2014/15, 2015/16, and 2016/17, see section general methodology for capture procedure). We collected 24 ml of milk by manual expression following an intramuscular injection of oxytocin (0.25 ml, 10 UI ml^{-1}). This was done 24 to 48 hours post-partum and anytime a seal was captured again during the breeding season (most of these were done when the instrument was recovered but additional samples in some females were obtained while retouching instruments during the

season). We then divided each milk sample into two 0.25 ml aliquots and stored them in a solvent-rinsed glass tube with 2 ml of chloroform ($CHCl_3$) with 0.01% butylated hydroxytoluene (BHT). Finally, we flushed the samples with nitrogen, sealed, and stored them frozen (-20°C) for later lipid extraction in the laboratory.

Lipid extraction

Once in the lab, we extracted lipids from milk samples according to Folch *et al.* (1957) and modified by Iverson *et al.* (2001). For further detail on the lipid extraction, a very well detailed description can be found in Polito and Goebel, (2010).

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Fatty acid composition analysis

To estimate fatty acid composition, we did duplicate analyses of fatty acid methyl esters by using a temperature-programmed gas-liquid chromatography and identified fatty acids and isomers from known standards mixtures, silver-nitrate (argentation) chromatography, and GC mass spectrometry using the same models and details as described in Iverson *et al.* (1992), Iverson *et al.* (1997b) and Iverson (2001). We expressed fatty acid levels as mass percentage of total fatty acids and designated them by shorthand nomenclature of the International Union of Pure and Applied Chemistry (IUPAC) for carbon chain length number of double bonds and location (n-x) of the double bond nearest to the terminal methyl group. More methodological details of this procedure can be found in Budge *et al.* (2006).

Fatty acid statistical analysis

Only those fatty acids found consistently in amounts higher than 0.5% were used for statistical analyses to account for potential noise contribution of trace fatty acids (Grahl-Nielsen *et al.*, 2011). Further, we excluded those fatty acids found in trace amounts and the fatty acid C22:5n-3, which is not recommended for diet analysis since it is assumed to be an intermediate of C20:5n-3 and C22:6n-3 (Iverson, 1993). Finally, the number of fatty acids used for characterization and proportional calculations was 12.

The assumption that the obtained milk represents what animals consumed in the previous trip was previously described in Arnould *et al.* (1995) and Iverson *et al.* (1997a). Based on this assumption, we did not incorporate samples of which we did not have information on the previous foraging trip. Samples were separated in two groups: "Perinatal sample" (hereby P samples) which are the milk samples obtained in the initial capture 24-48 hours after females gave birth, and "lactating trip" samples (hereby: L samples) which are those samples obtained after trips occurring during the breeding season. The obtained fatty acids represent diet of 40 L trips and 18 P samples, this last group represent the diet of the animal from previous seasons before arriving at Cape Shirreff (Iverson *et al.* 1997a; Polito and Goebel, 2010).

Initially, we performed a Hierarchical Clustering Analysis (HCA) among the fatty acid percentages to inspect naturally occurring diet clusters. We created a dissimilarity matrix based on the Euclidean distances between samples and using "hclust" and the Ward's linking Method we performed an agglomerative HCA (HCA package: Maechler *et al.*, 2013; factoextra package: Kassambara and Mundt, 2017) with all 58 fatty acids percentages obtained (P and L samples). We used the silhouette and elbow methods to determine the optimal number of clusters and to

assign each FA sample (and therefore each trip and female) to a specific cluster. Results confirmed that P samples were a separated group than L trips (see result section for details) and therefore, a new HCA with the same properties as described above was performed only between L samples, obtaining two clusters that represent prey consumed only during the breeding season To assess variations in fatty acid signatures between clusters, we performed Permutational Multivariate Analysis of Variance (PERMANOVA) using the R package "vegan" (Oksanen *et al.*, 2007). For a visual assessment of these differences in a multivariate space, we used nonmetric multidimensional scaling (MDS) analysis. To identify the individual fatty acids driving the segregation among groups, we applied the similarity percentages routine (SIMPER) using the vegan package.

Quantitative dietary estimations based on fatty acid data

Since little is known about prey types consumed by Antarctic fur seals before their arrival to Antarctica (but see Arthur *et al*., 2016), diet contributions were only estimated for milk samples obtained after the perinatal period, when females are conducting foraging trips within the Antarctic Peninsula not calculating diet contribution with the P samples. As potential prey species, we used Antarctic krill, *Euphausia superba* (Phleger *et al.*, 2002), and the myctophids *Electrona antarctica*, *E. carlsbergi*, and *Gymnoscopelus nicholsi* (Stowasser *et al.*, 2009).

To estimate diet proportions quantitatively, we used the Bayesian mixing tool MixSIAR GUI v3.1 (Stock and Semmens, 2016a). This framework requires three datasets to estimate posterior distributions: mixture data (consumer fatty acid data), source data (potential prey fatty acid data), and discrimination values (differences in fatty acid values between prey and predator, also

called calibration coefficients (CCs) according to Iverson *et al.*, (2004)). Using MixSIAR, Guerrero and Rogers, (2017) showed that the use of CCs derived from an animal eating a certain food source, led to an overestimation of that source in the predicted diet. Therefore, CCs are prey-specific and this can impact the estimated diet (Rosen and Tollit, 2012). Here, to avoid an overestimation of the contribution of fish or krill associated to the specificity of CCs, we used two sets of CCs: one applied to the three fish species used as potential food sources, and another applied to the only krill species used. For fish species, we used CCs derived from northern fur seals, *Callorhinus ursinus*, fed Pacific herring, *Clupea pallasii*, for at least a year (Rosen and Tollit, 2012). To the best of our knowledge, CCs have not yet been calculated for a marine mammal fed with a crustacean species. However, there is an Antarctic pinniped whose main source of food is krill, and therefore, their blubber fatty acids likely reflect a whole life history of krill-based diet. This species is the crabeater seal, *Lobodon carcinophaga*, whose diet is composed by nearly 90% of krill (Hückstädt *et al.*, 2020 and section 4 of Appendix B). Therefore, assuming that the only prey is krill, we used their blubber fatty acid from Guerrero and Rogers, (2017) to calculate CCs, using fatty acids of krill from different sites along the Antarctic Peninsula (Phleger *et al.*, 2002; Fricke *et al.*, 1984; Guerrero and Rogers, in prep (a)). This was done by dividing each consumer fatty acid (crabeater seal) by that of the krill (Iverson *et al.*, 2004 or Guerrero and Rogers, in prep (a)).

Prior to the Bayesian mixing model analysis, the fatty acid signatures of potential prey items were multiplied by their respective CCs (either from northern fur seals or crabeater seals). This was done prior to the analysis since MixSIAR treats discrimination data as additive values, whereas CCs are multiplicative values. Therefore, as the prey values already accounted for the 'enrichment' in fatty acids, we set discrimination values to zero.

MixSIAR requires sources values to be statistically different from each other prior to the analysis. For this, we checked the differences among sources by means of pairwise multilevel comparisons in the R package "pairwiseAdonis" (Martinez Arbizu, 2017).

Raw fatty acid values of each female, together with the mean and standard deviation derived from source data were input to run each MixSIAR model as recommended by Stock *et al.* (2018). The model is fit via Markov Chain Monte Carlo (MCMC), which uses the data provided to produce a simulation of possible values of the posterior distribution. We used a multiplicative process error structure, as this is a more ecologically realistic scenario (Stock and Semmens 2016b), and non-informative priors. Model convergence was assessed via Gelman-Rubin and Geweke diagnostics (Geweke, 1991; Gelman *et al.*, 2013).

Data analyses were conducted using JAGS and R software (Plummer, 2003; Team R Core, 2013). Posterior distributions obtained from the MixSIAR analyses are expressed as median (and range). Fish species other than *Gymnoscopelus nicholsi* did not represent more than 1% of the fish consumed so, for the next section fish proportions of all species were added up identifying two clusters: "krill" and "Fish" cluster.

Coupling behavior and diet

Diving behavior was obtained from TDRs as described in the "general methodology section". To characterize a krill or fish dive, we use seven diving variables namely Bottom time (s), Dive duration (s), Maximum depth (m), Ascent time (s), Ascent rate (m/s), Descent time (s), Descent rate (m/s). An additional categorical variable is included that state whether the dive occurred during the day or night since diving behavior is influenced by the diurnal/nocturnal migratory patterns of both preys targeted (Croxall *et al.*, 1985; Collins *et al.*, 2008). After identifying prey proportions from all FAs, we identify diving behavior associated to each prey type in three steps:

1. Constructing a random forest algorithm: In order to classify all the dives measured using the TDRs, we created a ML algorithm by constructing a Random Forest Model Analysis (RFA) using the open-source machine learning program KNIME (Berthold *et al.*, 2009). Figure 2 shows a flowchart of the steps taken to construct the random forest and to determine the classification of the dives.
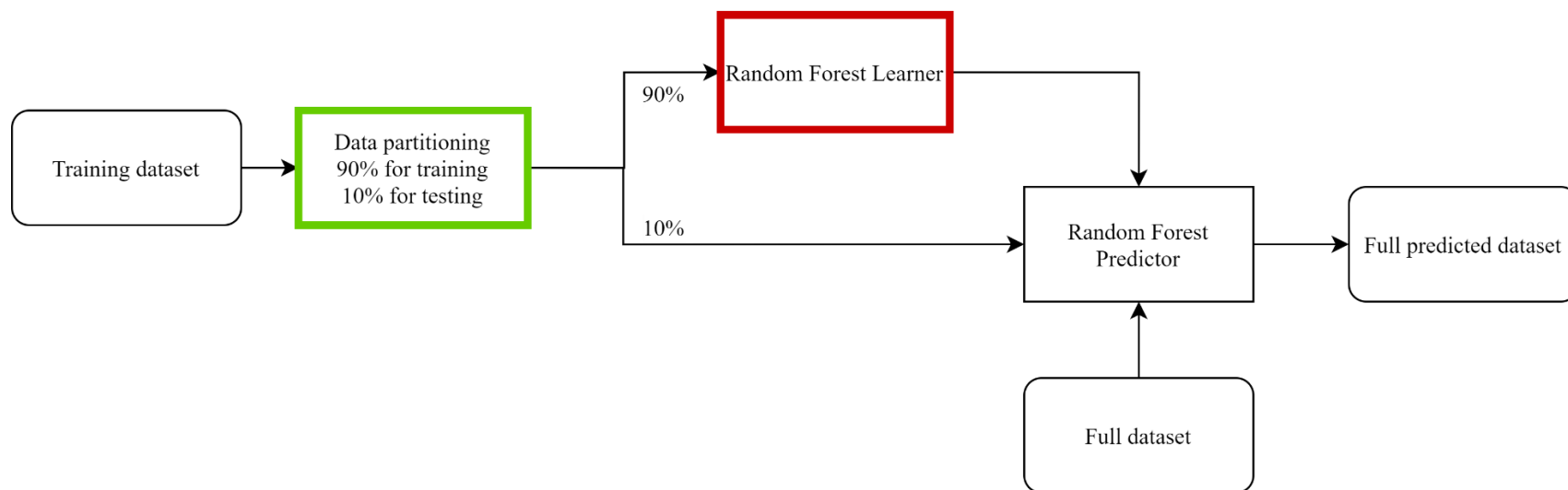
Figure 8. Flowchart for the construction of the random forest algorithm to determine diving behavior associated to each prey (Fish or Krill). The green square shows the node in which 90% of the data is defined to train the model and 10% of the data to test the model. The random forest learner (red square) is the node were details such as the splitting criteria, the number of trees, the index to select the splitting variable (Gain ratio), etc. are defined. The full dataset contains all the data that we want to predict and is the input for the random forest predictor.

Since the prey proportions are known for each trip and, in some of them, only one type of prey was mostly consumed, supervised classification is chosen. The random forest that is constructed for this study is a supervised classification algorithm that creates 100 different decision trees based on random selections of the data set of trips for which the proportions are known, called the training data set. Using RFAs instead of single decision trees leads to a higher classification accuracy and a higher robustness of the prediction because single decision trees are trained using the entire training data set whereas in this RFA, 100 decision trees are trained, each one on a subset of the original training data set. Using a random subset to train each decision tree eliminates the sensitivity to noise existing in the predictive outcome of the decision tree. Bootstrapping is performed by training trees on different training sets using random sampling with replacement of the original data to avoid correlation.

To create a training data set, ideally the type of prey is known for a few thousand dives. However, from FA we could only obtain proportions of consumed prey per trip. Females normally dive to capture a combination of fish and krill during each trip to sea. Therefore, if we look at, for instance, the Mean Maximum Depth (MMD) in a mixed-prey scenario (Figure 9A), the mean value obtained (red line) is a combination of MMDs registered for krill and fish target dives and would not represent any of the prey consumed separately. We assumed that using trips that contain samples with the highest proportion of prey obtained for each cluster, the MMD calculated would be closer to the actual krill (Figure 9B) or Fish (Figure 9C) MMD than those combined.

Following this assumption, to create the training data set we selected the trips that were associated to the FA samples showing the highest proportions of one prey item (Figure 9B-C):

More than 95% krill proportion from the krill cluster and 85% fish proportion from the fish cluster. Using a 95% cut in fish proportion leads to only one trip representing the cluster "fish" and using 90% leads to two trips. Therefore, to increase the sample size of the fish cluster, we allowed for a higher chance of wrongly classified fish dives in this category (15%). In total we used 12,945 dives for the RFA of which 90% is used to train the decision trees and 10% is used to test the performance of the random forest in terms of accuracy.
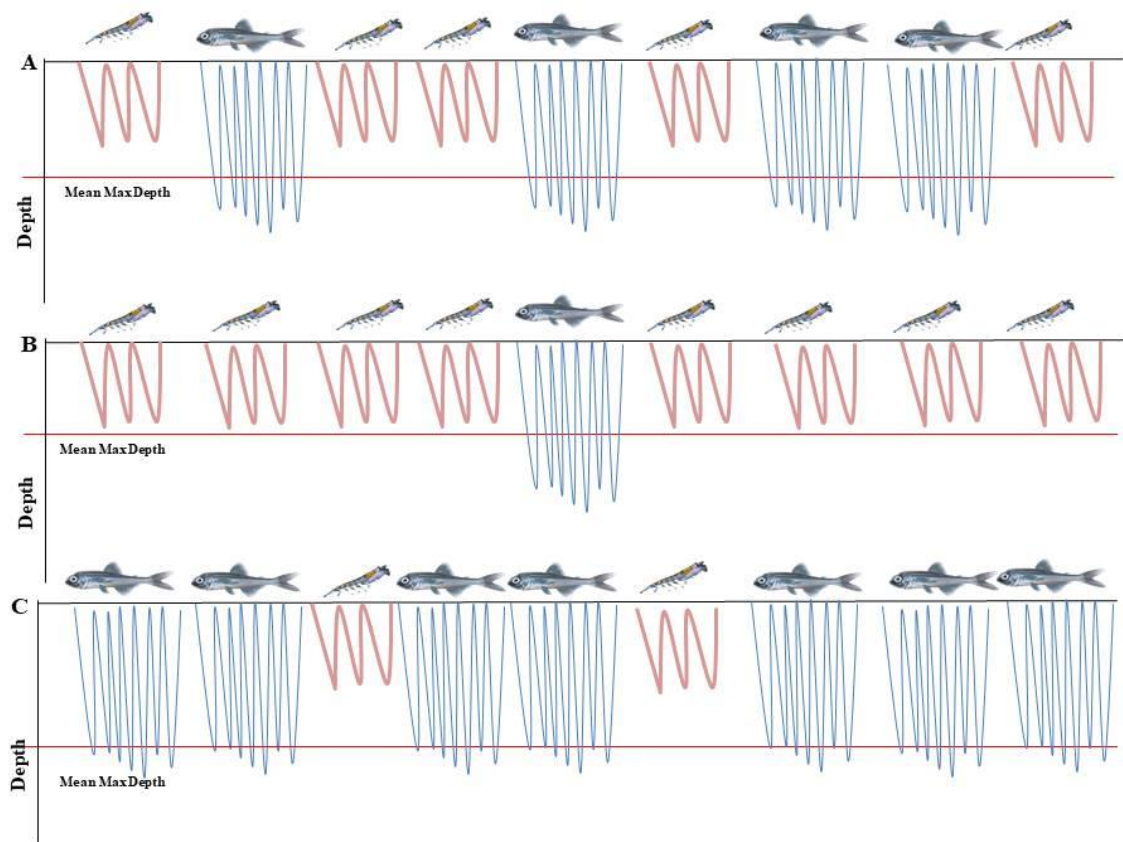
Figure 9. Representation of the approach used to characterize each prey group. The Y axis represents depth, and the upper line represents the surface of the ocean in all three figures. (A) represent a scenario in which animals would eat a combined diet of fish and krill. (B) represent a scenario in which females would mostly eat krill and (c) where females would mostly eat fish.

The input attributes (i.e. dive variables), can be different from node to node inside each tree of the random forest. When variables were numerical values such as the diving variables, the algorithm set a "candidate split point", which is the midpoint between consecutive values. The Gain ratio index is used to decide when to use which variable in order to split the data set on each level. The different trees produce slightly different predictions from the same total training data set because of the use of random subsets. We applied a "majority rule" to make the final decision, this is: the prediction obtained by most of the trees created is adopted as the final category.

2.- Implementation of the algorithm: To test and predict behavior using the RFA, we ran the algorithm in the remaining trips associated to the FA samples and compare the proportion of dive frequency and dive time that each female invested on each prey per trip. The final predicted prey proportions are compared with the prey proportions obtained from the FA quantitative analysis.

3.- Dive characterization: To characterize the differences in diving behavior when targeting krill or fish, we performed a Linear Mixed effect Models (LMM) using R (Team R Core, 2017) and lme4 (Bates *et al.*, 2018) to identify if each feeding cluster (fish or krill) influences the diving variable data (the seven dive variables used in the decision tree). Taking into account the difference between dives performed during day and night, we first separated the dives based on the category "DAY/NIGHT" and treated them separately. We used CLUSTER (Fish or Krill) and SEASON as fixed factors and used the identity of each female as the random intercept. We also included "Trip" as random factor in those variables where trip explained part of the variance of the random component of the model. Homoscedasticity and normality were tested by

visual inspection of residual plots. When basic assumptions were not met, we transformed the data using log or square root. In variables showing data "Gamma" Distributed (i.e. night dataset: maximum depth, descent time, ascent time) we performed Generalized Linear Mixed effect models (GLMM). Mass and age were not included in the models since mass did not differ between females (see Chapter 3) and age was controlled by selecting only fully mature animals for this study. We selected the best model for each variable according to Zuur *et al.* (2009) using the AIC criterion (MuMin R package, Barton, 2010; Team R Core, 2017). To determine if there was a significant contribution of clusters to each model, we obtained p values of fixed factors using a Type III Wald chi-square test from the "car" R package (Fox and Weisberg, 2019). Marginal means and confidence intervals are shown in the original scale of each variable and all data transformed in each model was back-transformed to the original values of each variable. Figures constructed in this section showed the mean and standard error of the entire data set used (not just marginal means of the models).

RESULTS

Diet analysis

The Hierarchical Cluster Analysis (HCA) results, using FA proportions of the entire data set (58 samples) and methods to determine the optimal number of clusters (Figure 2 of appendix B), suggest two distinctive clusters (Figure 10a and b). However, we found an additional pronounced break using the Elbo method within cluster 2 that suggests an inner break on two clusters, one of them containing most of the P samples (15 out of 18, Figure 10c and d). When samples were grouped based on the three clusters identified, fatty acid-based cluster explained 45% of the variance with significant differences in the overall fatty acid composition (PERMANOVA, $F2 = 22.94$, $P = 0.001$, Figure 11) and each cluster being significantly different from each other (Pairwise PERMANOVA, adjusted $P < 0.05$). This confirmed that P samples represent the diet of animals prior to their arrival at Cape Shirreff (Polito and Goebel, 2010) by showing that are substantially different from those samples obtained during the rest of the breeding season.
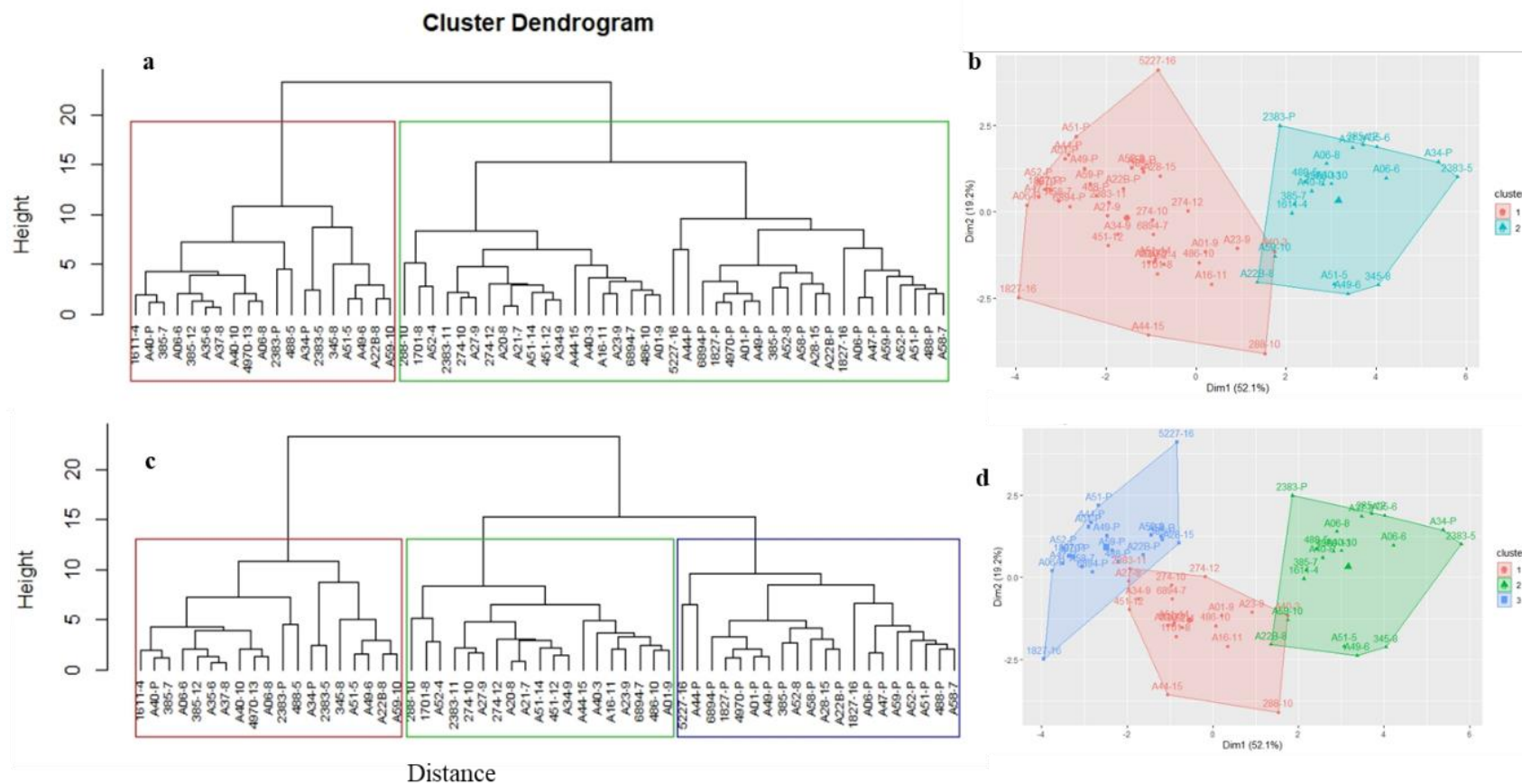
Figure 10. Hierarchical Cluster Analysis results obtained from all fatty acid samples. The results of the optimal number of clusters methods suggest two groups (2a) that can be observed in the MDS plotted (2b). However, an additional break within one of the clusters (green cluster of 2a) was observed using the Elbo method. Therefore, we diagramed these three clusters (2c) and identified an entire cluster that included most of the P samples (Blue color, also MDS figure 2d).
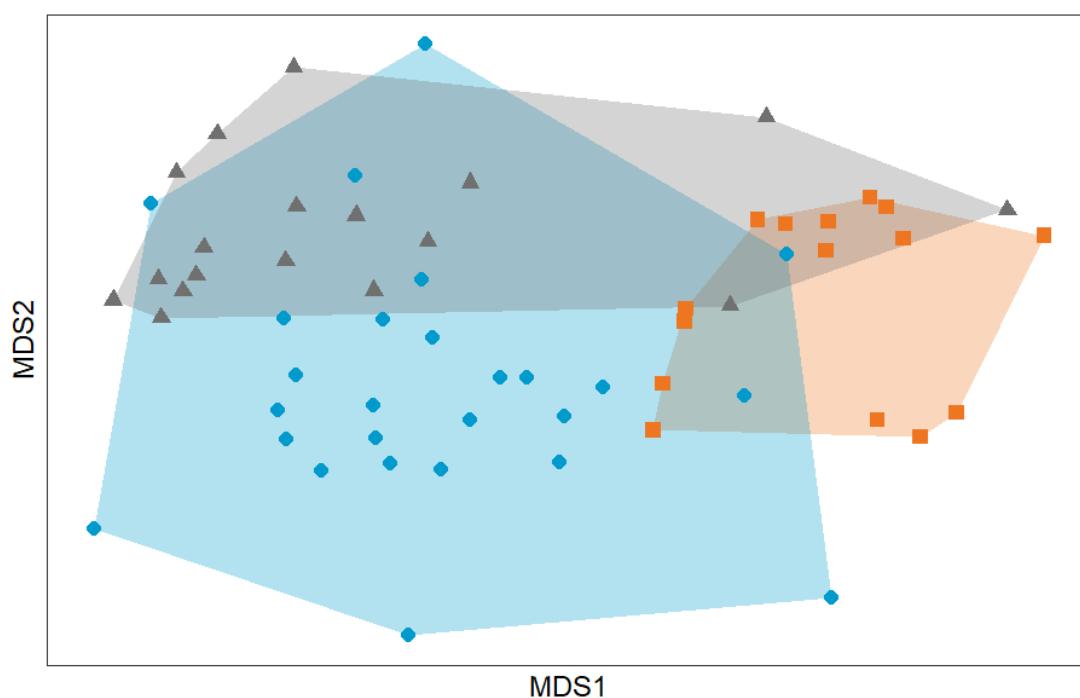
Figure 11. Multidimensional scaling analysis showing overall Fatty Acid composition differences between clusters obtained. The clusters were significantly different from each other (Pairwise PERMANOVA, adjusted $P < 0.05$).

According to the SIMPER analysis, the most influential fatty acids explaining the differences between clusters 1 and 2 are **C18:1n-9**, **C20:5n-3**, **C20:1n-9**, **C14:0**, **C16:0**. Their overall contribution to dissimilarity was 71% for the pairwise comparison between these two clusters. Milk fatty acids from seals in cluster 1 were richer in C20:5n-3, C14:0, and C16:0 compared to samples from seals of cluster 2 that showed higher values of C20:1n-9 and C18:1n-9 than cluster 1. The FA C18:1n-9 shows the highest proportion of all fatty acids in all three clusters (cluster 1: 20.6%, cluster 2: 26% and P cluster: 29.9%, Table 5) with no significant differences observed between clusters 1 and 2.

Table 5. Fatty acid proportions for dietary analysis.

	Cluster 1		Cluster 2		Perinatal	
	Mean	SD	Mean	SD	Mean	SD
C14:0	8.5	1.1	6.3	1.0	5.8	1.7
C16:0	18.4	1.1	16.5	1.1	16.9	1.2
C16:1n-7	6.4	1.2	5.7	1.1	6.6	0.8
C18:0	1.6	0.2	2.0	0.5	1.6	0.2
C18:1n-9	20.6	1.6	26.3	2.8	29.8	4.7
C18:1n-7	7.4	0.4	7.1	0.4	6.1	0.9
C18:2n-6	2.1	0.2	1.7	0.3	1.6	0.3
C18:4n-3	1.4	0.3	0.9	0.3	0.6	0.5
C20:1n-9	2.6	1.2	6.0	1.5	5.4	1.9
C20:5n-3	9.1	0.9	6.5	1.0	5.6	1.9
C22:1n-11	0.3	0.2	0.8	0.3	0.7	0.3
C22:6n-3	8.7	1.4	7.4	1.5	6.5	1.3

With enough results suggesting that P samples were not representative of prey consumed during the breeding season, we decided to run a second HCA only including the L trip samples (41 samples). The optimal number of clusters is two (Figure 12a and b). The new HCA shows two distinctive clusters and re-classified 5 samples that were originally classified within the P cluster (Figure 12c and d).
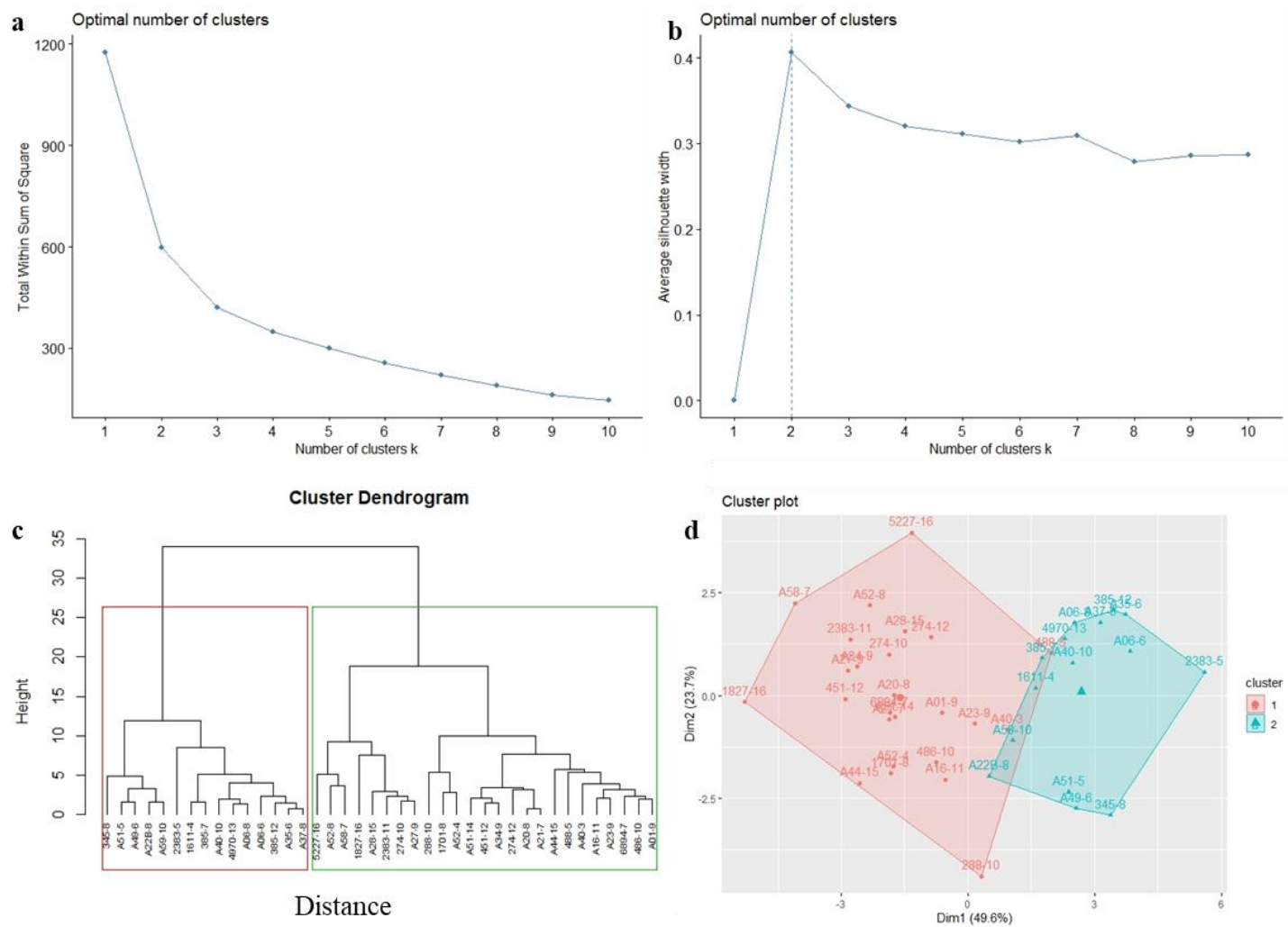
Figure 12. Cluster analysis performed with the fatty acid samples obtained during the lactating period of Antarctic fur seals. Optimal number of clusters methods suggested two groups (2a and b). 2c.- Cluster analysis using the ward method. 2d.- Multidimensional scaling analysis showing the two different clusters obtained.

Dietary predictions

All source species (potential preys) are significantly different from each other (Pairwise PERMANOVA, adjusted $P < 0.05$, Figure 13), and therefore, to calculate proportions there was no need to combine species into groups. Proportional values of samples from cluster 1 are closer to values of the source species *E. superba* (Krill) whereas values of cluster 2 are closer to fish species *G. nicholsi* and *E. electrona*.
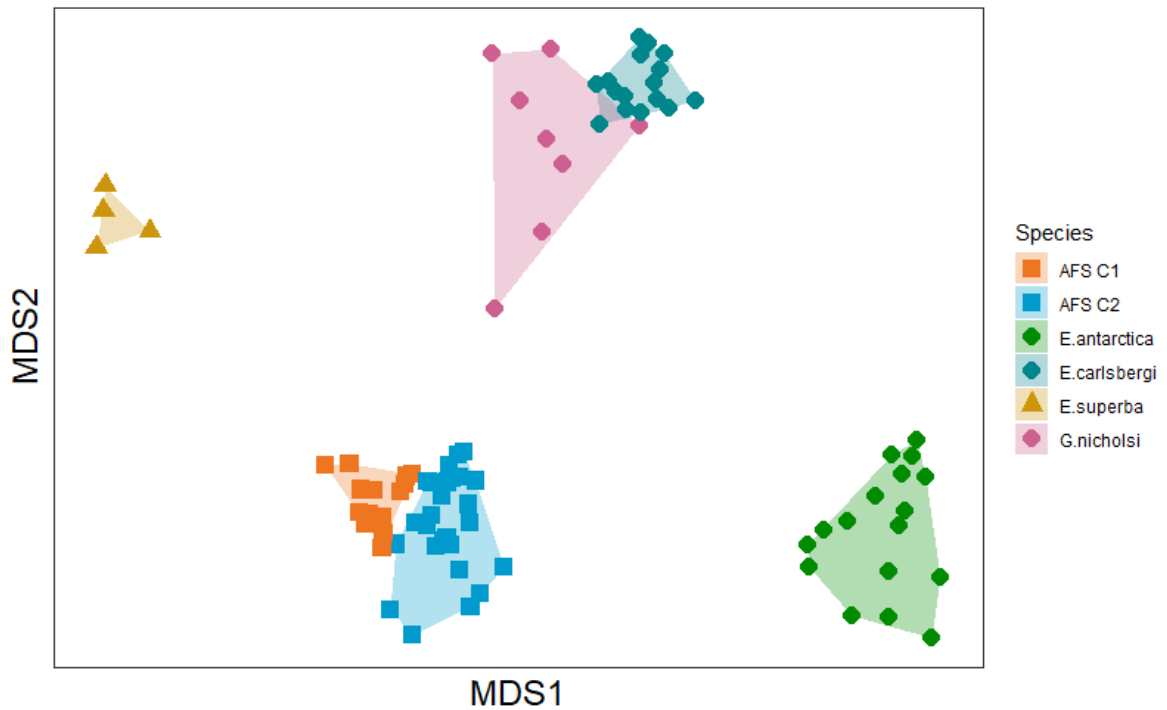
Figure 13. Multidimensional scaling analysis (MDS) using both consumer and source Fatty acid proportional data. Consumer's fatty acid proportional values are raw data from this study: Cluster 1 (orange, AFS C1) and Cluster 2 (Blue, AFS C2) whereas source proportional data were input as means and standard deviations obtained from the literature. The model is fitted via Markov Chain Monte Carlo (MCMC), which uses the raw data provided to produce a simulation of possible values of the posterior distribution which are plotted here for one krill species: *Euphausia superba* (brown triangles) and for three fish species: *Electrona antarctica* (green circles) *Electrona carlsbergi* (blue circles) and *Gymnoscopelus nicholsi* (pink circles).

The FA clusters identified produce very different dietary predictions (Table 6). Using MixSIAR

we estimated Cluster 1 to consume almost exclusively *E. superba* (93%, Figure 14a) whereas

cluster 2 is estimated to consume 80% of *G. nicholsi* and only 19% of *E. superba* (Figure 14b).

The remaining fish species together, *E. carlsbergi* and *E. Antarctica,* accounts for only 3% of

the mean diet proportion.

Table 6. Percentages of prey consumed (median and range) based on milk fatty acids from AFS
females classified as cluster 1 (Krill dominant) and 2 (Fish dominant).

Prey species	Cluster 1 (Krill dominant) [%]	Cluster 2 (Fish dominant) [%]
E. antarctica	2.6 (0.1 – 5.5)	0.5 (0.001 – 2.4)
E. carlsbergi	2.2 (0.1 – 5.9)	0.4 (0.001 – 1.4)
E. superba	93.6 (90.1 – 95.2)	19.1 (14 – 24.6)
G. nicholsi	1.6 (0.01 – 6.8)	80 (74.1 – 85.0)
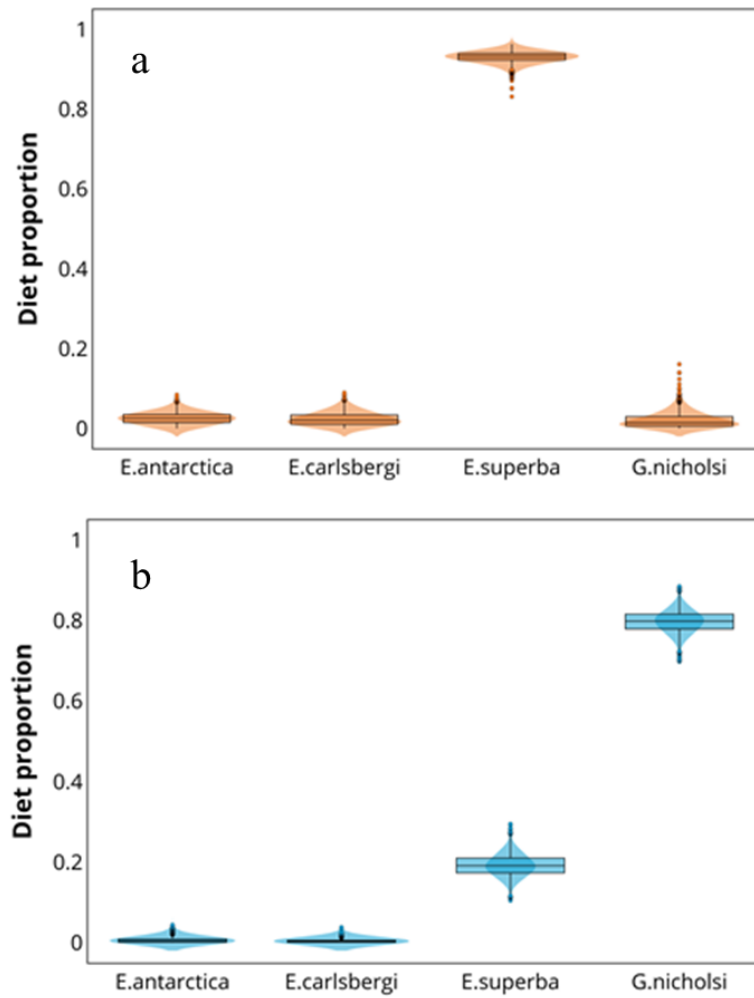
Figure 14. Prey species proportions per cluster obtained from the quantitative fatty acid analysis. a.- Cluster 1 showed a 93% mean of krill (*E. superba*) and b.- Cluster 2 showing ~80% proportion of the fish species *G. nicholsi*. Mean ± SD.

Coupling behavior with diet proportions

After obtaining the diet proportions per sample, we selected females that represented the maximum proportional values for each cluster (cluster 1 is further called krill cluster and cluster 2: fish cluster, Table 7). Within the fish species found in the FA samples, *G. nicholsi* represents most of the fish diet proportion. The other fish species account for less than 3% of the diet. Therefore, the different fish proportions in the fish cluster were pooled together, accounting for the total proportion representing fish consumption. For the Krill cluster, we used all females with equal or more than 95% of their diet composed by krill (6 females with a krill mean proportion of 97.6± 1.5 % and a fish mean proportion of 2.4 ±1.5 % representing 6 trips and a total of 6,292 dives). For the fish cluster, we used a threshold of 85% fish proportion or higher (8 females with a fish mean proportion of 88.7 ± 3.6% and a krill mean proportion of 11.3 ± 3.6% representing 8 trips and a total of 6,653 dives).

Table 7. Females, trip number, and diet proportions of subset trips selected for the coupling between behavior and diet.

Clusters	Female ID	Trip Number	Fish%	Krill %
Krill Cluster	2383	5	0.8	99.2
	385	12	2.4	97.6
	A06	6	1.4	98.6
	A35	6	1.9	98.1
	A37	8	5.1	94.9
	A40	10	2.9	97.1
Fish Cluster	1827	16	95.6	4.4
	2383	11	88	12
	451	12	86	14
	6894	7	86	14
	A34	9	87	13
	A44	15	85.7	14.3
	A52	8	88.6	11.4
	A58	7	92.8	7.2

Random forest analysis

The total supervised data set used contains 12,945 dives. To build the multiple trees, the program used 90% of these dives to trained the decision trees and 10% (1,295 dives) for testing. Out of 100 trees constructed, the average depth (number of levels) was 42 levels with a minimal depth of 33 levels and a maximal depth of 51 levels. The average number of nodes was 4,657 with the minimal number of nodes of 4,363 and the maximal number of 4,825.

The output of the RFA is the prediction of dives targeting krill or fish and is performed with 76.2 % accuracy. This means that, out of the 1,295 dives used in the testing section of the model, 987 dives were correctly classified, and 308 dives were wrongly classified. Within the fish cluster, 75% of the dives were correctly classified as fish dives (502 dives of 666 dives), and within the krill cluster, 77% of the dives were correctly classified as krill dives (485 dives out of 629 dives). Therefore, the final algorithm is slightly better (2%) predicting krill dives than fish dives.

Table 8 shows the relevance of each variable to classify the dives. We only present the level 0 (first decision level) which is the most important level for classification. The column "Candidate" is the number of times that a specific variable was proposed as a splitting node and the column "splits" show how many times that variable was chosen as a splitting node in level 0. The most important variable is the ascent rate (m/sec) in which the variable was chosen 100% of the times that it was proposed as a splitting node. Ascent time is the second most important variable (81.8%), followed by Maximum depth (69.2%) and Descent rate (60%).

Table 8. The relevance of each diving variable using random forest analysis. The column candidates show how many times each variable was proposed as a splitting node in the most important level of classification (Level 0) and the column "Splits" shows how many times the variable was chosen as a splitting node.

Variables	Candidates	Splits	% of times chosen
Day or Night	22	2	9.1
Maximum Depth	26	18	69.2
Dive Duration	27	5	18.5
Bottom Time	20	5	25
Descent Time	31	12	38.7
Descent Rate	30	18	60
Ascent Time	22	18	81.8
Ascent Rate	**22**	**22**	**100**

We ran the final version of the algorithm obtained from the RFA in the entire known-diet proportion dataset. From this, we calculated the percentage of time invested targeting each prey (Time Invested Diving, TID), and the percentage of dives performed targeting each prey (Dive Frequency, DF). We found a higher percentage of TID and DF performed when we observe higher proportional values of FA of each prey (Table 9). When targeting Krill (Cluster Krill), the mean FA krill proportion is 93% ± 5.3% and the mean FA fish proportion is 6.7%. This is correlated to higher percentages of TID to capture krill (76.7 ± 26.57%) than fish (23.25 ± 22.8%). Also, the DF targeting krill (73.15 ±24.3%) over fish (26.85± 24.29%) is consistent with the FA proportional values of prey capture in this cluster (Table 9). Furthermore, similar conclusions can be drawn from the fish cluster (mean diet percentage fish: 79.7±9.9% over krill: 20.3±9.9%). In this case, the TID when targeting fish (68.53±26.57%) is higher than that invested in krill (31.46±26.57%). Also, the DF targeting fish is higher (71± 24.3%) than when targeting krill (28.7 ± 24.31%, Table 9). Altogether, this confirms that the random forest

machine learning approach applied to behavioral data can accurately be used as a predictive tool for behavior in the absence of dietary data.

Table 9. Means diet proportions and behavior per cluster. Mean prey proportions obtained from fatty acids proportions of time invested diving and dive frequency calculated for each trip on each cluster obtained using the algorithm constructed. Mean ± standard deviations are presented.

Cluster	Prey Proportion		Dive time invested		Dive frequency	
	Fish%	Krill %	Fish%	Krill %	Fish%	Krill %
Krill	6.7 ± 5.3	93.3 ± 5.3	23.3 ± 22.8	76.7 ± 26.6	26.8 ± 24.3	73.2 ± 24.3
Fish	79.7 ± 10	20.3 ± 10	68.5 ± 26.6	31.5 ± 26.6	71.3 ± 24.3	28.7 ± 24.3

Prey specific diving behavior

Diving behavior is associated with the vertical distribution of prey and therefore, it differs for dives occurring during the day or during the night. During the day, krill is targeted in deeper waters than fish (Krill: 37.3±15m, Fish: 28.3±16m, X2=29.8, P value < 0.001) and females perform longer dives ((Krill: 107.2±28.6 sec, Fish: 86.7±26.3 sec, X2=79.3, P value < 0,001) than when capturing fish. Those longer dives cannot be explained by an increase in bottom time (Table 10) and are more likely explained by an increase in ascent time (Krill: 31.07±11.7 sec, Fish: 20.5±10.46 sec, X2=187.9, P value < 0.001) and descent time (Krill: 24.7±9.7 sec, Fish: 18.7±9.7 sec, X2=13.3, P value=0.0002) when capturing krill in deeper waters. During the night, both preys are captured closer to the surface and no significant differences were found in the maximum depth reached (Table 10). In night time, dive duration is slightly shorter when capturing krill than fish (Krill: 55.4±34.6 sec, Fish: 59.4±42.2 sec, X2=79.3, P value < 0.001) even though a higher ascent time was found when targeting krill (X2=86.1, P value < 0.001). These differences between clusters are only a few seconds and do not differ much when means

of the total data set are calculated (ascent time: krill: 15.6± sec, fish: 14.7± 11.8 sec, Figure 15).

We find a higher speed when targeting fish than krill when ascending (Krill: 0.9 ±0.4 m/sec, Fish: 1.2±0.4 m/sec, X2=236.1, P value < 0.001) and a slight increase in speed while descending during day and night dives when capturing krill over fish. These differences are a result of the model (Table 10) but the means obtained from the full dataset (Full dataset: Descent rate during day: Krill: 1.3 ±0.2 m/sec, Fish: 1.2±0.4 m/sec, X2=47.9, P value < 0.001, during the night: Krill: 1.1 ±0.3 m/sec, Fish: 1.3±0.4 m/sec, X2=10.89, P value < 0.001, Figure 15) suggest that these differences may not be as important as other variables when working with mean values.

Overall, both krill and fish are captured in deeper water during the day than during the night. Females targeting krill increase the ascent and descent time when reaching deeper areas extending the duration of their dives (dive duration) compared to dives at night. However, when we compare both preys during the day, fish is captured in shallower waters than krill using less time capturing fish than krill (ascent or decent time) and therefore, performing longer dives to capture krill. At night, both preys can be found in shallower waters but krill is captured in less time than fish. When capturing fish at night, animals chase their prey going upward to the surface increasing their ascending speed as opposed to capturing krill which mostly occurred from the surface down (Table 10, Figure 15). This highlights two important strategies associated to each prey targeted and the limitations existent by the life history and characteristics of each preys.

Table 10. Model marginal means for all variables with 95% confidence intervals for day and night of both clusters: krill and fish. Means and intervals were back-transformed and recovered in the original unit.

Time of the day	Diving Variables	Krill Cluster	Fish Cluster	P values[#]
Day dives	Dive Duration (sec)	105.1 (97.0-113.1)	84.8 (77.1-92.6)	**<0.0001***
	Ascent Rate (m/sec)[b]	1.04 (0.79-1.32)	1.07 (0.84-1.33)	0.799
	Descent Rate (m/sec)	1.4 (1.32-1.46)	1.25 (1.18-1.32)	**<0.0001***
	Ascent Time (sec)[b]	29.8 (25.8-34.1)	18.7 (15.5-22.1)	**<0.0001***
	Descent Time (sec)[b]	20.9 (18.0-24.1)	18.3 (15.6-21.1)	**0.0003***
	Bottom Time (sec)	48.0 (38.5-57.5)	49.2 (42.4-55.9)	0.7696
	Maximum Depth (m)[b]	33.2 (28.0-38.9)	26.8 (22.2-31.8)	**<0.0001***
Night Dives	Dive Duration (sec)	63.0 (54.6-71.4)	56.5 (48.2-64.8)	**0.004***
	Ascent Rate (m/sec)[b]	0.87 (0.006-3.21)	1.24 (0.72-1.89)	**<0.0001***
	Descent Rate (m/sec)	1.3 (1.20-1.4)	1.23 (1.13-1.33)	**0.0009***
	Ascent Time (sec)[a]	18.6 (16.1-21.9)	12.7 (11.6-14.2)	**<0.0001***
	Descent Time (sec)[a]	13.8 (12.2-15.8)	13.7 (12.3-15.6)	0.984
	Bottom Time (sec)	25.6 (13.8-37.5)	31.2 (23.5-39.0)	0.2
	Maximum Depth (m)[a]	19.4 (16.5-23.4)	18.7 (16.1-22.3)	0.51

[a]Results from Generalized Linear Mixed model fit by maximum likelihood (Laplace Approximation) performed in data gamma-distributed
[b]LMM fitted in sqrt transformed data
[#]P value only for the variable cluster
*Significant P-values less than 0.05
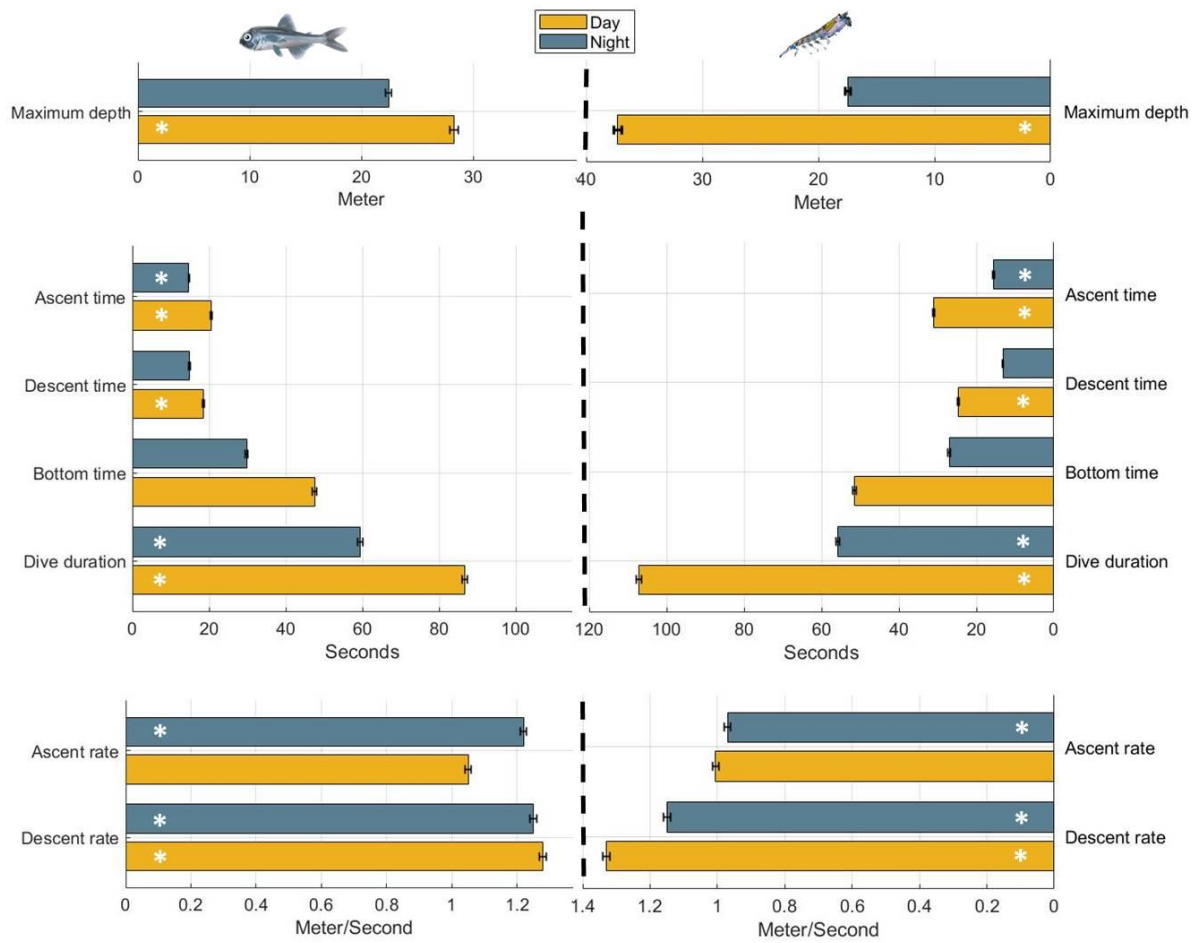
Figure 15. Means of diving variable for both clusters (Fish and Krill clusters). Fish: left panel, krill: right panel for both Day (yellow) and night (Blue) dive performances. White asterisks represent those variables in which cluster significantly explain variance based on the mixed model analyses per variable. Means and standard errors are presented.

DISCUSSION

Inferring foraging success and predator's habitat selection using only spatial data and qualitative diet analysis can be misleading (Bastille-Rousseau *et al.*, 2010). When diving data is collected, most ecological studies have also inferred prey capture success from diving metrics (e.g. Boyd *et al.*, 1995a; Croxall *et al.*, 1985; Fedak *et al.*, 2001) speculating also about the prey captured in specific locations based on the way predators behave. Diving behavior needs to be associated with prey capture success when assessing prey-habitat selection or when a full description of foraging strategies is pursuit. Previous studies were able to validate feeding attempts using diving behavior (Viviant *et al.*, 2014; Volpov *et al.*, 2016) but these attempts would only apply to specialist individuals since they have assumed that every capture attempt, despite the prey been targeted, involved the same diving modifications, not recognizing the influence that different preys targeted or prey vertical distribution may have in predator diving behavior. We have successfully link foraging success to species-specific diving behavior without the need of using sophisticated additional instruments (Viviant *et al.*, 2010; Suzuki *et al.*, 2010; Hooker *et al.*, 2002; Volpov *et al.*, 2016) or complex analytical tools. Instead, we use a methodology that can be easily implemented in other data sets in which TDRs have been used (see the implementation in Chapter 3). Further, we have been able to fully describe the behavior of the

dive phase associated with the most abundant prey species captured by Antarctic fur seals in the WAP.

To validate the relationship between diet proportional data and diving information obtained from the preceding trip to sea, we worked with the underlying assumption that prey proportional data obtained from FA analysis represent the prey captured in that preceding trip. Behaviorally, the rate of milk energy production on land and the total estimate energy delivered during an attendance event has been positively correlated with the duration of the previous trip (Arnould and Boyd, 1995). This means that AFS would mostly produce the milk while pups are suckling on land, producing one-fifth of the total production at the previous trip while females forage (revised in Sharp *et al.*, 2005). Furthermore, milk fatty acids have been tested to be derived mostly from immediate dietary intake (Iverson *et al.*, 1997a; Lea *et al.*, 2002b). All this information was solid enough for us to suggest that behavior in the preceding trip was indeed associated with the preys consumed during the previous trip.

Fatty acids

FA composition of each cluster identified in our study is consistent with what has been found in previous FA studies on the species. Within the krill cluster, C20:5n-3, C14:0, and C16:0 account for ~35.6% of the total fatty acid composition, ~5% more than the percentage found in the fish cluster (~30%). A higher proportion of these FAs have been linked to a krill diet in previous studies (Iverson *et al.*, 1997a; Brown *et al.*, 1999), and when compared to the fish cluster, small differences are expected since fish species found in this area are also thought to

feed on krill (Gon and Heemstra, 1990). In contrast, monounsaturated Fatty Acids (MUFAs) proportions were higher in the fish cluster (C20:1n-9 and C18:1n-9) than the krill cluster. MUFAs are found in high concentrations in myctophids (Lea *et al.*, 2002c and references in) and therefore associated with diets that incorporate a high consumption of these fish species (Iverson *et al.*, 1997a; Brown *et al.*, 1999; Lea *et al.*, 2002b). *Gymnoscopelus nicholsi* and *Electrona Antarctica*, the most abundant species found in this study (this Chapter and Chapter 3), account for most MUFAs concentration found in the fish cluster. *G. nicholsi,* the largest and one of the most lipid-rich species of the genera found in Antarctica (Lea *et al.*, 2002b; Lea *et al.*, 2002c) was the most abundant of the two species according to the proportional analysis. The two most abundant FA of the fish cluster have also been described as major FAs found in squid species collected at Sub-Antarctic islands (Phillips *et al.*, 2002). This may lead us to wrongly link behavior to this cluster due to the misclassification of the species based on the FAs found, since they may represent other species besides those considered in this study. However, other diet estimators of this study (scats, Chapter 3) and previous diet descriptions at this location (Osman *et al.*, 2004; Polito and Goebel, 2010), show very low quantities of squid found in their diet, therefore, it is very unlikely that these FA could represent squid. With all this information, we are confident to suggest that behavior associated with both clusters do represent mostly two species; *E. superba* (krill) and *G. nicholsi* (fish) and therefore, the behavior found in the precedent trip would represent the capture of either of these two species.

Machine learning

There is an overwhelming amount of machine learning (ML) methods for data classification but all of them can be summarized in two types; unsupervised and supervised ML methods. Unsupervised ML methods rely on direct observation of a phenomenon (e.g. feeding events) and from it, they identify repetitive patterns (Chimienti *et al.*, 2016; Ladds *et al.*, 2016; Norris, 2019), whereas supervised ML methods are trained with pre-defined behavior (Leos-Barajas *et al.*, 2017) and then tested within a known data set (Chimienti *et al.*, 2016). We choose a supervised ML method because by knowing the prey targeted and the proportion of prey consumed by each individual, we were able to inform and train the algorithm to be tested later, whereas unsupervised ML methods cannot be validated (Sur *et al.*, 2017). Our approach provides a highly accurate predictive tool but, three important assumptions were made: 1.- We assumed that every dive performed was a feeding dive, 2.- When calculating the proportional time invested diving targeting each prey, we also assumed that there were no failed capture attempts, and 3.- By training the algorithm specifying each dive with each prey, every predicted dive would only be classified to one of the two options given (fish or krill) and therefore, unknown behavior can either not be classified or be wrongly classified (Chimienti *et al.*, 2016; Ladds *et al.*, 2016; Norris 2019). All these points need to be explored more in-depth to make the classification process more reliable, however, we can assume that these assumptions remain a constant error within the process of classification and rely on the fact that, out of all methods to classify behavior, RFA seems still to have a good balance between been an accurate predictor and produced the best outcome when is applied to predict behavioral data in long-term data sets

(Ladds *et al.*, 2016; Bao and Intille, 2004, chapter 3) and have been validated with fine-scale behavioral data (Kleanthous *et al.*, 2019).

Diving behavior

The most important diving variable to predict species-specific dives was ascent rate followed by ascent time, then maximum depth, and finally, descent rate with bottom time scoring very low as a predictive split node. This suggests that most of the diving modifications to target one or the other prey occur in the transit phase of a dive over the bottom phase. Although we assumed that all dives were successful attempts, our results are consistent with previous findings, in which prey capture attempts were usually associated to changes in descent or ascent rate at a dive scale (Viviant *et al.*, 2014), and where increasing ascent rate has been linked with greater foraging intensity (Volpov *et al.*, 2016). This is opposed to other studies inferring that the bottom phase is the most important phase for feeding in this (Hooker *et al.*, 2002; Iwata *et al.*, 2012) and several other species (Kuhn *et al.*, 2009; Austin *et al.*, 2006; Watanabe *et al.*, 2003 among others). Instead, our results agree with previous studies that show that the bottom phase of a dive seems to be a poor predictor of foraging success (Viviant *et al.*, 2016).

The studies of Viviant *et al.* (2014; 2016) were performed in AFS females targeting fish so it can be assumed that most of the capture attempts were associated with fish and that those foraging attempts found in the vertical component are only associated to this prey. We added to this that differences in vertical behavior when different preys are targeted can also be observed

and may be related to differences in chasing behavior or time spend diving to capture multiple preys per dive.

When capturing fish at night, Viviant *et al.* (2014) found descent rate to be the most constant and reliable predictor of foraging success. However, when capturing fish, we found that dives were performed accelerating from deeper waters swimming upward and with this increasing the ascent rate rather than the descent rate as previously reported. We think this may have to do with the depth differences in which fish is captured at Cape Shirreff compared to The Kerguelen Plateau where this study was conducted (Viviant *et al.*, 2014). Foraging at this location occurs at 50 ± 17 meters at night (Lea *et al.*, 2002a) twice deeper than at Cape Shirreff during the night. The depth at which fish is found in the Kerguelen Plateau may force animals to target fish from surface waters toward deeper waters, increasing their descent rate, whereas at Cape Shirreff, the proximity of the prey to the sea surface, especially at night, may force them to ambush the prey from below. This may also be true when capturing krill, although slower when ascending than when capturing fish, animals would spend longer ascending time compared to those dives when fish is captured.

The extension of time when capturing krill could be related to multiple attempts of krill capture per dive which would implicate longer dives than when capturing fish as we found here. Viviant *et al*. (2016) suggest that most of the time it is only one capture attempt that is performed per every dive when capturing fish. However, we do not have this information for krill capture attempts. Video camera footage suggest that multiple krill are capture per dive by doing zig-zag swimming usually capturing krill in direction to the surface (Borras-Chavez pers obs), but further validation is necessary to test this assumption. Altogether, our study is in line with the

findings of Viviant *et al.* (2014), where the vertical phase of the dive may be playing a key role in the capture of prey over the bottom duration of a dive that do not necessarily relate to successful prey capture in surface waters (Viviant *et al.*, 2016) but diving behavior associated to other activities.

CONCLUSIONS

We have successfully determined how AFS dives when capturing two of their most important prey species at Cape Shirreff. This was done by validating behavior with novel dietary proportional estimations in a species that allow us to link diving behavior with the prey consumed in the previous trip. We hypothesized that capturing fish would demand more time than capturing krill due to the swimming and escaping behavior of fish compared to krill. On the contrary, Krill captures demand more time at a dive scale and this is presumably related with multiple preys captured per dive. When capturing fish, animals use less vertical time and increase their ascent speed compared to when consuming krill. This happens at such a consistent rate throughout the total number of dives that, according to the ML algorithm, ascent rate was the best predictor when classifying dives between krill or fish. This may indeed represent a tradeoff between strategies, in which diving longer but acquiring multiple less lipid-rich prey (krill) would compensate the energy spent when swimming faster to capture a single but lipid-richer prey (Fish). For this, further validation is necessary using video cameras (Hooker *et al.*, 2002; Naito *et al.*, 2013; Volpov *et al.*, 2015) or other instruments that would allow us to match visually the specific dive with the exact prey capture.

Our ML approach is relatively easy to implement (free online source tool) and can be extended to other individuals of the same species or otariids species of which we may have fatty acid information. We are aware that other ML methods may work as good as RFA and exploration of multiple methods should (and would) be applied to this data set (Ladds *et al.*, 2016). Finally, simple proxies such as this or those provided by Viviant *et al.* (2014), allow us to work with larger data sets, improve future energetic models, and analyzed in retrospective all the data already collected using TDRs by multiple monitoring programs in the last decades. The implications of these findings are further tested and discussed in the third and final chapter of this thesis where we test the validity of our algorithm in a larger data set, unveiling the applicability of these tools when defining foraging strategies, habitat used, and real time prey captures.

CHAPTER 3. LIVING AT THE EDGE. COPING WITH ENVIRONMENTAL VARIABILITY IN ALREADY HIGHLY HETEROGENEOUS ENVIRONMENTS

ABSTRACT

In the Southern Ocean, predator´s prey availability is highly responsive to environmental variability and atmospheric events. Antarctic fur seals (AFS) females mitigate negative effects of environmental variation by being efficient at provisioning and/or foraging. This has been observed studying the behavioral response of predators to prey inter-annual variation triggered by atmospheric events such as El Niño Southern Oscillation (ENSO) or the southern annular mode (SAM), compared to normal years. However, there is little understanding on colonies living at the edge of their breeding distribution which are already facing highly heterogeneous environments and operating at its highest field metabolic rate. We evaluated how the southernmost breeding colony of AFS copes with additional environmental variability and adjusts behavior while living near their metabolic ceiling. We instrumented, measured and compared feeding and foraging behavior of 15, 15, and 11 AFS females between the breeding seasons of 2014/15, 2015/16, and 2016/17 respectively. Seasons represent highly variable environmental conditions considering that both an ENSO (2015-2016) and an intense SAM event (2016) occurred within this time frame. In addition, we identified the foraging strategies used by females at this colony by coupling spatial data (trip duration, distance from colonies, foraging areas utilized, and haul-out time) with prey captured by applying the algorithm obtained in Chapter 2 and checked if different strategies are used between seasons. Foraging behavior is limited by prey availability at the edge of the AFS breeding distribution. In seasons where krill is found in reduced densities (2014, 2016), or when previous spring conditions led to reduced krill availability in summer (ENSO-SAM, 2016), we observed that foraging behavior shifts toward a higher rate of fish consumption compared to 2015, when a higher krill abundance is available and a higher consumption was found. This is observed by (1) a higher percentage of fish-associated fatty acids (FA) in 2014 and 2016 than in 2015 and (2) a higher use of fish-associated foraging strategies in 2014 and 2016, even in phases within the breeding season in which mostly krill has been found in previous studies.

We did not observe changes in diving behavior presumably due to the constraints of breeding at their physiological limits been the shifting of prey the only remaining alternative. This highlights how sensitive AFSs can be to changes in prey availability, which is concerning considering the current projected changes in sea ice extent and temperature that may reduce krill spawning habitats and the observed reduction of myctophid populations in certain areas. Continuous monitoring of AFS behavior in edge colonies provides valuable information on the capacity of predators to respond to future intensification of atmospheric events.

INTRODUCTION

Marine predators are conditioned to their prey abundance, distribution, and size and everything that affect prey conditions will shape predator's behavior. Preys of Southern Ocean predators are highly responsive to environmental variability impacting the upper trophic levels directly (Fraser and Hofmann, 2003; Atkinson *et al.*, 2004; Clarke *et al.*, 2007; Costa *et al.*, 2010b). Moreover, the Antarctic mesopelagic food web is mostly sustained by one single species: Krill. We have explored and reviewed the relevance of krill for both pinnipeds, and fisheries in the additional chapter of this thesis (Appendix A) which can be revised for further information on the importance of krill in this ecosystem. Essentially, several Antarctic predators rely substantially on this resource and some of them, such as Crabeaters and AFS, rely almost exclusively on krill (Hückstädt *et al.*, 2020 and Section 4.1 Appendix A). For this, any change of abundance and availability of this resource would severely impact species both at an individual (behavior) and a population scale (Morris *et al.*, 2009).

In the Southern Ocean, the availability of prey is directly related to natural atmospheric processes (Forcada and Trathan, 2009), such as El Niño Southern Oscillation (ENSO) or the Southern Annular Mode (SAM), since these events have a direct impact on the formation and extent of sea ice (Forcada *et al.*, 2006; Murphy *et al.*, 2007; Le Boeuf and Crocker, 2005;

Forcada and Trathan, 2009). In addition, during the last 50 years, the polar ecosystem has faced the biggest ecological changes observed in the region due to climate change (Constable *et al.*, 2014; Schofield *et al.*, 2010) affecting marine mammal prey availability and distribution at multiple scales.

Behaviorally, modify trip duration is one of the most common response to resource variability and changes in the environment (Costa *et al.*, 1989; Boyd *et al.*, 1991; Trillmich *et al.*, 1991; Merrick and Loughlin, 1997; Boyd, 1998; Georges and Guinet, 2000; Beauplet *et al.*, 2004; Costa, 2008). However, these modifications are also less desired because the energy delivered upon return from a trip is constant (Costa, 1991) and therefore, with a longer trip duration, the overall energy received by the offspring gets reduced (Costa, 2008). Alternatively, animals could forage energy-richer prey (if they are generalists) or increase the amount of prey consumed, but both decisions may demand a higher effort by changing foraging areas or modifying diving behavior to capture energy-richer or more prey (Feldkamp *et al.*, 1991; Boyd, 1996; Boyd *et al.*, 1999; Costa and Gale, 2003, Merrick and Loughlin, 1997; Mattlin *et al.*, 1998; Beauplet *et al.*, 2004). Whether these behavioral modifications are spatial or temporal, they will all carry changes in their field metabolic rate (reviewed in Costa, 2008), increasing the energy used. This, however, represents a challenge in colonies that are already operating in highly heterogeneous environments of which we have little understanding of their behavioral response to additional variability delivered by atmospheric events and changes in prey abundance and distribution.

Females also mitigate environmental variation by been efficient on provisioning and/or foraging (Boyd *et al.*, 1994; Lea *et al.*, 2002a; Mcdonald *et al.*, 2009). In the AFS, the effect of environmental variability in prey conditions and therefore foraging success, has been studied by observing the behavioral response to inter-annual variation associated to atmospheric events such as ENSO (e.g. Lea *et al.*, 2006). AFSs change aspects of their provisioning patterns such as trip duration (Costa *et al.*, 1989; Francis *et al.*, 1998) and modify diving patterns when they face complex years, forcing females to perform deeper dives and reduced their catch per unit effort of their prey (Lea *et al.*, 2006). Additionally, atmospheric anomalies can also directly affect the offspring. In some cases, females would reduce offspring production (Forcada *et al.*, 2005) or pups would not gain mass at the same rate than normal years during the breeding season (Lea *et al.*, 2006). Under extreme weather events, the dispersal and timing of weaning can be affected, risking the first-year survivorship (Lea *et al.*, 2009). Further, when conditions are not suitable, abandonment of offspring can be one of the consequences (Costa, 2008). Therefore, all these changes at the individual level (both on females and their offspring) can have an impact later at a population scale.

At its most southern breeding range, the Antarctic fur seal (AFS) operates at its highest field metabolic rate (Costa *et al.*, 2000), challenging its physiological limits for energy acquisition. Females forage in three general areas: over the continental shelf, along the shelf break, and, in some cases, in oceanic waters (Goebel *et al.*, 2000). In other locations where the species is found, foraging strategies respond to energy distance trade-off in normal years (Staniland *et al.*, 2007) whereas in areas where food acquisition is already limited by their physiological capacity, there is little room for modifications in behavior and the behavioral decisions are limited only to the prey characteristics within the foraging areas (i.e. prey vertical distribution, diel migratory

patterns, prey spatial distribution) but with little capacity to increase effort by diving harder, deeper or exploring new areas. Identifying how these edge colonies cope with additional environmental variability is challenging since simultaneous quantification of behavior and prey captured during the entire breeding season demands on-the-field quantification of diet at the same time as behavior is registered.

Current and more sophisticated instruments have successfully associated behavior with prey capture success (Viviant *et al.*, 2014; Volpov *et al.*, 2016; Kleanthous *et al.*, 2019) but, as discussed in Chapter 2, the autonomy and memory use of these instruments still complicate long-term monitoring of foraging activities. Also, animals do not just consume one prey species per foraging trip and therefore, single time estimations or capture attempts evaluation do not represent long-term strategies such as compensation between preys that could help animals to cope with variability. The algorithm provided in Chapter 2 allows us to test differences in behavior that are directly linked with the prey consumed by quantifying behavior when long-term monitoring instruments such as TDRs have been used. This does not require quantifying prey consumption for all dives register as it is already validated by the training dataset within the algorithm. With this, an accurate and dynamic estimation of the relationship in time between spatial, diving, and feeding behavior in long-term datasets is possible.

The following chapter has three main objectives:

1.-To identify the behavior within each breeding seasons that is used in response to the progressive differences in krill and fish availability.

2.-To understand differences in foraging behavior between contrasting years in colonies living already in highly heterogeneous environments and limited capacity to modify their foraging behavior.

2.-To fully describe foraging strategies used by AFS at the edge of their breeding distribution, including the relationship between each strategy and the prey targeted by applying and testing the algorithm designed in Chapter 2 in a long-term data set.

We hypothesize that animals respond to the conditions of the prey on each season (availability and abundance), showing no modifications in foraging effort. In complex years, females would only increase the number of times they use strategies that lead to a more energy-rich prey acquisition (fish consumption) but do not incorporate new strategies as they are limited by living at the edge of their breeding distribution.

MATERIALS AND METHODS

Were the years different?

To compare feeding strategies and behavior of animals in contrasting years we first evaluated if our underlying assumption of working in contrasting years was legitimate. To achieve this, we (1) measured on land atmospheric conditions, (2) measured morphometric conditions of females upon arrival to the beaches and followed pup's conditions throughout the breeding seasons, (3) characterized prey consumed by analyzing feces while on the field (here after scats), and (4) use any data available in the literature and/or databases to described prey availability in the area, characterizing prey density, krill length and other proxies within the time frame the study was conducted.

Atmospheric conditions

We sampled atmospheric conditions each year from the first week of November until the second week of March by using a land-based meteorological station provided by NOAA. We then calculated the mean values per week for several atmospheric variables and select those that may

influence more in the maintenance of thermoregulation and metabolism while onshore (and therefore could modify behavior to obtain more or better food) to later evaluate differences between seasons. Variables incorporated in this section were: Temperature (°C), wind speed (knots), wind direction (see below for details on the calculation) and precipitation (mm). After, we calculated weekly means and plotted them for visual inspection.

We calculated the mean weekly wind direction first by calculating the mean proportional time that wind direction presented East, West, North, or South within each week. Assuming that North is at a 90° angle in a cartesian plane, we then calculated the predominant direction (D) per week expressed in degrees from North using the equation:

D= $\tan^{-1}$ ((North-South)/(East-West)).

For statistical purposes, we pooled the week means of each variable arbitrarily in three groups: Early-season (hereafter, ES: first week of November to Mid-December), Mid-season (hereafter, MS: from the third week of December through the end of January), and Late-season (hereafter, LS: from the beginning of February to the second week of March). Then we compared each atmospheric variable between seasons per group (ES, MS, LS) by using a non-parametric Kruskal-Wallis analysis.

Female and pup conditions

Morphometric variables such as mass and length can give us an index of the initial "health" condition of an animal upon arrival (females) or birth (pups). As mentioned in the overall methodology of this thesis, we obtained morphometric data of all females and pups of the study. With this, we calculated Body Condition Indexes (BCI) of the studied animals by dividing body

mass (M) by the total length of each individual (L) (BCI = M/L) which has been validated as a reliable index of the condition for this species (Arnould, 1995). Using the initial and final mass of females and pups, we also calculated the mean daily mass loss (in grams) of each mother and its offspring dividing the difference between initial (M_i) and final mass (M_f) by the number of days between both measures. Caution must be taken in the interpretation of this data, especially for pups, since the daily rate of mass loss/gain may vary depending on how many days went between the sampling days and differences have been found associated to the sex of the pup ((Vargas *et al.*, 2009; Osman *et al.*, 2010). For this reason, the daily mass loss/gain in pups was not treated statistically. Instead, we obtained a population estimate by measuring 100 pups randomly (in an even number between females and males) every 15 days starting 30 days after the median pup parturition date. Median pup parturition date (MPPD) refers to the median date between the first and the last pup born at Cape Shirreff during one breeding season. Depending on the season, we were able to weight between 40-60 pups of each sex each sampling day. We treat sexes separately since differences in mass are closely related to sex (Vargas *et al.*, 2009; Osman *et al.*, 2010) and there are sex-based differences in energy delivered by mothers (Lunn *et al.*, 1993).

We then compared the mean values of all measurements between seasons (i.e. Initial Female BCI, Initial Pup BCI, Female daily weight loss, and pups mass taken every two weeks since the median pupping date), by using one-way Analysis of Variance (ANOVA).

Prey characteristics per season

Scats analysis

We characterized prey consumed during the study seasons and overall diet composition by analyzing scats. We collected opportunistically 10 fresh scats per week starting the third week of December when most of the females returned from their first trip. After, we collected scats for 10 consecutive weeks, reaching 100 scats per season. This is a higher sample size than what Trites and Joy, (2005) reported to be the minimum to identify principal prey remains and therefore, results obtained are representative of the diet of these colonies during this time. Scat collection and calculation of prey frequency of occurrence were done following Osman *et al.* (2004). Briefly, we collected the scats in areas used predominantly by lactating individuals (See Polito and Goebel, 2010 and Klemmedson *et al.*, 2020 for details) collecting all scats immediately in front of the researcher and one meter on either side to avoid bias associated to brightly-colored krill scats. After, we washed the scats under running water through a 3-tiered sieve (1mm, 0.5mm, and 0.25mm mesh size), small enough to retain otoliths of the principal fish taxa that compose AFS diet (myctophid fish), cephalopod mandibles (not identified taxonomically) and other prey hard parts. We count all otoliths per scat and identify the species at the lowest taxonomic level possible according to Hulley, (1981) and Hecht, (1971).

Krill size determination

For krill sex and reproductive stage determination, we followed Goebel *et al.* (2007). We selected and measured 20 non-broken carapaces haphazardly from each scat and recorded Length (RCL) and Width (RCW). Carapaces smaller than 12.5 mm RCL were classified as "Juveniles" and on those larger than 12.5 mm RCL we applied a discriminatory function (D= -10.68 + 0.43RCL + 0.29 RCW, Goebel *et al.*, 2007) to distinguish sexes (Female or Male) of adult carapaces individuals. Individuals showing a negative discriminant function score were classified as males and those showing a positive discriminatory function score, females (Reid and Measures, 1998). Then, to determine total krill length (TKL), we used the following formulas depending on the reproductive stage and sex of each sample: $TKL_{Juveniles}$= 10.43+2.26RCL, TKL_{Males}= 0.62+3.13RCL, and $TKL_{Females}$= 11.6+2.13RCL (Goebel *et al.*, 2007).

After defining sex and stage on each carapace, proportions of each group (juveniles, males, and females) were calculated by counting the numbers of each group multiplied by 100, then divided by the total amount of carapaces per week (~200 carapaces/week) and express them in percentage per season.

We calculated the frequency of occurrence (expressed as the percentual frequency of occurrence %F of krill, fish, or squid) based on the scat's proportions containing each prey taxon and divided by the total scats collected. We adjusted a binomial generalized linear model to evaluate differences between years in the occurrence of krill, fish, and squid using the "lme4" and "Carr" packages for R Studio (Team R Core, 2017; Bates *et al.*, 2018). We also separated each breeding season in two phases and compared if prey occurrence was different within each breeding

season. Finally, when differences were found between phases or seasons, we conducted Tukey post hoc tests to identify which seasons or phases differ from each other.

Prey availability. Published data

To the best of our knowledge, no summer cruise studying krill were performed in the vicinities of Cape Shirreff during our study seasons. To accomplish an understanding of krill availability and abundance, we conduct two approaches.

We revised krill fishery reports (CCAMLR, 2020) to see if there were differences in biomass extracted between our years. We obtained the total annual krill catch (tons) captured in the small-scale management unit "APDPW" from sub-area 48.1, which represents the direct surrounding waters of Cape Shirreff (see Figures 1 and 3 of Appendix A). The data gathered represent the total catch of each year right before the animals were instrumented (for instance, for our breeding season 2014/15, we obtained total annual catch of 2014, which included total krill catch between the beginning of January and the end of November of 2014). In addition, we obtained from the Antarctic bulletin archives (data download from www.ccamlr.org) specific catch data from the area 48.1 occurring during January and February of our three breeding seasons that was declared by all countries performing krill fisheries in this area. We only included the data of those countries that declared their catch within these two months in all three seasons (2014, 2015, and 2016) and in which the gear employed by their vessels to catch krill was consistent throughout the seasons (otter trawls-mid water). We sum up all catches per country occurring within this timeframe and divide it by the number of days work by each of the countries within those two months to estimate tons per day worked.

Because fisheries behave like a predator, and the "sampling" is biased only toward areas where krill is available, we also included a non-bias proxy to calculate krill density and length. The long-term Palmer Station Antarctica LTER program (PSA-LTER, an interdisciplinary polar marine research program created by the National Science Foundation), perform annual krill surveys within a grid area approximately 250 kilometers south from Cape Shirreff southward, covering most of the WAP (for more details on the grid, see Waters and Smith 1992). Some of the sampled points represent the downstream pathway flow existent along the WAP shelf break (Piñones *et al*., 2013). Therefore, krill obtained from those points very likely represent krill conditions in the surrounding waters of Cape Shirreff. We obtained krill total length (PSA-LTER & Steinberg 2020a), krill density, and fish density (PSA-LTER & Steinberg 2020b) from all sample points between 64° latitude (the closest latitude sampled from Cape Shirreff) and 66.6° latitude (last points before Marguerite Bay, a region where local krill recruitment has been proposed: Daly 2004, Pakhomov *et al*., 2004 and other oceanographic processes define krill conditions, Piñones *et al*., 2013). The sampling was performed during the mid-summer surveys (the entire month of January) and we extract the data of our three seasons (surveys dates: 2014: 1-Jan to 2-Feb, 2015: 10-Jan to 11 of Feb and 2016: 1-Jan to 31-Jan). With this data, we evaluate krill availability by calculating the krill stage (juveniles or adults), sex of the adults, and the krill density observed during our three study seasons.

In situ krill stage and sex estimation

The program collected krill using a 2m, 700-um net towed from the surface to 120 meters. They measured standard length (distance between the tip of the rostrum and blunt end of uropod) in a random subsample of up to 100 krill per tow or all krill present in tows with less than 100 individuals. The presence of the red thelycum identified mature females. Siegel and Loeb (1994)

established that males reach maturity between 43.35-43.71 mm, therefore, in the remaining non-classified individuals, we categorized all krill smaller than the middle point between this two values, 43.53 mm as juveniles and those larger than this number as Males. Finally, we calculated each stage and sex percentage out of the total number of krill measured.

In situ krill and fish density

We used the density data (number of individuals/ 1000m^3) registered by the program from all tows occurring within the mid-summer surveys of our seasons. After, we compared both fish and krill density between years by using a non-parametric Kruskal Wallis test. When differences were found, we performed a Dunn post-hoc test to identify which season(s) was driving the differences observed. Although described by the program, cephalopods represented less than 0.5% of the data collected and therefore not included in this section.

Foraging behavior

We evaluated the four components of marine mammals foraging behavior defined by Austin *et al.* (2006): Vertical behavior (diving), habitat utilization, horizontal behavior (spatial behavior), and prey captured in all three years. By analyzing scats, we partially cover the prey species composition and the differences in availability within and between seasons (feeding behavior section). At the studied area, krill was the most consumed prey item during the entire breeding season but two phases are clearly observed: a first half of the season in which diet is mostly composed by krill (hereby called K phase) and a second half in which the presence of fish is higher in the AFS diet than the first phase (hereby called F phase) these two phases have also

been observed in previous studies at this (Goebel and Polito, 2010; Osman *et al.*, 2004; Santora, 2013 and other locations (Iverson *et al*., 1997a, Lea *et al.,* 2002a; Tarroux *et al*., 2016). We divided the breeding season in these two phases based on the occurrence of fish and krill found in the scats and account for behavioral differences associated to each phase. The section "Diving behavior" described the vertical component by also exploring the dives associated to each prey targeted implementing the algorithm developed in chapter 2. The "spatial behavior" section described the horizontal component as well as the habitat utilization. Behavior has been proved to be very different on the first trips to sea. Thus, initial trips performed within the first 24 hours after instruments were installed were not included in any of these analyses. Finally, we determined foraging strategies used by animals using feeding, diving, and spatial behavior of all three years and then evaluate the use of these strategies within and between seasons.

Feeding behavior

Fatty acids

The section "Materials and Methods" of Chapter 2 showed the methodology for fatty acid extraction, processing, description, and quantification of each prey proportion consumed and associated to each sample obtained in all three seasons. To assess variations in fatty acid proportions between seasons we pooled all samples obtained per season without including the P samples and performed a PERMANOVA using the R package "vegan" (Oksanen *et al.*, 2007). To determine which seasons differed among each other in the fatty acid composition of samples, we conducted pairwise comparisons between seasons with the R Package "pairwiseAdonis" (Martinez Arbizu, 2019). To identify the individual fatty acids driving the segregation between

seasons (if any), we applied a similarity percentages routine (SIMPER) using the vegan package. For a visual assessment of these differences in a multivariate space, we used nonmetric multidimensional scaling (MDS) analysis.

The final capture of females and therefore, the time of collection of milk for fatty acid analysis, depends on 1.- the status of the instruments (we captured back females when the conditions of the instrument and the risk of losing them was too high) and 2.- the survivorship of the pup (females may leave the breeding colony risking losing the instrument). Therefore, most of the samples were obtained closer or within the F phase. This must be considered since the results indicate that fish otoliths are mostly concentrated in the F phase and therefore, fatty acid samples do not represent the entire breeding season but only the specific timeframe in which they were collected. Furthermore, we only obtained a limited fatty acid sample size per season (2014: 15, 2015: 16 and 2016: 11 samples). Therefore, we did not compare proportions of diet between years but instead, we indirectly measured diet from behavior within the "foraging strategies" section using our algorithm that validates diving behavior with our fatty acid data in Chapter 2.

Diving behavior

Diurnal/Nocturnal diving activity

We calculated whether dives occurred during the day or night as described in the general methodology section and visually compared the proportions of day/night dive frequencies between seasons. TDRs provided the time intervals that animals would spend diving (dive duration) and the time they spend at the surface (Post Dive Time Intervals PDI). With this information we calculated the total amount of time diving and the total time spent at the surface

per trip per female and calculated differences of these variables between years. Furthermore, we plotted the relationship between the maximum dive depth and the frequency of dives per season as this is related to prey targeted and effort of the females. Finally, we calculated dive frequency per hour as described in the general methodology section for all trips and females per season and evaluated differences explained by season using the trip means of all females by fitting a Linear Mixed Model (LMM) with season and day/night as fixed factors and each female identity as a random factor.

Time invested per prey

To quantify the relationship between diving behavior and prey targeted we applied the machine learning algorithm obtained from the random forest analysis in Chapter 2 to the entire data set in all trips and females of the study. Using the TDR diving data of the whole data set, the algorithm evaluated and categorized all dives and labeled them as a krill or fish dive. After, we calculated the proportion of dives (frequency) performed when targeting krill or fish per trip and calculated also the proportion of time invested diving when targeting each prey as these two were identified as good behavioral predictors associated with each prey in Chapter 2.

With the proportional time of behavior separated per prey, we only use the proportional values of fish since krill proportions account for the complementary proportional value and therefore, statistical results would be equal to what is obtain from the fish proportion. We ran LMM as suggested by Zuur *et al.* (2009) to see if there were differences in proportion explained by seasons. Season (2014, 2015, or 2016) and prey type (krill or fish) nested within each season were proposed as a fixed factor in the model with female identity as the random effects. When the data did not meet assumptions, it was transformed (log or square root) before running the

model. Results were back-transformed to proportions and summarized per year presenting the mean ± SD for each season. Homoscedasticity and normality were tested by visual inspection of residuals plots using q-q plots and histograms for LMM (Zuur *et al.*, 2007).

Spatial behavior

We evaluated spatial behavior by exploring five variables in all completed L trips: trip duration (days), Haul-out time (days), maximum distance from Colonies (maxdist: km), mean transit rate (km h^{-1}: kilometers per hour traveled), and niche utilization (utility distribution calculations). Trip duration and haul-out time were calculated as described in the general methodology section of this thesis. Maxdist and mean transit rates were compared between seasons for females carrying a GPS sensor (see next section).

Tracking data processing

Only a subset of females was carrying TDRs with GPS sensors registering tracking data (2014: 7 females, 2015: 8 females and 2016: 5 females). We filtered tracking data using a particle filter (Tremblay *et al.*, 2009). We then calculated per trip: the mean transit rate (km h^{-1}: kilometers per hour traveled), the maximum distance to colonies (Km: the straight-line distance from the farthest foraging location to the haul-out beach), and the mean total distance traveled (Km).

Utilization distribution

To evaluate the use of the foraging areas, we calculated utilization distribution probabilities (UDs, kernel analysis) based on the tracking data (See Costa *et al.*, 2010c and Hückstädt *et al.*, 2012a for details). Briefly, the total foraging area of each female contains 95% of the total

amount of geo-location data points. We projected the areas containing 95, 75, and 50% of locations and defined the area containing ≥ 50% of the geo-locations as the most utilized area where most likely foraging activities occur. Areas were projected using ArcGIS 10 pro (Esri *et al.*, 2011).

Foraging strategies

Mean transit rate did not differ between animals despite the season in which trips were performed. Therefore, we did not use this variable for the identification of foraging strategies. We used seven variables (trip duration, haul-out time, mean dive rate, mean maximum distance to colonies, percentage of time diving, percentage of time invested diving to capture fish (TID-Fish), and the percentual number of dives performed per trip to capture fish (DF-Fish). We could not calculate "mean distance from colonies" for all females and trips of the study since not all females carry GPS sensors. However, in females with tracking data, we found that trip duration was associated with maxdist, just as it been observed in early studies on the species, where trip duration showed to be a good predictor of the maximum distance from colonies reached (Boyd, 1999). Therefore, a regression between maxdist and trip duration was performed using data from females with tracking information. The resulting equation showed an adjusted R^2 value 0.77 (results of the regression analysis are shown under the section "Chapter 3" of Appendix B including figure 3 of the same Appendix). The linear equation used to calculate maxdist from trip duration on the females with no tracking data was:

Maxdist = -21.771 + 71.07*tripduration

After pooling all seven variables, we checked for cross-correlation among variables (Pearson correlation) and performed a principal component analysis (PCA) using the R package Factominer (Husson *et al.*, 2009): we retained principal components that explained 90% or more of the variation, as determined from a scree plot of the percentage of variance explained by each eigenvalue (contribution). Five Principal Components (PCs) account for 91.6% of the variance. We loaded all scores of each trip of all five PCs into an Agglomerative Hierarchical Cluster Analysis (HCA) using a Ward Linkage method and Euclidean distance (cluster package HCA package: Maechler *et al.*, 2013; factoextra package: Kassambara and Mundt, 2017) as used with fatty acids in Chapter 2. We obtained the optimal number of clusters by using both the Elbo and Silluette method provided by the R packages described. All statistical tests were performed in R (Team Rcore, 2017)

Clusters obtained from the HCA were considered for each strategy used by the animals and therefore, to describe and identify the differences between strategies, we performed LMMs for all variables that contributed more to the variance explained by the PCs obtained in the PCA. The LMMs considered "cluster" and "Season" as a fixed factor and each female as a random factor. Assumptions and data transformations were met the same way they have been described in previous sections. LMMs were fitted via restricted maximum-likelihood estimation (REML).

RESULTS

Were the years different?

Meteorological data

Table 11 and Table 12 show all means ± standard deviations, the Kruskal-Wallis comparison results and the p values of the meteorological variables obtained on land. We compared Early, Middle, and Late seasons (ES, MS, and LS respectively) for all three seasons studied. Early in the season, mean temperature (Figure 16, chi-squared =6.7371, df=2, p-value=0.041) and mean wind speed (Figure 17, chi-squared= 9.556, df=2, p-value=0.008) are significantly different between 2014 and 2015 compared to 2016, showing particularly very low mean temperature and higher wind speeds in 2014 at the beginning of the breeding season. The low temperature was sustained during MS in 2014 (Figure 16, chi-squared=8.230, df=2, p-value=0.016). In addition, maximum temperatures are higher in 2016 than the other two years during the entire breeding season (Figure 16, ES: chi-squared =8.230, df=2, p-value=0.016, MS: chi-squared=7.833, df=2, p-value=0.02 and LS: chi-squared=8.703, df=2, p-value=0.013). Mean minimum temperatures during MS are also significantly lower in 2014 and 2015 compared to 2016 (Figure 16, chi-squared=9.556, df=2, p-value=0.008). No significant differences are

observed in precipitation for any of the phases (Table 12, Figure 18). Together, these differences show that meteorologically, the breeding seasons of 2014 and 2015 are significantly different from 2016 with lower temperatures, mostly concentrated in the first and second quarter of the seasons especially in 2014 (Figure 16), likely driven by the period when females are giving birth and performed their first trip to sea (ES).

Table 11. Summary table of all meteorological variables measured for all 3 phases of the breeding seasons. Data presented correspond to mean ± Standard deviation. ES= Early Season, MS= Mid-Season, and LS=Late Season.

Season	Stage	Mean T (C°)	Max T (C°)	Min T (C°)	Mean wind speed (knots)	Precipitation (mm)
2014	ES	-1.25 ± 0.74	1.62 ± 0.79	-3.76 ± 1.3	15.35 ± 2.72	3.09 ± 2.88
	MS	0.8 ± 0.5	3.85 ± 0.37	-1.28 ± 1.02	10.18 ± 2.89	5.58 ± 5.22
	LS	1.7 ± 0.75	4.67 ± 0.97	-0.55 ± 1.13	11.43 ± 1.70	13.63 ± 15.23
2015	ES	-0.68 ± 1.16	3.38 ±1 .99	-3.22 ± 1.97	14.1 ± 2.05	3.47 ± 5.74
	MS	0.67 ± 0.39	5.35 ± 1.52	-1.78 ± 0.84	10.08 ± 1.5	3.68 ± 1.13
	LS	1.2 ± 0.39	4.4 ± 1.01	-1.1 ± 0.80	12.2 ± 2.28	9.69 ± 6.53
2016	ES	0.1 ± 0.65	4.18 ± 1.49	-1.87 ± 1.1	9.55 ± 2.4	6.05 ± 7.57
	MS	1.57 ± 0.27	6.23 ± 0.62	-0.58 ± 0.29	9.4 ± 0.56	6.13 ± 4.12
	LS	2.2 ± 1.22	5.85 ± 0.40	-0.65 ± 1.6	10.01 ± 1.09	11.56 ± 9.99

Table 12. Kruskal-Wallis results of all three breeding seasons (2014, 2015, and 2016) of each of the phases evaluated. ES= Early Season, MS= Mid-Season, and LS=Late Season. Significant differences (P-values less than 0.05) are presented in bold with an asterisk*.

Variable	Stage	Chi-squared	DF	p values
Mean T (C°)	ES	6.371	2	**0.041***
	MS	8.230	2	**0.016***
	LS	5.275	2	0.072
Max T (C°)	ES	8.265	2	**0.016***
	MS	7.833	2	**0.02***
	LS	8.703	2	**0.013***
Min T (C°)	ES	4.697	2	0.096
	MS	6.622	2	**0.036***
	LS	1.495	2	0.474
Mean wind speed (knots)	ES	9.556	2	**0.008***
	MS	0.009	2	0.996
	LS	4.592	2	0.101
Precipitation (mm)	ES	0.591	2	0.744
	MS	0.832	2	0.66
	LS	0.144	2	0.931
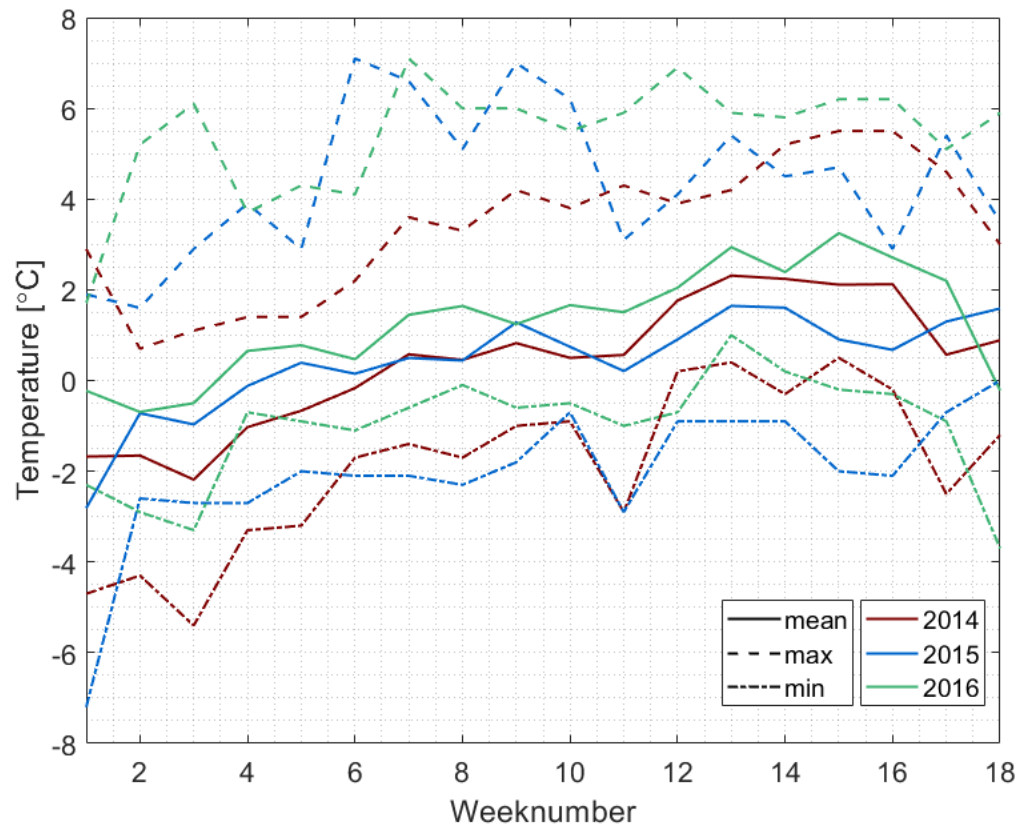
Figure 16. Weekly mean temperature, mean maximum temperature, and Mean minimum temperature of all seasons studied. Weekly mean temperature (continuous lines), Mean maximum temperature (long dashed lines), and mean minimum temperature (short dashed lines) expressed in degrees Celsius (°C) for 2014 (red), 2015 (blue) and 2016 (green) during the entire breeding season.
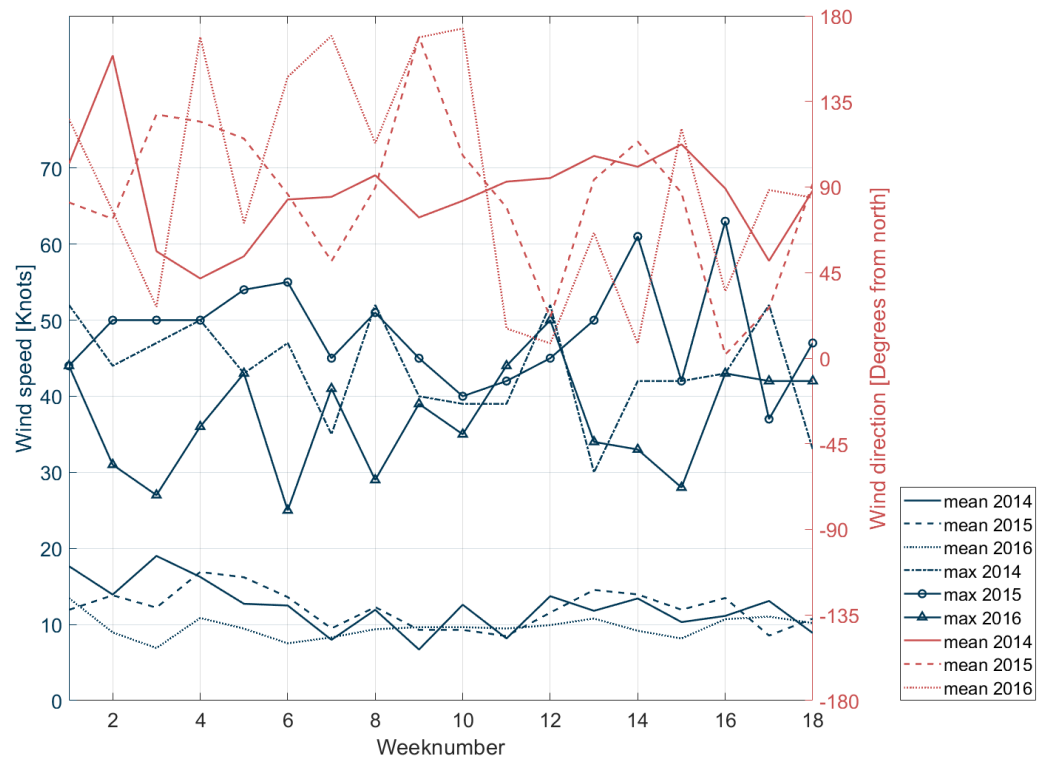
Figure 17. Weekly mean wind characteristics during all three breeding seasons. Mean wind speed (in knots, 2014: continuous blue line, 2015: long dashed blue line and 2016: light blue line), mean maximum wind speed (in knots, blue axis, 2014: short dashed line, 2015: continuous line with circle and 2016: continuous line with triangles) and mean wind direction calculated in degrees from North (red Y-axis and red lines: 2014: continuous lines, 2015: long dashed line and 2016: short dash lines).
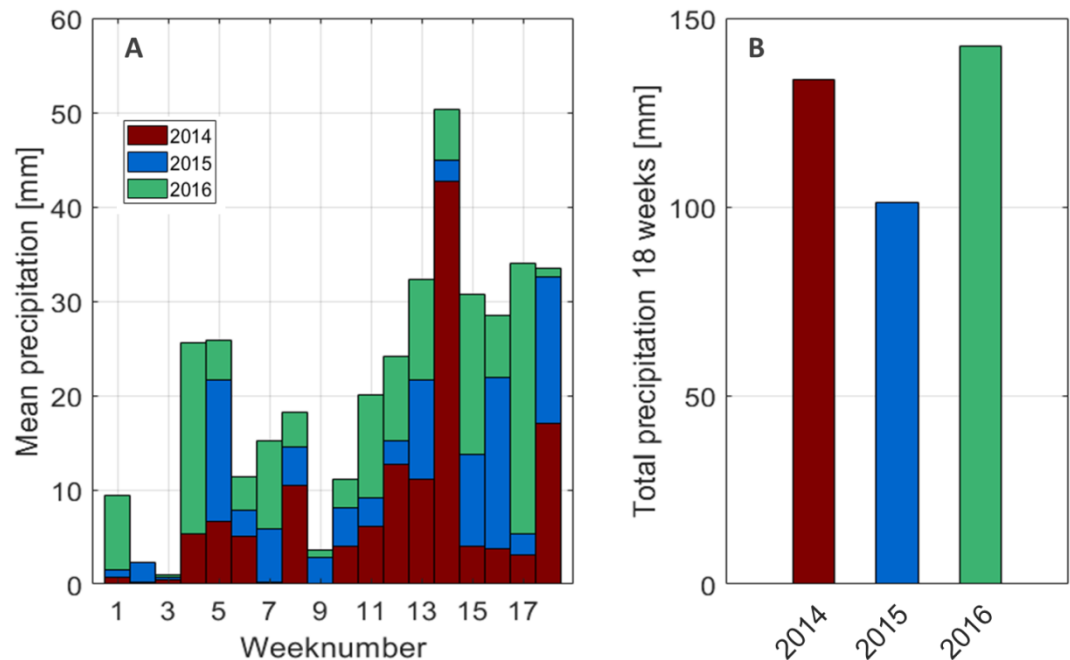
Figure 18. Precipitation during all three breeding seasons. A) Weekly mean Precipitation (mm) and B) Total precipitation of the breeding season per year (2014: Red, 2015: Blue and 2016: Green).

Female initial conditions

We captured and instrumented a total of 15 females in 2014, 14 in 2015, and 12 in 2016. Table 13 showed the means ± standard deviation of all general morphometrics obtained from all the females captured per season. After performing a Kruskal Wallis test we found no significant differences in the initial BCI of the females after giving birth (chi-squared=3.629, df=2, p-value=0.163), suggesting that all females were relatively similar in size and initial conditions prior to each breeding season (Figure 19). We found a significant difference in mean daily mass loss of females between seasons (Kruskal-Wallis: chi-squared=10.234, df = 2, p-value = 0.005994), where 2015 females show less mass loss than 2014 (Post-hoc Wilcoxon rank-sum test: p-value= 0.0064) and a statistical tendency (p values less than 0.1 but no lower than 0.05)

of females to lose less mass on average in 2015 than in 2016 (Post-hoc Wilcoxon rank-sum test: p-value= 0.0929). No differences are observed between females from 2014 and 2016 in mean daily mass loss (Post-hoc Wilcoxon rank-sum test: p-value= 0.2147). Mass loss results however need to be treated with caution since we were not able to perform measurements in all females at the end of the breeding seasons (2014: 13 individuals, 2015:11 and 2016: 10) and the low sample size might have caused the significance of these differences (see figure 4 under the section "Chapter 3" of Appendix B).

Altogether, these results suggest that females were in similar conditions upon arrival, but the mass loss was lower in animals from 2015 than from 2014 with also a statistical tendency to be lower on females in 2015 than from 2016. Detailed morphometric values per female can be found in table 1 of the "Chapter 3" section of Appendix B.

Table 13. Mean ± standard deviation female adults morphometric measures. Weight, Length, and Body Condition index (BCI=Mass/Length) for all three seasons (2014, 2015 and 2016).

Season	Initial Weight (Kg)	Total Length (Cm)	Body Condition Index (BCI)
2014	54.55 ± 3.99	132.08 ± 4.44	0.41 ± 0.02
2015	50.87 ± 6.24	129.14 ± 5.40	0.39 ± 0.04
2016	51.65 ± 4.57	131.5 ± 4.50	0.39 ± 0.03
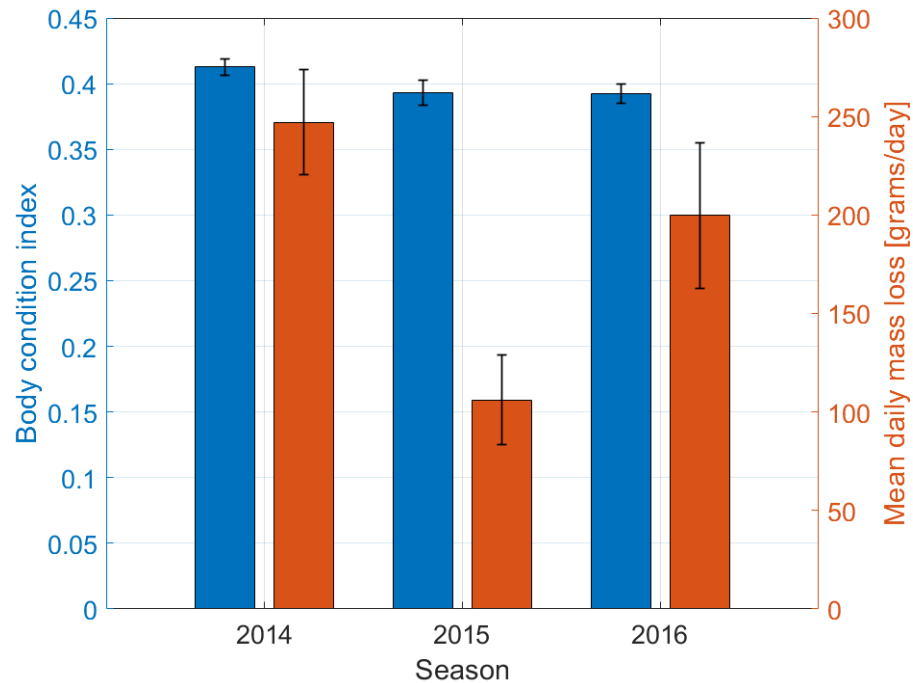
Figure 19. Mean body condition Index (blue) and mean mass weight loss (orange) of all females studied in all three seasons. Body condition index (blue), mean mass weight loss (orange). Mean ± Standard error are presented.

Pup conditions

As mentioned in the methods section, we did not treat mass loss estimates for the studied pups statistically, since conclusions could be misleading, however, information on the initial conditions of the newborn pups is available in both table 2 and figure 5 of the section "chapter 3" of Appendix B. We present the data from the 100 pups weighted every 15 days starting 30 days after the median pup parturition date (MPPD), in Table 14 and Figure 20 for all male and female pups.

Table 14. Pup Mass (Kg) grouped by sex calculated for all three breeding seasons. Values are expressed as mean ± standard deviation. MPPD=Median pup parturition date.

Season	Days after MPPD	Male Mass (Kg)	Female Mass (kg)
2014	30	9.2 ± 1.5	8.1 ± 1.3
	45	10.88 ± 1.8	9.68 ± 1.4
	60	12.6 ± 2.26	11.4 ± 1.35
	75	15 ± 1.93	12.8 ± 1.4
2015	30	10.1 ± 1.5	8.8 ± 1.0
	45	11.9 ± 1.7	10.8 ± 1.5
	60	13.3 ± 1.7	11.4 ± 1.2
	75	15.1 ± 2.4	13.1 ± 1.5
2016	30	9.98 ± 1.57	8.8 ± 1.24
	45	11.43 ± 1.88	10.03 ± 1.39
	60	13.17 ± 1.97	11.67 ± 1.50
	75	15.14 ± 2.03	13.01 ± 1.48
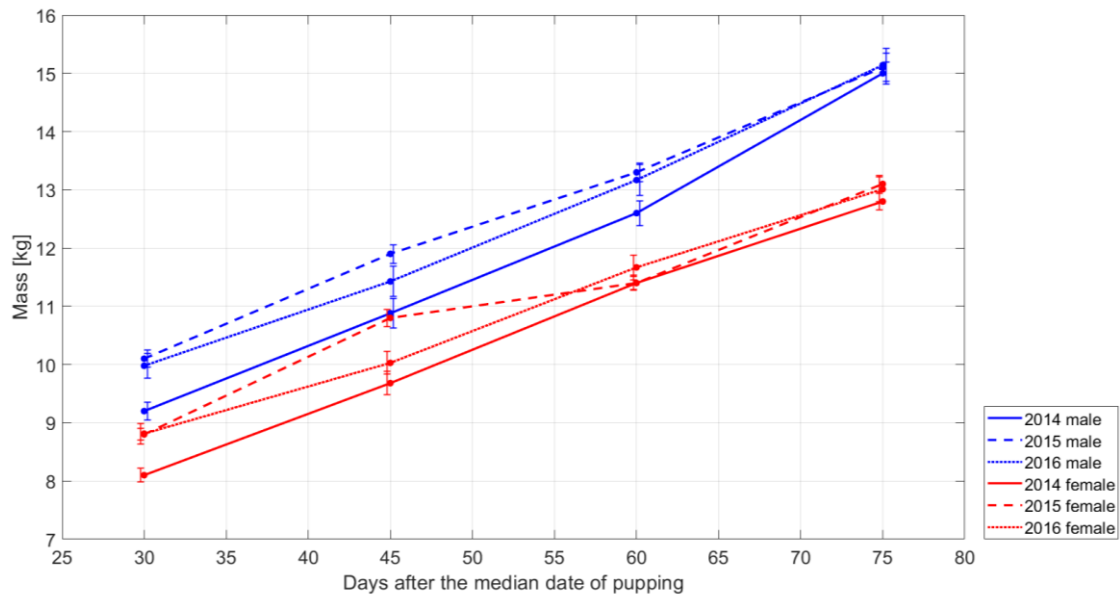
Figure 20. Pup Mass (Kg) grouped by sex obtained during each breeding season. Females pups: red, male pups: blue. 2014: continuous line, 2015: long dashed lines, 2016: short dash lines. Measurements started 30 days after the median date of parturition and every 15 days after. Bar lines represent the standard error.

Overall, we found significant differences between years for both female and male pups during the first half of the breeding season (i.e. 30 and 45 days after MPPD, Table 15) and no differences during the second half (i.e. 60 and 75 days after median pup parturition date, Table 15 and Figure 20). Specifically, there are no significant differences in mass between pups from 2015 and 2016 in any of the days sampled except in female pups after 45 days of MPPD, with females almost one kilogram heavier in 2016 than 2015 (pairwise Tukey comparison 45 days MPPD, Females: 2015-2016: p value=0.0209) but not males (p-value 0.4). Therefore, differences in mass observed in the first half of the breeding period are driven mostly by values from 2014. In 2014, both female and male pups presented significantly less mass (~1 kg less, Table 15) at 30 days after MPPD compared to 2015 and 2016 (Pairwise Tukey comparison, Females: 2014-2015: p value= 0.0086, 2014-2016 p value=0.007; Males: 2014-2015: p value= 0.0103, 2014-2016 p value=0.0227). 45 days after MPPD, these differences remain to be significant between 2014 and 2015 (pairwise Tukey comparison, Females: 2014-2015: p value= 0.0003; Males: 2014-2015: p value= 0.0124) but no longer between 2014 and 2016 (pairwise Tukey comparison, 2014-15: females: p value=0.446; Males: p value=0.2675). After 45 days, there are no significant differences in pup mass at 60 nor 75 days after MPPD between seasons (Table 15). All p values of the post hoc Tukey comparison are provided in detail in Table 3 of appendix B.

Table 15. Analysis of variance (ANOVA) results between breeding seasons (2014, 2015, and 2016) at 30, 45, 60, and 75 days after the median pup parturition date (MPPD) for female and male pups. Significant p values were obtained using a confidence level of 0.95 and highlight in bold and with an asterisk (*). M=Male, F=Female.

Days after MPPD	Sex	Multiple R^2	df	F-ratio	P-value
30	F	0.27	2	6.109	**0.003***
	M	0.254	2	4.954	**0.008***
45	F	0.312	2	7.72	**0.001***
	M	0.224	2	4.047	**0.019***
60	F	0.099	2	0.778	0.461
	M	0.155	2	1.922	0.15
75	F	0.089	2	0.703	0.496
	M	0.032	2	0.067	0.936

Prey characteristics

Krill sex-age determination

We found important differences in the krill sex ratio between years (Figure 21). 2014 shows 41.4% of juveniles against 15.4% in 2015 and 7.9% in 2016. Adult krill ratio (both females and males) also differs between years. Females represent 6.5% of the total krill ratio in 2014 against 25.7% in 2015 and 13% in 2016. Male ratio is considerable higher in 2016 (79.1%) than in 2014 (52.1%) and 2015 (58.9%). Although there is some overlap at certain size classes between females and males when age determination is linked with sex, a robust conclusion can be drawn when considering only the size of krill: large (females and males) or small krill (Juveniles). We found larger krill in 2016 and 2015 than in 2014, the former, a year dominated by juvenile krill

in the diet (adult krill= 92.1% in 2016, 84.6% in 2015 against 58.6% in 2014, Figure 21).

Implications are discussed ahead in the chapter.

Figure 21. Diet analysis. Krill sex ratio for all three breeding seasons. Dark yellow= Juvenile krill, Blue= Male krill, and grey= Females. Data is presented in percentages.

Table 16 and Figure 22 show the prey frequency of occurrence (%F) expressed in proportion out of 100 scats collected per year. Krill is the dominant prey been present in more than 90% of the scats in all years and no significant differences are found between seasons (p values= 0.7). Fish otoliths, however, are present in 15% more scats in 2014 than 2016 (post hoc Tukey comparison: 2014-2016: p value=0.0121 and Figure 22). Within breeding seasons, all years present a higher presence of otoliths (and therefore fish) in the F phase of the breeding season than the K phase (post hoc turkey comparison: 2014, 2015, and 2016: first half-second half: p value<0.004, Figure 23). We found no differences in squid consumption between years (p-value:

0.127) or between phases within seasons (pairwise turkey comparison **2014**: first half-second half: p value= 0.9939, **2015**: first half-second half: p value=0.9943, **2016**: first half-second half: p value=0.2.22, Figure 23). With such a small contribution of squid to AFS diet at Cape Shirreff, we did not incorporate this prey item in further analysis.

Table 16. Prey frequency of occurrence (proportion) for all seasons. Values are expressed as mean proportion ± Standard Deviation.

Prey Proportion	2014	2015	2016
Krill	0.93 ± 0.08	0.96 ± 0.08	0.97 ± 0.07
Fish	0.32 ± 0.31	0.3 ± 0.28	0.17 ± 0.18
Squid	0.08 ± 0.12	0.03 ± 0.05	0.05 ± 0.05
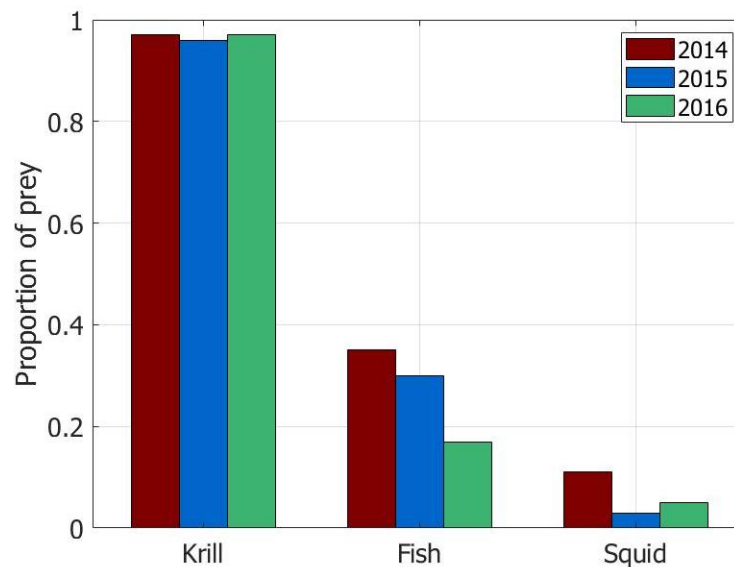
Figure 22. Prey proportion found in scats for all three seasons (2014: red, 2015: blue and 2016: green). 100 scats were collected per year and the presence/absence of krill, fish, or squid was assessed.
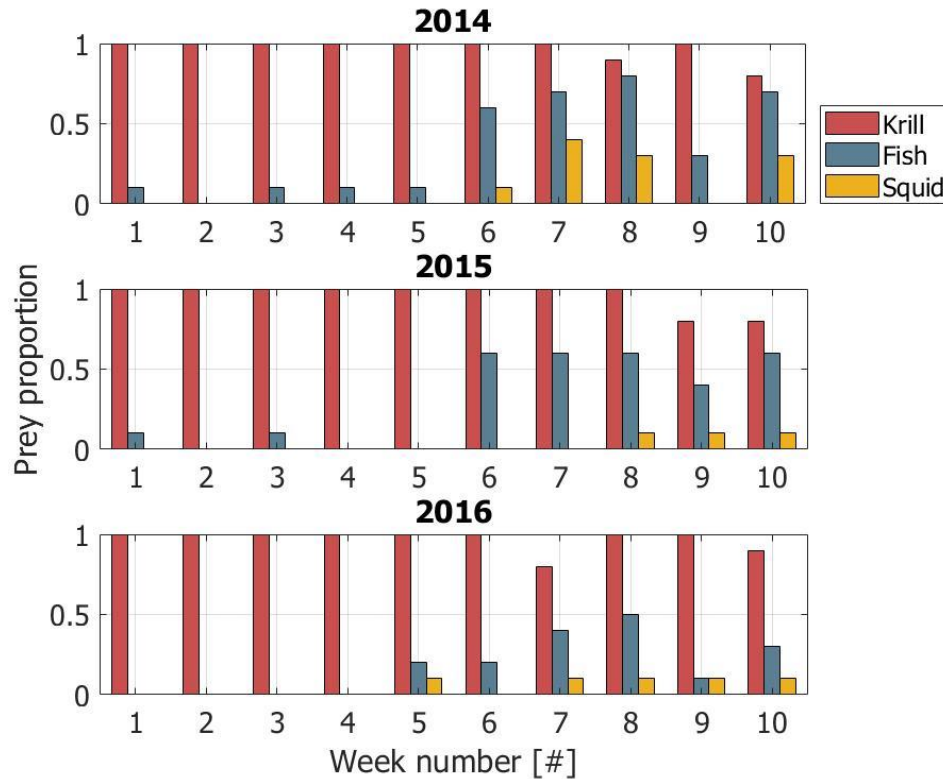
Figure 23. Scat prey proportion of occurrence for all three seasons of this study. Krill (red), fish (blue), and squid (yellow). Proportions were calculated based on the occurrence of each prey in 10 scats collected per week.

Fish taxonomic identification

Two myctophid species; *Electrona antarctica* (Günther, 1878) and *Gymnoscopelus nicholsi* (Gilbert, 1911) account for more than 98% of the otoliths identified in all three seasons (

Table 17). The number of otoliths found in 2014 and 2015 almost double the number of otoliths found in 2016. Within these two species, *G. nicholsi* is the dominant species found in 2014 (55%) and 2016 (67%) and *E. Antarctica* the dominant species in 2015 (66%). Further details on fish species, age distribution and fish population dynamics based on this data can be revised in Klemmedson *et al.* (2020).

Table 17. Species identified in the scat analysis and total amount of otoliths found per season in all 100 scats collected.

Species	2014	2015	2016
E.antarctica	116	193	32
G. braueri	3	0	0
G.nicholsi	146	96	66
E.carlsbergi	0	1	0
Squid Beaks	15	3	3

Prey availability. Published data

Krill fisheries

The annual catch declared from the surrounding waters of Cape Shirreff (small scale management unit APDPW, see figure 3 of Appendix A) during the year before each breeding season started, decreased continuously from 2014 to 2016 (**2014**: 19,780 tons, **2015**: 340 tons, **2016**: 0 tons, see Figure 24). In 2016, total catch reported was 0 tons meaning that attempts of fishing were conducted but no krill was found. This is consistent with the catch declared for the larger sub-area 48.1, that includes, among others, APDPW. Here, the same overall pattern is observed, and the mean tons captured per day decreased from 2014 to 2016 in January and February (**2014**: 114 tons/day, **2015**: 91 tons/day and **2016**: 83.5 tons/day, see Figure 24). For the sub-area 48.1, we only included the total catch declared by China (**2014**: 114.2 tons/day, **2015**: 109.3 tons/day and **2016**: 83.9 tons/day), Korea (**2014**: 116.7 tons/day, **2015**: 63.7 tons/day and **2016**: 101.3 tons/day) and Ukraine (**2014**: 111.4 tons/day, **2015**: 100 tons/day and **2016**: 65.5 tons/day). The other two fishing countries were not included since Chile did not declare any catch in January or February of breeding season 2016, and Norway changed the gear used between years and therefore, data is not comparable between years. Korea was the

only of the three countries that increased the tons catch from 2015 (63.7 tons) to 2016 (101.7 tons).
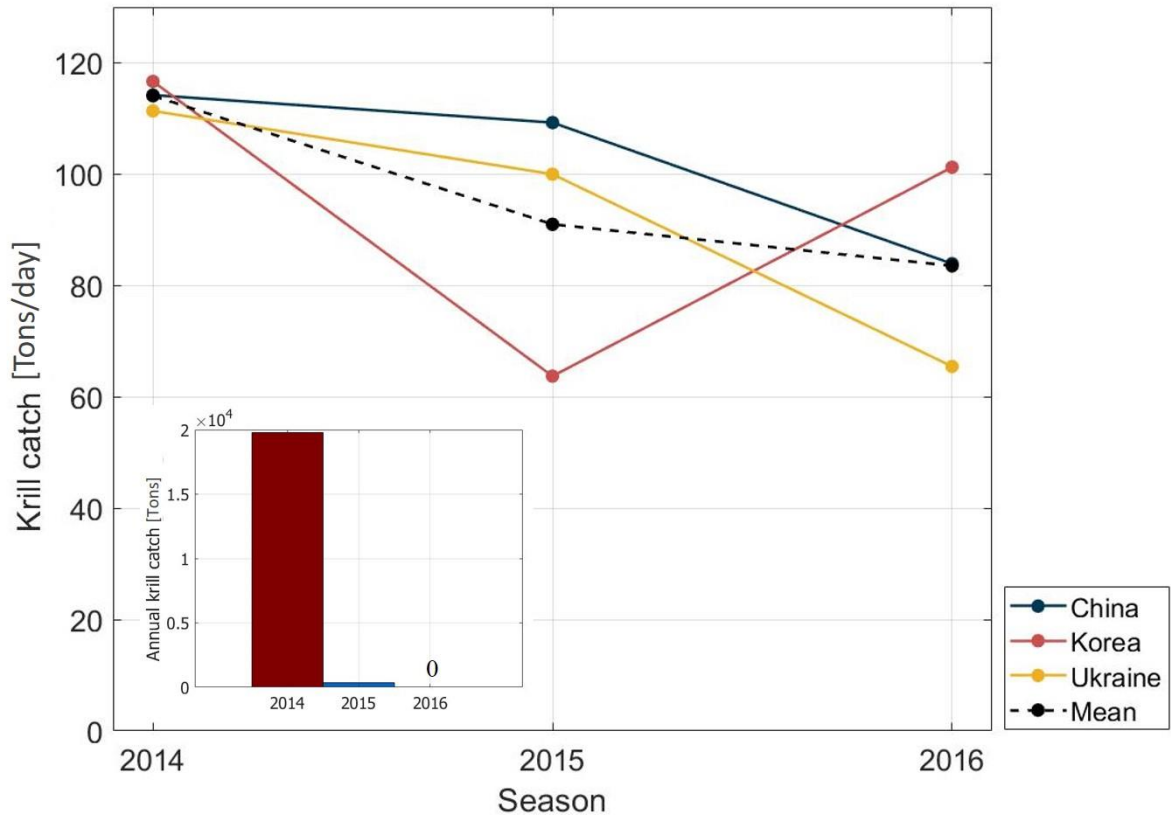
Figure 24. Fisheries krill catch occurring close to Cape Shirreff. The inner graph shows the total annual krill catch of each year previous to each breeding season within the small-scale management unit area APDPW. In 2016 total catch reported was 0 tons meaning that attempts of fishing were conducted but no krill was obtained. The outer graph shows catch per day within the total sub-area 48.1 specifically, between January and February of each of the three Antarctic fur seal breeding seasons included in this thesis. The catch of China (blue line), Korea (red line), and Ukraine (yellow) are presented for all three seasons. The black dash line shows the mean catch/day of these three countries together. For details on the location of APDPW and sub-area 48.1, see figures 1 and 3 of appendix A.

In situ krill stage and sex estimation

This section included 580 krill individuals of those measured in 2014, 1,921 in 2015, and 1,240 in 2016. Percentages of juveniles and males available in 2014 (Juveniles: 39%, Males: 42.1%, Figure 25) are very similar to those consumed by AFS in that season (Figure 21). By 2015, when krill was abundant (see the next section), a reduction in the consumption of smaller stages (juveniles) is observed (Figure 21) despite the high percentage available (Juveniles:56%, Figure 25). Instead, a larger quantity of adult krill is consumed that season (Figure 21). In 2016, juveniles available decreased considerably compared to the previous two seasons (Juveniles: 15.6%, Figure 25), which is consistent also with the high consumption of adult stages observed in 2016 (Figure 21).
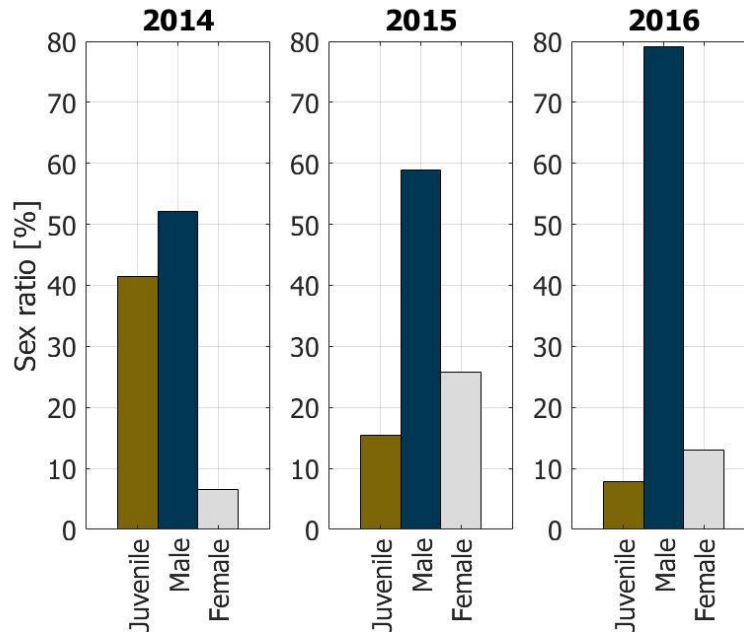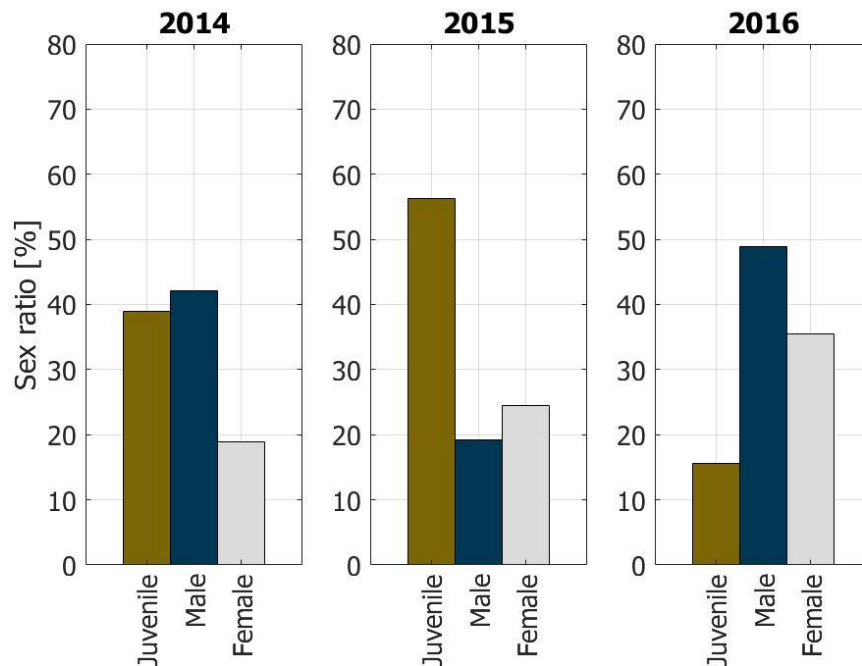

Figure 25. *In situ* krill availability. Krill sex ratio found in January of all three breeding seasons. Dark yellow= Juvenile krill, Blue= Male krill, and grey= Females. Data is presented in percentages. Data was obtained from PSA-LTER & Steinberg (2020a).

In situ krill and fish density

We used both krill and fish density from 16 sample points in the WAP cover by the program (see methods section). Krill density was significantly different between years (chi-squared: 10.99, p value= 0.004), and was driven by a higher density in 2015 (161.5±298 individuals/1000m^3) than in 2014 (23.3±45.8 individuals/1000m^3) or 2016 (22.8±20.8 individuals/1000m^3. Post hoc Dunn test: 2014-2015: p value= 0.0033, 2014-2016: p value= 0.27, 2016-2015: p value= 0.05, Figure 26). In the case of fish, no significant differences were found between seasons (chi-squared: 0.35, p value= 0.84), with average presence of fish (2014: 2.3±3.7, individuals/1000m^3, 2015: 4.4±11.1 individuals/1000m^3, 2016: 2.8±5.6 individuals/1000m^3, Figure 26), similar than the reported in previous years (see full data set from 2009-2019 in (PSA-LTER & Steinberg 2020b). Caution should be taken interpreting fish data as it does not just includes myctophids but all teleost fishes found.
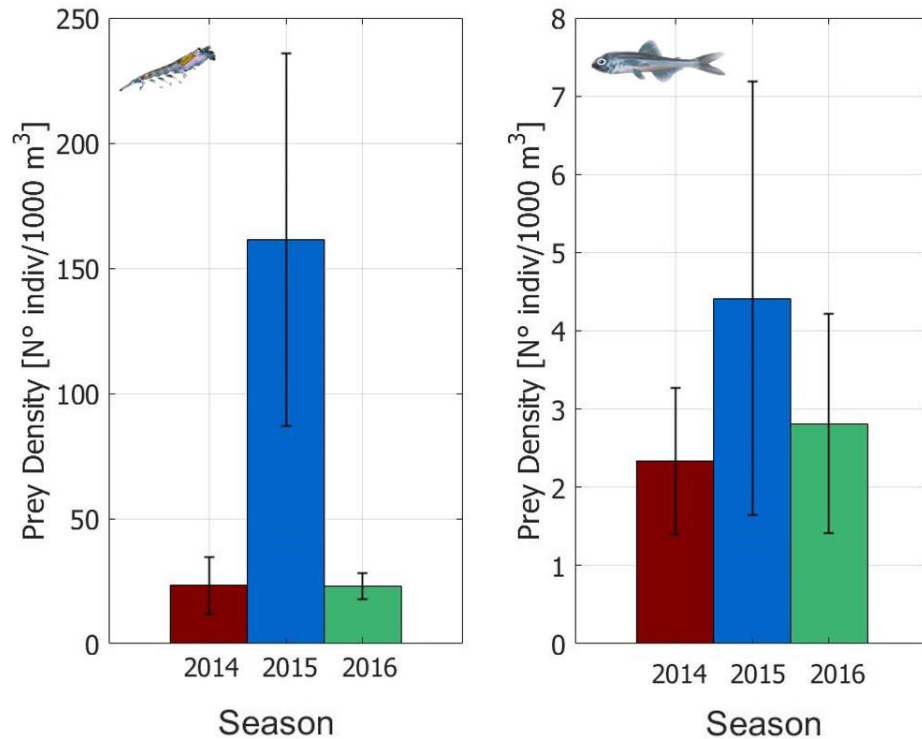
Figure 26. *In situ* krill and fish density south from Cape Shirreff. Left panel shows mean krill density (number of individuals/1000 m^3) and the right panel mean fish density (Number of individuals/1000 m^3) from 16 sample points between 64° latitude (the closest latitude sampled to Cape Shirreff) and 66.6° latitude during January of each breeding season. Data was obtained from PSA-LTER & Steinberg (2020b).

Together, the differences between seasons of prey consumed, and prey available can be described as follows: 2014 and 2015 are characterized by almost 50% presence of juvenile but only in 2014 females consumed a high number of juveniles (40%). This may be associated with the reduced krill density found in 2014 compared to 2015, which leaves no other alternative but to consume more juvenile krill in 2014. In 2016, despite the low density of krill observed compared to 2015, only adult krill is consumed and also more available than juveniles. The alternative in the two low krill density years (2014 and 2016) can also be fish consumption. Fish seems to be available similarly during all three seasons. However, because this prey is mobile,

local abundance could be substantially different from the one obtained south from Cape Shirreff, and caution should be taken when interpreting this data.

Feeding behavior

Fatty acid

Fatty acid composition differs among seasons (PERMANOVA, $F_2 = 4.35$, $P = 0.003$; Figure 27). Pairwise comparisons revealed that only seasons 2015 and 2016 are significantly different from each other (Pairwise PERMANOVA, adjusted $P = 0.03$) and 2014 samples did not show clear pattern that could distinguish more consumption of one (krill) or the other (fish) prey type. Therefore, differences were only further tested between these two seasons. The SIMPER analysis showed that the differences in FA composition only explained an average dissimilarity of 13% between these two seasons. Furthermore, the most influential fatty acids explaining the differences between 2015 and 2016 are **C18:1n-9**, **C20:5n-3**, **C20:1n-9**, **C14:0**, **C22:6n-3** with an overall contribution to the dissimilarity of 70% for the pairwise comparison. Milk FAs of females in 2016 are richer in C18:1n-9 and C20:1n-9 (Table 18) which have been previously associated with fish consumption (Chapter 2). Moreover, out of the most abundant FAs, those from females of 2015 are richer in C20:5n-3 and C14:0 than those of females in 2016 (Table 18). These fatty acids have been identified previously with krill consumption (Chapter 2). We did not count with enough FA samples representing both phases (F or K) of all seasons and most of the milk samples were collected during the F phase, showing a higher consumption of krill in 2015 than 2016 at this phase.

Table 18. Similarity percentages routine analysis between 2015 and 2016 of all fatty acids incorporated in this section. Significant p values were obtained using a confidence level of 0.95 and highlight in bold and with an asterisk (*).

Fatty Acid	Average	SD	Ratio	2015 (%)	2016 (%)	p-value
C18:1n-9	0.034	0.025	1.4	24.8	28.2	**0.008***
C20:1n-9	0.015	0.0089	1.7	4.1	5.5	**0.004***
C205n-3	0.014	0.0092	1.5	7.5	6.1	**0.006***
C14:0	0.013	0.0089	1.5	7.5	5.8	**0.001***
C22:6n-3	0.01	0.0074	1.4	7.1	7.5	0.39
C16:0	0.009	0.0061	1.5	17.8	16.7	0.052
C16:1n-7	0.008	0.0057	1.3	6.8	5.8	**0.006***
C18:1n-7	0.006	0.044	1.3	7.1	6.5	**0.001***
C22:5n-3	0.004	0.0031	1.2	1.9	2.1	0.65
C18:4n-3	0.0034	0.0023	1.5	1.1	0.7	**0.007***
C18:2n-6	0.0024	0.0014	1.6	1.9	1.6	**0.001***
C18:0	0.0023	0.0024	0.9	1.7	1.8	0.27
C22:1n11	0.0022	0.0014	1.5	0.5	0.7	0.82
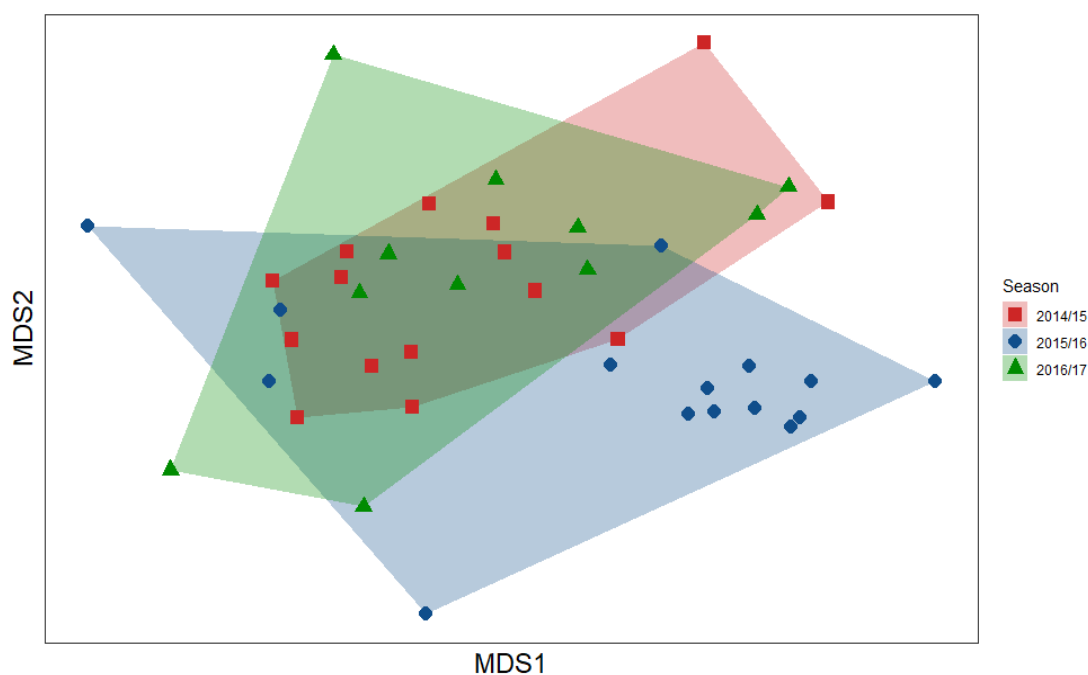
Figure 27. Nonmetric multidimensional scaling (MDS) plot for milk fatty acids of Antarctic fur seals. Samples were obtained during the breeding seasons of 2014 (red squares), 2015 (blue circles), and 2016 (green triangles).

Diving behavior

A total of 281 trips to sea for all three seasons is included in this section (89, 111, and 81 trips from 2014, 2015, and 2016 respectively). Excluding transit time, the mean percentage of time invested diving on each trip, never extents more than 50% of the total time at sea (24±6.7 %, 23.5±4.7 %, 32.4±14.5 % in 2014, 2015, and 2016 respectively). A tendency (p value less than 0.1 but larger than 0.05), suggest that differences in total time diving could be partially explained by the differences in season (X2= 4.7, p value= 0.09, Figure 28), but was only significant when phases were taken into account (Season(Phase)= X2= 6.4, p value= 0.04). These differences are observed at the K phase, in which females from 2016 (32.4±14%) spent ~10% more time diving than animals from both 2014 (23±6.8%) and 2015 (24±4.4%, Post hoc Tukey test: 2016-2014: p value= 0.013; 2016-2015: p value= 0.02).
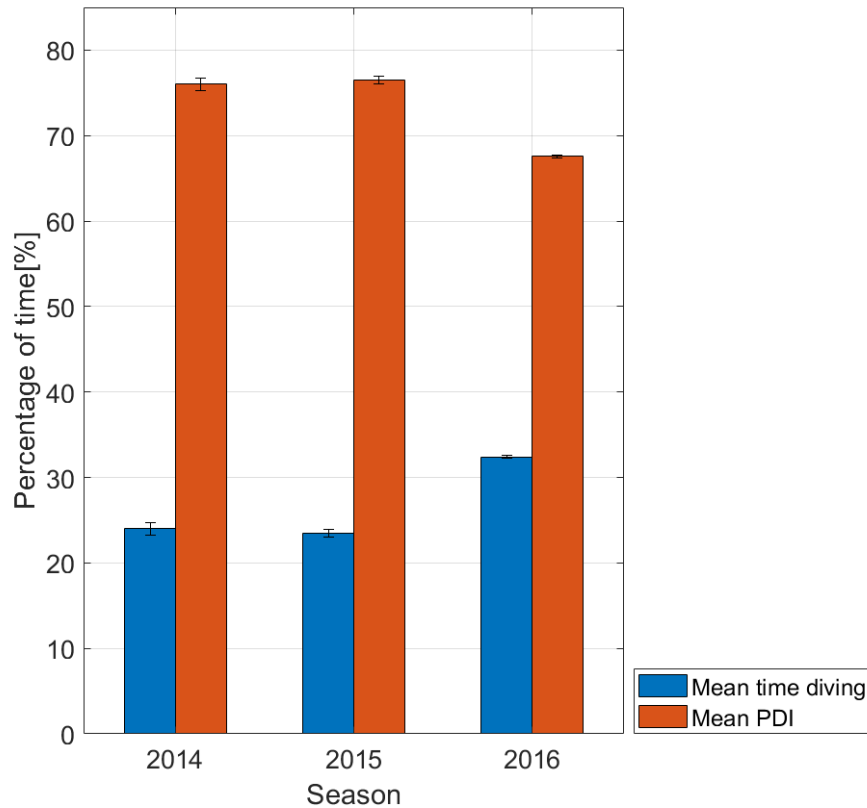
Figure 28. Mean percentage of time invested diving and time spent at the surface between dive bouts of Antarctic fur seals for all seasons. Time invested diving (Orange) and time spent at the surface between dive bouts (Post dive intervals: PDI, Blue). The total time used to calculate these two variables does not include the transit time from the colonies to the areas were foraging takes place.

The proportion of dives performed during the day and the night are similar (**2014**: day=51,7% night=48.3%; **2015:** day=50,3% night=49.7%; **2016**: day=56,1% night=43.9%, Figure 29). However, night time during summer is only ~5 hours long, so all three years exhibit a higher frequency of dives per hour during nighttime than during daytime. These frequencies do not differ between seasons (X2= 0.07, p value= 0.78, Figure 29).
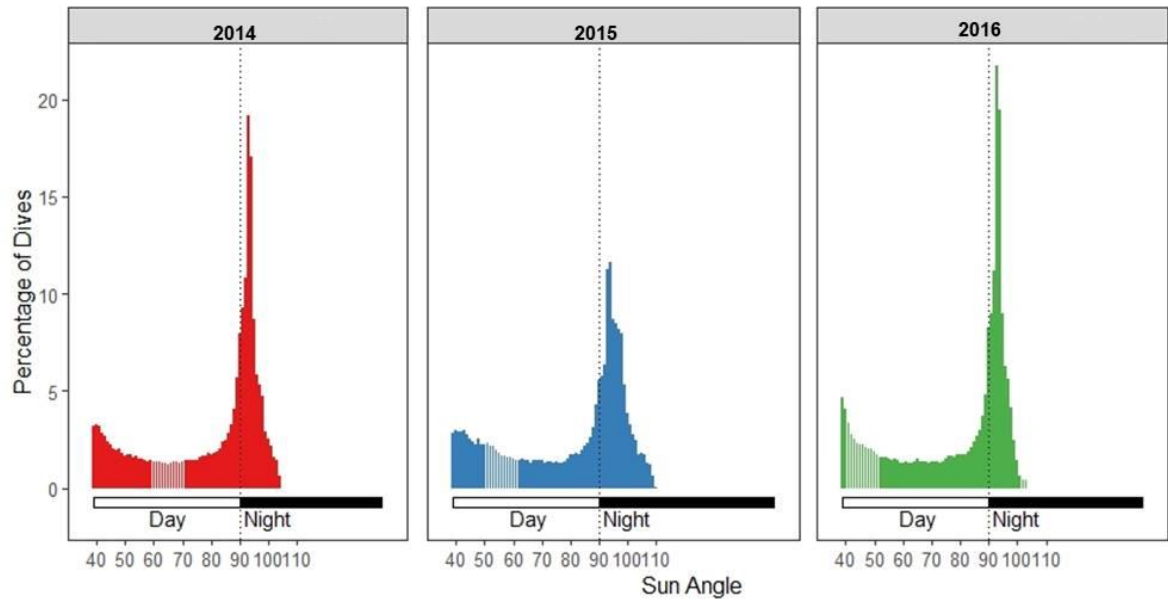
Figure 29. Percentage of dives occurring during day or night in all three breeding seasons. 2014: red, 2015: Blue and 2016: Green. The dashed line marks the 90-degree sun angle that separates daylight from Night.

Most of the dives are concentrated within the first 50 meters below the surface and no more than 12% of them occurred below 50 meters, with less than 1% occurring below the 100 m (Figure 30). The deepest dive measured was performed in 2014 (213 m), with similar maximum depths registered in the coming two seasons (**2015**: 181,5 m; **2016**: 211 m). We observed ~10% more dives between the 30 and 50 meters in 2015 than in 2014 and 2016. On the other hand, ~10% more dives occurred within the first 20 m in 2014 and 2016 compared to 2015 (Figure 30). The longest dive recorded occurred in 2014 (5.3 min) followed by 2015 (4.7 min) and 2016 (4.4 min).
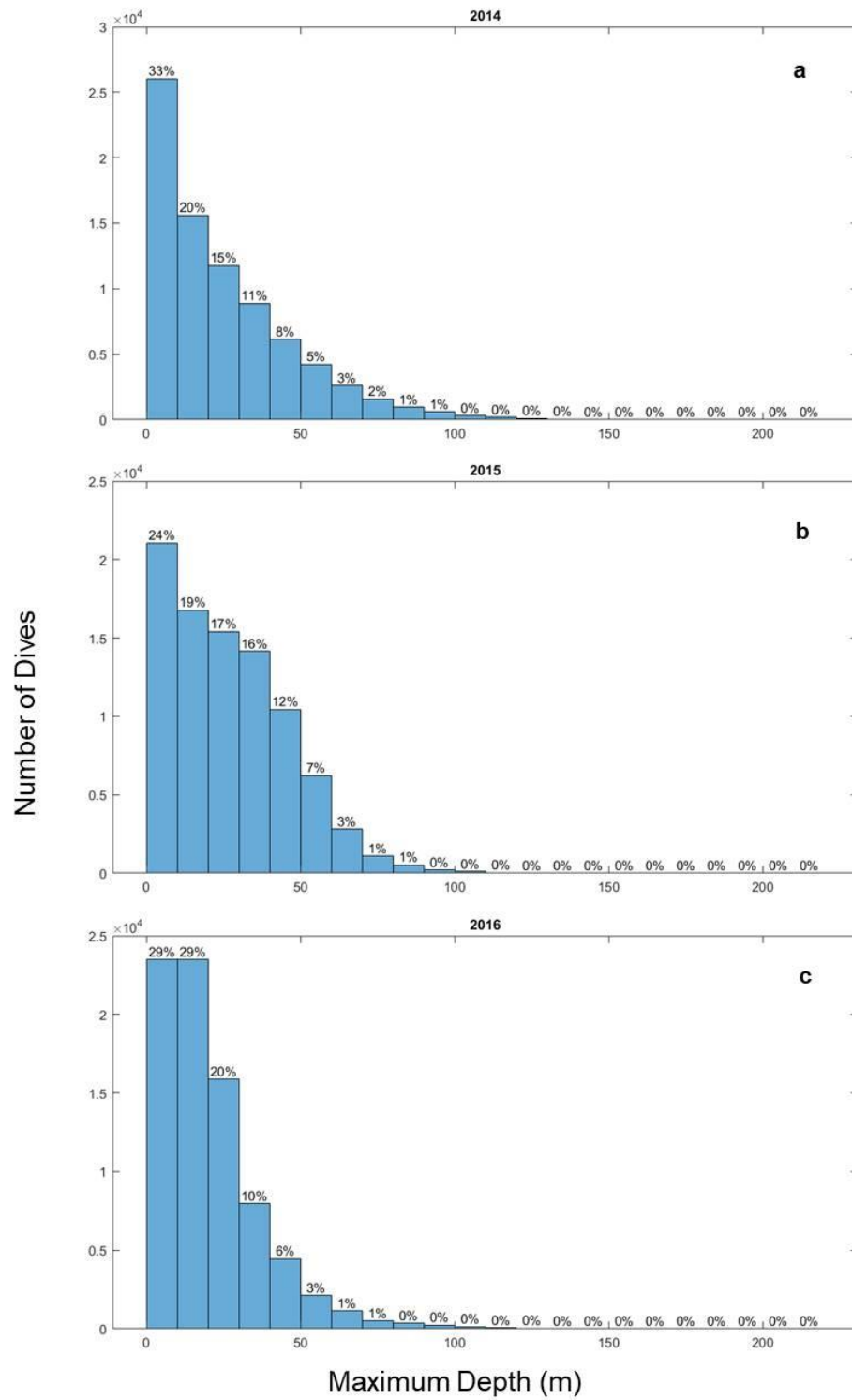
Figure 30. Percentages of dives performed every ten meters from the surface in all three seasons. 2014: top, 2015: middle and 2016: bottom graph.

Within each season, differences in mean dive rate (dives per hour) per trip can be explained by the phase in which dives were performed (K or F phase, X2= 9.2 p value= 0.002). These differences are found between phases in 2014 (F: 13.2 ± 4.5 dives/hr and K: 10.7 ± 4 dives/hr, post hoc turkey test p value= 0.008) and 2015 (F: 12.7 ± 6.7 dives/hr and K: 9.8 ± 2.4 dives/hr, post hoc turkey test p value= 0.03) but not between phases in 2016 (F: 11 ± 2 dives/hr and K: 13 ± .6 dives/hr, post hoc turkey test p value= 0.1). Therefore, differences between seasons are only observed when phases are included in the analysis (Season(Phase): X2=11.3, P Value=0.004). Specifically, only in the K phase between 2016 and both 2014 and 2015 differences are significant (Post hoc Tukey test**: 2016-2014**: p value= 0.03; **2016-2015**: p value= 0.03). Although statistically relevant, biologically, differences of ~ 2-3 dives/hr between phases or seasons do not represent an increase in effort per unit of time and therefore overall mean dive rate per trip may not be a good predictor for calculating differences in effort between seasons. However, these results are consistent with the additional time invested diving in 2016 showed in the previous section.

Behavior associated to capturing each prey (krill or fish)

The diving behavior associated to target fish or krill was evaluated using two indexes derived from Chapter 2: the proportional time invested diving (TID) and the proportional number of dives performed targeting each prey (dive frequency: DF). Both indexes are different between prey phases within each of seasons (TID: Phase: chi-square= 16.5, P value<0.0001. DF: chi-square =85.4, P value< 0.001). The percentages of TID and DF targeting krill at the K phase are higher than targeting fish in all three seasons (Table 19, Table 20 and Figure 31). Likewise, at the F phase, the percentages of TID and DF percentages targeting fish are higher than targeting krill, also in all three seasons (Table 19, Table 20 and Figure 31).

Table 19. Percentage of total time invested (% TID) capturing each prey and percentage of dives targeting each prey (preys: Krill or Fish) in both phases (K phase and F phase). K phase represents all trips to sea occurring between the third week of December and the third week of January and the F phase from the Fourth week of January until the end of the breeding season (second week of March) in all 3 seasons of this study (2014, 2015 and 2016). Results are Mean ± Standard Deviation.

Season	% TID-Krill	% TID-Fish	% FD-Krill	% FD-Fish
Krill Phase				
2014	57.31 ± 17.1	42.68 ± 17.1	50.2 ± 16.3	49.8 ± 16.3
2015	76.54 ± 9.7	23.45 ± 9.7	71.5 ± 9.8	28.5 ± 9.9
2016	54.17 ± 17.5	45.83 ± 17.5	49.1 ± 16.3	50.9 ± 16.3
Fish Phase				
2014	43.1 ± 12.05	56.9 ± 12.1	36.1 ± 11.2	63.9 ± 11.2
2015	60.7 ± 19	38.24 ± 19	55.6 ± 17.5	44.3 ± 17.5
2016	24.6 ± 17.34	75.4 ± 17.3	22.87 ± 15.8	77.1 ± 15.8

Table 20. Post hoc Tukey test results evaluating intra-seasonal variation between both phases (K phase and F phase) of total time invested diving ratio (TID) and Frequency of dives ratio (FD). Total dive time invested Ratio is the percentage of dive time invested performing krill dives divided by the percentage of diving time invested performing fish dives and Dive frequency ratio is the percent of dives capturing krill divided by the percentage of dives capturing fish for all three seasons (2014, 2015 and 2016). P values smaller than 0.05 were considered significantly different and are presented in bold and with an asterisk.

TID Ratio	Phases	estimate	SE	df	t ratio	p-value
2014	K-F	-14.8	3.66	42.8	-4.04	**0.0002***
2015	K-F	-14.2	2.59	42.5	-5.5	**<0.0001***
2016	K-F	-23.4	3.72	37.1	-6.29	**<0.0001***
DF Ratio						
2014	K-F	-15.8	1.72	39.8	-9.22	**<0.0001***
2015	K-F	-15.8	1.72	38.8	-9.22	**<0.0001***
2016	K-F	-15.8	1.72	35.5	-9.22	**<0.0001***
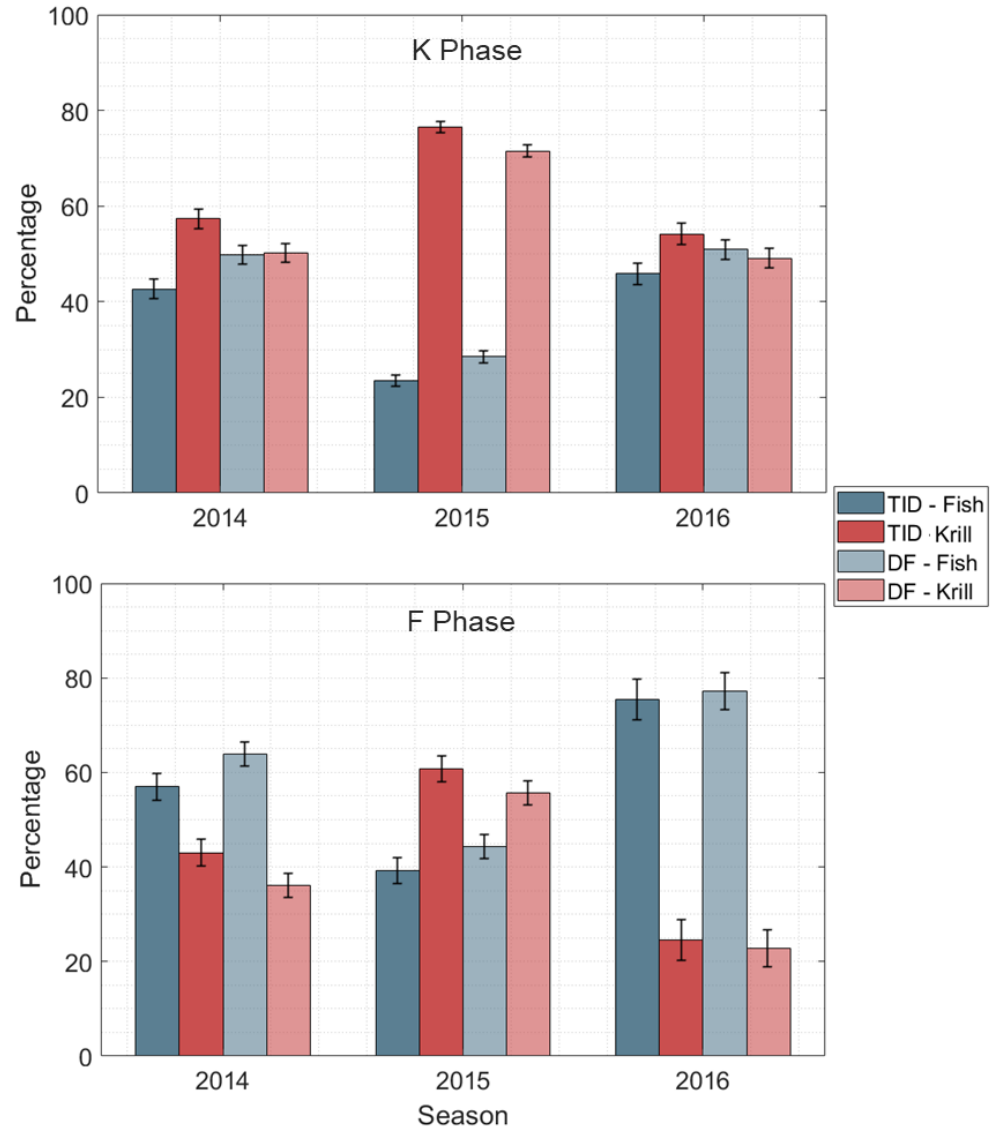
Figure 31. Behavioral indexes associated to prey capture. Percentage of time invested diving (TID) and percentage of number of dives performed (DF) targeting Krill (pink bars) or Fish (blue bars). The upper graph shows the behavioral indexes within the first half of the breeding season (K phase) and the lower graph shows the behavioral indexes in the second half of the season (F phase).

When we evaluate between-seasons differences, females also present differences in their behavior in both indexes (TID: chi-squared= 28.19, p value <0.0001 and FD: chi-square = 29.8, p value= <0.0001, Figure 32). The proportion of both behavioral indexes targeting fish are less in 2015 (TID-Fish: 30.4±16.5%, FD-Fish: 35.5±15.8%) than in the other two years (**2014**: TID: 45.7±17%, FD-Fish: 52.8±16.4%, **2016**: TID: 51.7±21.04%, FD-Fish: 56.1±19.2%), which highlights that krill was consumed in higher proportions in 2015 than the other two years (**2015**: TID: 69.6±16.5%, FD: 64.5±15.8%, **2014**: TID: 54.2±17%, FD: 47.2±16.4%, **2016**: TID: 48.3±21%, FD: 56.1±19.2%, Figure 32).
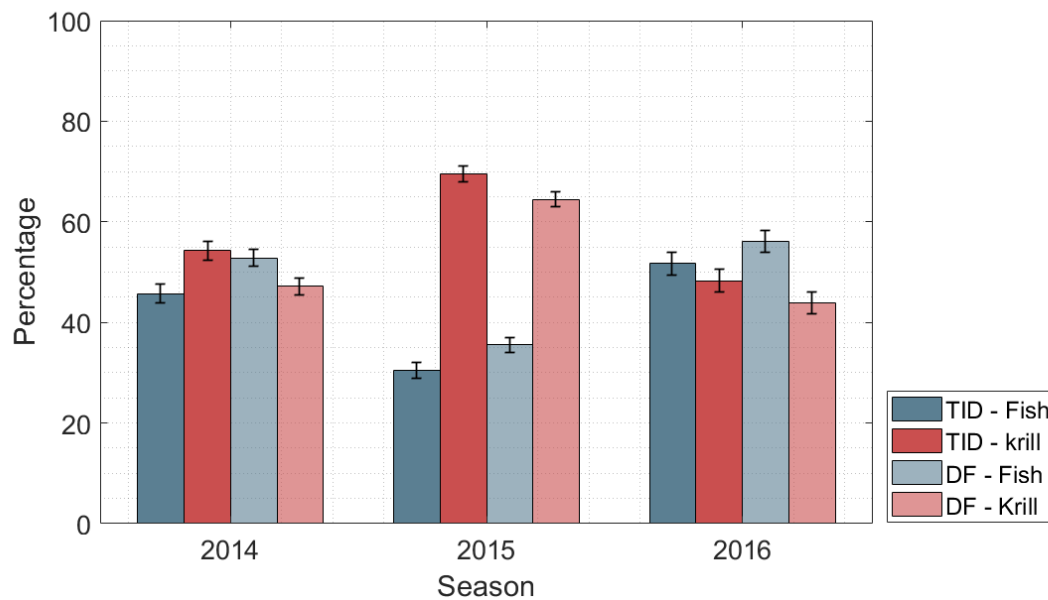
Figure 32. Seasonal means of behavioral indexes associated to each prey capture. Percentage of time invested diving (TID) and percentage of dives performed (DF) targeting Krill (pink bars) or Fish (blue bars) for all three seasons (2014, 2015 and 2016).

During the krill phase, we found the highest TID targeting krill in females from 2015 (70±16.5%), with females at the other two seasons showing values close to ~50% of the mean total TID for krill and no differences observed between females of 2014 and 2016 (Table 21). Likewise, the FD targeting krill was also higher in females of 2015 (64.5±15.8%) than females from the other two years, with no differences found between females of 2014 (47.2±16.4%) and 2016 (56±19.2%, Table 21). Therefore, females at the krill phase of 2015 shows a higher proportion of time diving for krill than at the krill phases of 2014 and 2016, and less than 30% of the time (both TID and FD) targeting fish. During the F phase, animals target more fish in 2016 (TID: 75.4±17.3% DF: 77.1±15.8%) than during the other two years (**2014**: TID: 56.9±12.1% DF: 63.9±11.2%, **2015**: TID: 39.2±19 % DF: 44.4±17.5%). Interestingly females from 2015 also showed the highest percentage of TID and DF targeting krill in the F phase compared to the other years, similar to what happened in the K phase (TID: 60.7±19%, DF: 55.6±17.8%). Table 21 shows all post hoc Tukey test results when comparing years of both indexes in both phases (see also Figure 31).

Table 21. Post hoc Tukey test comparisons between seasons in both phases (K phase and F phase) of total time invested diving ratio (TID) and Frequency of dives ratio (FD). Total dive time invested Ratio is the percentage of dive time invested performing krill dives divided by the percentage of diving time invested performing fish dives and Dive frequency ratio is the percent of dives capturing krill divided by the percentage of dives capturing fish for all three seasons (2014, 2015 and 2016). Phases with p values smaller than 0.05 were considered significantly different and are presented in bold and with an asterisk.

Time Invested Diving (%)				
K Phase	**Estimate**	**SE**	**df**	**p-value**
2014-2015	-18.33	4.74	42.5	**0.011***
2014-2016	2.650	4.96	37.1	0.8545
2015-2016	20.99	4.99	37.1	**0.005***
F Phase	**Estimate**	**SE**	**df**	**p-value**
2014-2015	-18.89	5.57	51.8	**0.004***
2014-2016	11.28	6.37	92.1	0.19
2015-2016	30.17	5.94	51.8	**0.0005***
Frequency of dives (%)				
K Phase	**Estimate**	**SE**	**df**	**p-value**
2014-2015	-20.3	0.44	38.8	**0.0001***
2014-2016	2.3	0.23	35.5	0.8775
2015-2016	22.6	0.44	35.5	**0.0001***
F Phase	**Estimate**	**SE**	**df**	**p-value**
2014-2015	-20.3	0.44	43	**0.0001***
2014-2016	2.3	0.23	46.2	0.8774
2015-2016	22.6	0.44	43	**0.0001***

Spatial behavior

Trip duration and time ashore

We found no differences in mean trip duration between seasons (chi-square= 2.21, p value= 0.3307) nor within each season (K-F phases, Season(phases): chi-square = 3.18, p-value = 0.37). On average, females spent ~ 3.5 days at sea (**2014**: 3.6±1.6 days; **2015**: 3.7±1.4 days and **2016**: 3.3±1 days). Furthermore, differences on the time spent ashore could not be explained by overall differences between seasons (chi-square= 0.10, p value=0.94, **2014**: 1.4±0.6 days; **2015**: 2±1.2 days and **2016**: 1.7±0.7 days) but it could be explained by differences between phases (chi-square= 11.4, p value=0.003). This difference was only observed in the K phase between seasons 2014 and 2015 (Phase= poshoc Tukey test 2015-2014= p value = < 0.0001) were, in 2014, animals would stay ~ 20 hours less time hauling out than in 2015 (Table 22). Figure 33 shows the relationship between trip duration and time spent ashore. In all three seasons, animals tend to maintain the same time onshore despite the extension of their foraging trips (but see section "foraging strategies").

Table 22. Mean trip duration and mean time ashore observed per phase. Fish phase: "F" and Krill Phase: "K" for all seasons studied (2014, 2015, and 2016).

Season	Phase	Sample Size	Mean Trip Duration	Mean Time Ashore
2014	F	19	3.5 ± 1.3	1.8 ± 0.8
	K	70	3.6 ± 1.7	1.3 ± 0.6
2015	F	49	3.8 ± 1.7	1.8 ± 1.1
	K	62	3.6 ± 1.1	2.1 ± 1.2
2016	F	16	3.5 ± 1.1	1.9 ± 0.8
	K	65	3.2 ± 1.1	1.6 ± 0.7
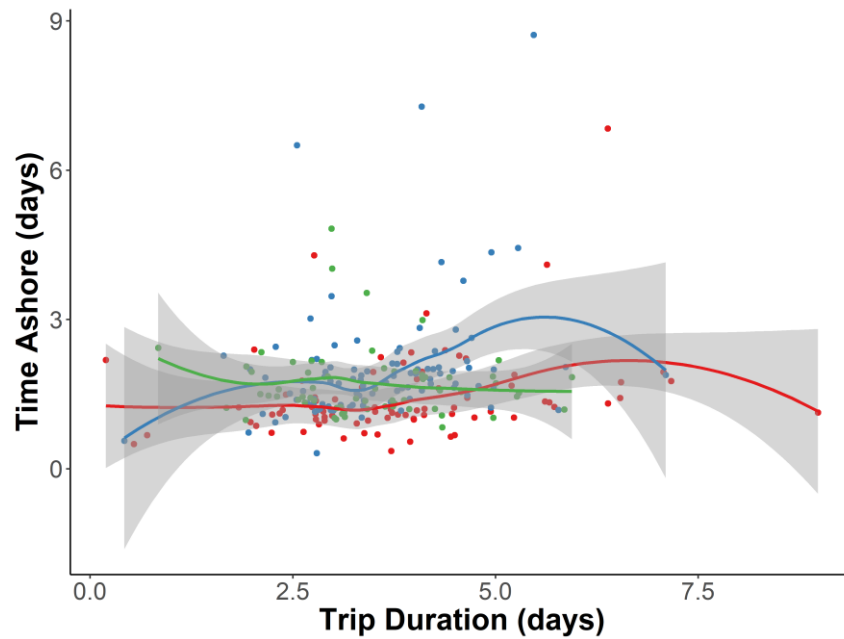
Figure 33. Relationship between trip duration and time spent ashore after each foraging trip in Antarctic Fur seals for all three seasons. 2014: red, 2015: Blue and 2016: Green.

Tracking data

Geolocation data was obtained from a subset of females for which instruments also incorporated a GPS sensor. We registered a total of 20 trips in 2014, 39 in 2015, and 36 in 2016 with geolocation. The mean maximum distance travelled cannot be explained by differences between seasons (Table 23, chi square= 3.7, p value= 0.15) nor differences between phases within each season (phase= chi-square: 0.4 p-value = 0.5). The maximum distance traveled registered, occurred in 2015 (774 km) by a female on a trip performed after the pup died. Besides this trip, the maximum distance traveled from the breeding colonies in 2014 and 2015 reached 532 km and 515 km, respectively. In 2016 only one trip of over 300 km (301 Km) was performed out of the 36 trips obtained in 2016 whereas in 2014 and 2015, 25% and 30% of the trips, respectively, were over 300 km.

The transit rate could also not be explained by differences between seasons (Table 22, chi square= 4.16, p value= 0.12) nor phases (chi square= 3.6, p value= 0.07, Poshoc Tukey test between K-F phase per year: 2014: p value= 0.0839; 2015: p value= 0.0858; 2016: p value= 0.09, Table 23).

Table 23. Mean maximum distance from the colonies (Km) and mean transit rate (Km/hr-1) observed by phase. Fish phase: "F" and Krill Phase: "K" for all seasons (2014, 2015 and 2016).

Season	Phase	Mean Max Distance (Km)	Mean Transit Rate (Km/hr^{-1})
2014	K	193.9 ± 168	2.9 ± 0.7
	F	214.3 ± 60	2.4 ± 0.5
2015	K	280.8 ± 62	3 ± 0.3
	F	272.3 ± 141	2.6 ± 0.4
2016	K	186.2 ± 73	2.5 ± 0.5
	F	116.3 ± 112	2.6 ± 0.5

Foraging strategies

We used seven variables to perform the principal component analysis (PCA): mean trip duration (days), maximum distance from colonies (km), proportional time invested diving targeting fish (TID, %), proportional number of dives targeting fish (DF%), mean time ashore (days), mean dive rate (dives/hr) and overall percentage of time diving. The PCA revealed four principal components (dimensions) that explained all together 90.5 % of the total variance (Figure 34).
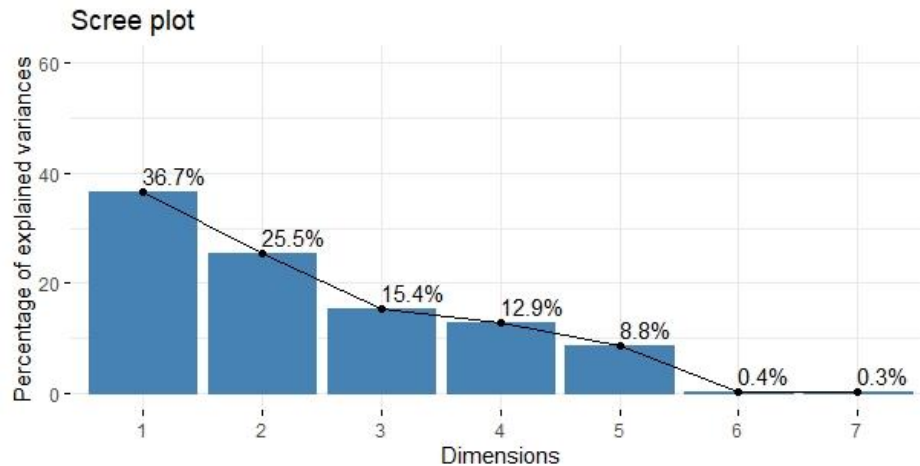
Figure 34. Scree plot obtained from the Principal component analysis between foraging variables. The scree plot presents the first seven principal components (Dimensions) and the percentage of the explained variance of each dimension. 90.5% of the variance is explained by the first 4 dimensions and therefore these were further used in the classification of the foraging strategies.

The maximum distance from colonies (Maxdist), trip duration, DF, and TID contributed most to the variance explained by dimensions 1 and 2 which represented 62.2% of the variance (Figure 35). We expected that Maxdist and trip duration would have a similar contribution to the variance since maximum distances to colonies were partially inferred from trip duration itself (figure 3 of appendix B). Haul-out and overall mean proportional time diving per trip (prop

dtime) were the highest contributors to the variance explained by dimensions 3 and 4 which represented 28.3% of the variance (Figure 35). Details on the contribution of each variable to the variance of each dimension can be revised figure 6 of appendix B.
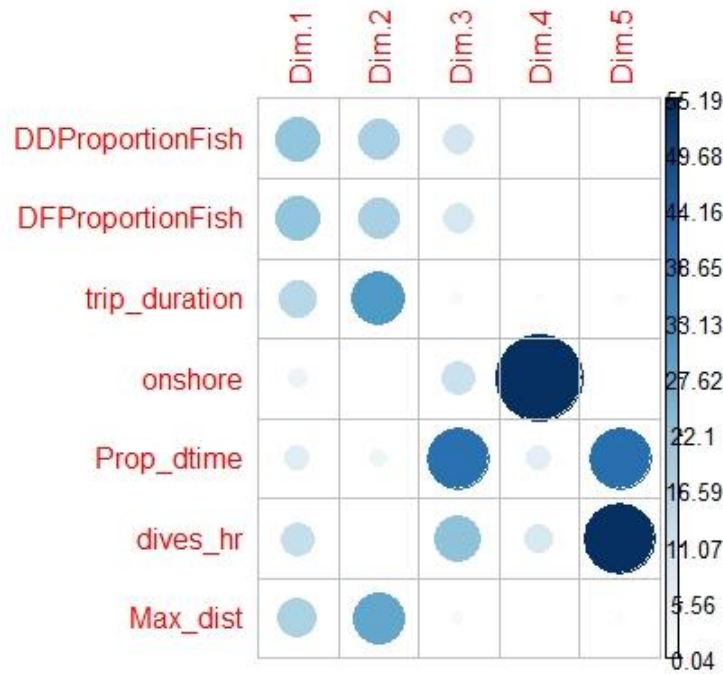
Figure 35. Contribution of all variables to the variance explained by each dimension obtained from the principal component analysis. Larger darker circles represent variables explaining more variance than those lighter small blue circles on each dimension. Further detail can be found in Figure 6 of appendix B.

Hierarchical Cluster Analysis (HCA)

The results from the Elbo and silhouette method to evaluate the optimal number of clusters were not as evident as expected, suggesting either two, four or, five clusters. (See figure 7 of appendix B). We decided on the final number of clusters after performing multiple LMMs in the most important variables that defined foraging strategies (Those explaining most of the variance of the 4 PCs found to be important from the PCA) and evaluating the explanatory power of clusters

in every foraging variable. We started with five clusters. When differences were not explained by two or more clusters in any foraging variable, those clusters were merged. The total number of clusters in which we found significant differences in at least one of the foraging variables was four. These four clusters account for four behavioral strategies (Figure 36 and Figure 37).

Figure 36. Cluster Dendrogram of all trips from all three seasons (2014, 2015, and 2016). Clusters are represented by a different colored square and include all trips showing that behavior.

Figure 37. Nonmetric multidimensional scaling (MDS) grouping the four clusters identified from the hierarchical analysis (HCA).

To see if behavioral strategies were different from each other, we performed LMM with every behavioral variable obtained in the PCA analysis that contributed to explain most of the variance of the four most important dimensions (see figure 6 of appendix B). As explained in the methodology of this chapter, we only have a few FA samples and therefore, a few prey proportion estimations per strategy. Therefore, only the mean percentages of these FA samples per strategy are shown (Figure 38 of this chapter, and Table 4 of appendix B), but no statistics were performed on FA samples and instead, prey targeted was more robustly determined from behavior using the algorithm developed in Chapter 2. The use of each strategy calculated from the total number of trips performed per season is shown in Figure 39.
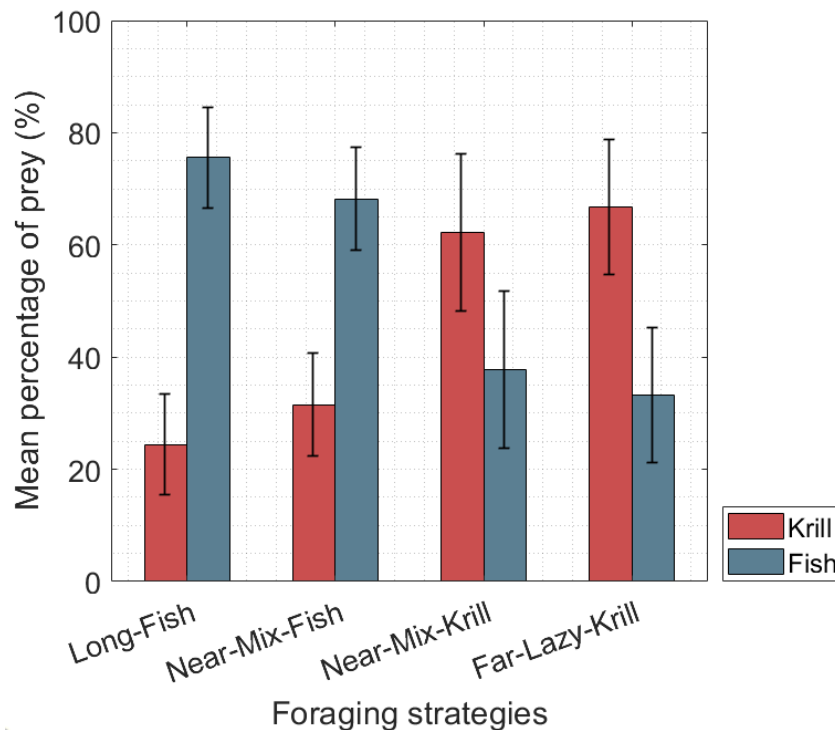
Figure 38. Mean and standard error of prey proportions calculated from milk fatty acid samples. *Euphausia superba* (krill)-red bars and all three species of fish merged as "Fish"-blue bars. We had a small FA sample size per strategy (from left to right: 9, 7, 7, and 9 samples) so caution needs to be taken when interpretating this figure. Mean and standard error presented.
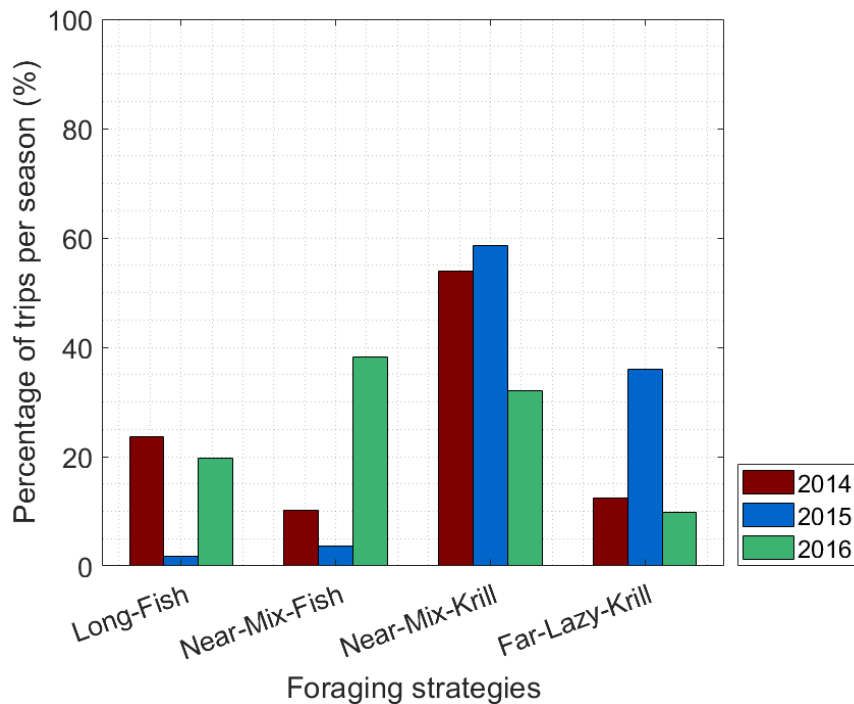
Figure 39. Percentage of trips per season performing each strategy used by Antarctic fur seals at Cape Shirreff. Red: 2014, Blue: 2015, and Green: 2016.

Spatially, female's strategies obey to three explored areas; 1.-two groups of females forage over the continental shelf but mostly associated to the 500 meters shelf break (two strategies named with the word "Near" as a reference of been closer to colonies than the other strategies, Figure 40a), 2.- females foraging mostly between the shelf break and the South Shetland Trough (one strategy with the word "Long" in the name as reference of long and far trips to sea, Figure 40b), and 3.- females foraging from the South Shetland Trough reaching even farther oceanic waters (one strategy named with the word "Far" since is the farthest that females would go from their colonies compared to other strategies, Figure 40c and Figure 41). Behavior associated to each prey was used to further described the strategies. Based on behavior, most of the trips showed a combination of prey targeted (fish and krill) but two of them were significantly higher in one

prey or the other and in those, the words "fish" or "krill" was designated to each of these two strategies ("Long-fish" and 'Far-Lazy-krill' strategies). The word "mix" was only designated to the name of those strategies that did not presented significant differences in the prey targeted but do show a tendency to be targeting more of one prey than the other (strategies "Close Mix-Krill" and "Close-Mix-Fish" strategies). Is interesting to see that despite the lower sample size of milk FAs obtained from females carrying GPS sensors, percentual values of prey consumed obtained from FA (Figure 38) are consistent with the behavior associated to each prey targeted by each strategy (Table 24 and Table 25). Table 24 summarized means and standard error of all variables per strategy used by females.

Table 24. Mean values of all foraging variables per foraging strategy identified for females at Cape Shirreff during 3 breeding seasons. Results are presented showing the mean ± Standard Deviations.

Cluster	Strategy	Number of trips	Number of Females	Trip Duration (Days)	Time Ashore (Days)	Maximum Distance travelled (Km)	TID-Fish (%)	TID-Krill (%)	DF-Fish (%)	DF-Krill (%)	total time diving (%)
1	Long-Fish	39	15	4 ± 1.2	1.8± 1	256± 92	70.2± 13	29.8± 13	73.5 ± 10.8	26.5 ±10.8	22 ±4.2
4	Far-Lazy-Krill	59	24	4.8 ± 1.6	2.4 ± 1.4	330 ± 110	23.9 ± 10	76.1 ± 11.7	29.5 ± 11.7	70.5 ± 11.7	21 ±0.04
3	Near-Mix-Krill	139	33	3.1 ± 1	1.4± 0.5	194± 64	35 ± 12.3	65 ± 12.3	41.4 ± 12.7	58.6 ± 12.7	25 ± 5.5
2	Near-Mix-Fish	44	14	2.8 ± 1.1	1.4 ± 0.4	179 ± 80	59.8 ± 15.2	40.2 ± 15.2	64 ± 13.5	36 ± 13.5	40 ± 16
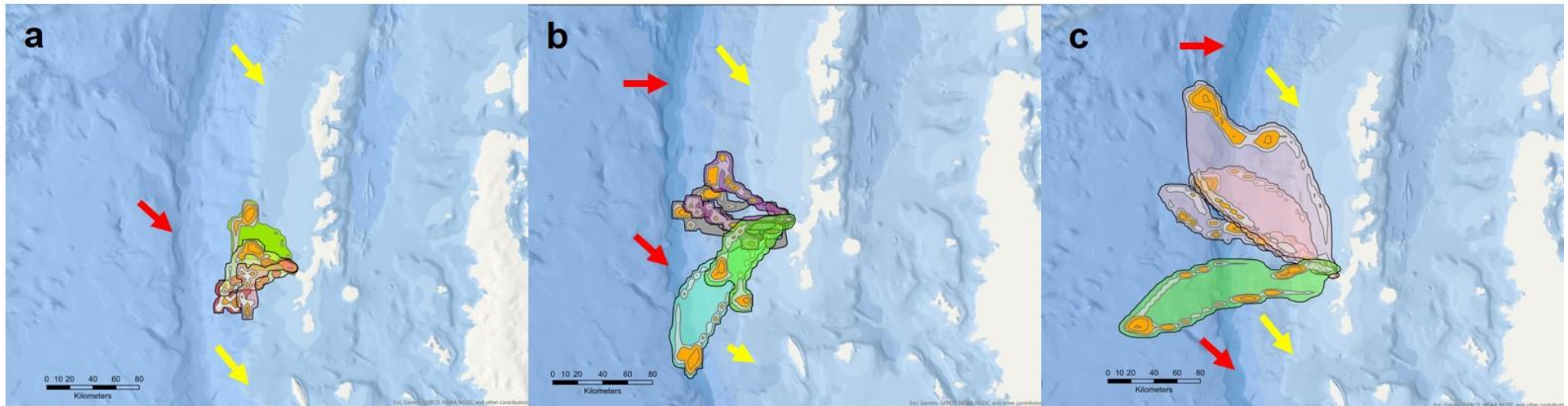
Figure 40. Foraging areas utilized in three of the four strategies identified for female Antarctic fur seals breeding at Cape Shirreff. Each color represents a different trip and female. The orange areas of each trip represent the most utilized area (foraging area), which containing 50% of the total GPS points registered per trip. Yellow arrows point out the 500 m shelf break and red arrows point out the South Shetland Trough a remnant of a subduction zone a.- Areas utilized by females performing "Mix-fish" and "Mix krill strategies" in 2014. B.- Females performing the "Long-fish" strategy in which they use but also go over the continental shelf break and utilized farther areas closer to the subduction zone. C.- Females performing the "Far-Lazy-krill" strategy in which they mainly focused their foraging activities in the subduction zone and even farther toward oceanic waters (see Figure 41 for more details on this strategy).
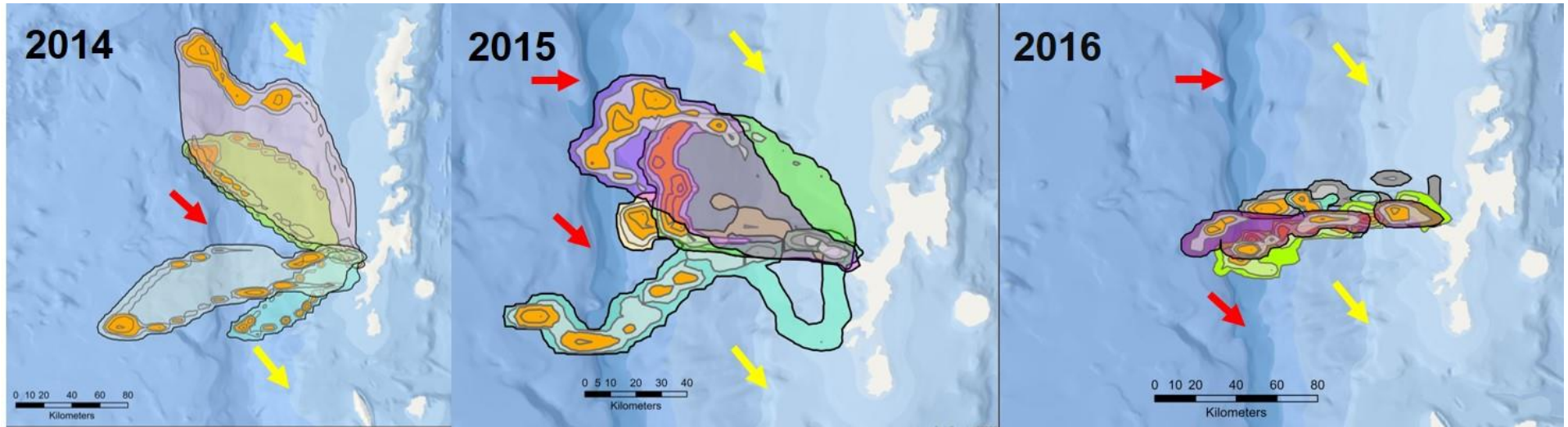
Figure 41. Foraging areas utilized by females performing the "far-Lazy-krill" strategy on each season (2014, 2015, and 2016). Each color represents a different trip and female. The orange areas of each trip represent the most utilized area (foraging area), which containing 50% of the total GPS points registered per trip. Yellow arrows point out the 500 m shelf break and red arrows point out the South Shetland Trough a remnant of a subduction zone. Despite the season, most of the areas utilized are associated with the subduction zone and some trips even pass it toward farther oceanic waters.

In all three seasons, the most used strategy was the "Near-Mix-Krill" Strategy (33 females and a total of 139 trips) in which behaviorally, animals are targeting more krill than fish (Table 25) in areas over the continental shelf close to the colonies and the shelf break (Figure 40a). Out of all trips performed in 2016, females use this strategy in fewer trips than what was observed in 2014 or 2015 (Table 25, Figure 39).

Table 25. Percentage of trips from the total trips performed per season using each strategy.

Season	Strategies			
	Long-Fish	Near-Mix-Fish	Near-Mix-Krill	Far-Lazy-Krill
2014	23.6	10.1	53.9	12.4
2015	1.8	3.6	58.6	36.04
2016	19.8	38.3	32.1	9.9

The "Near-Mix-Fish" strategy shows a tendency of targeting more fish than krill also closer to the colonies, with the highest percentage of time invested diving of all strategies (Table 24). Overall, it was used by 14 animals in 44 trips using feeding grounds in the continental shelf and mostly the shelf-break similar to the "Near-mix-krill" strategy (Figure 40a). Actually, half of the female from 2016 (7 out of 14 females) use the "Near-Mix-Fish" strategy (38% of the total number of trips of 2016, Table 25). The "Long-Fish" strategy was used by 15 animals in 39 trips within all seasons (Table 25). Animals using this strategy were performing trips pass the continental shelf break up to the South Shetland Though (Figure 40b) and based on their behavior, capturing more fish than krill (Table 24). This strategy was almost never used in 2015 (1.8% of the total trips performed in 2015, Figure 39).

At last, the "Far-Lazy-Krill" strategy was used by 24 females in 59 trips of all seasons. This strategy showed similar mean trip duration than the long-fish strategy, but reaching far-off distances from the colonies. The strategy consists of trips performed pass the shelf break and more than half of them even pass the subduction zone (Figure 40c and more detail per season in Figure 41). As a consequence of those long trips, females spend significantly more time hauling-out than animals using any other strategy (Table 24). Diving behavior of this strategy, suggests a high frequency and dive time used targeting krill than fish (TID-Krill: $76.1 \pm 11.7\%$, DF: $70.5 \pm 11.7\%$), which is consistent with the proportion of the few fatty acid samples obtained from trips using this strategy (Figure 38). Females measured in 2015 showed higher use of this strategy than females measured in 2014 and 2016 (Table 25) which suggests the existence of krill patches expanded into the oceanic area pass from the shelf break in 2015 as opposed to the other seasons in which animals did not explore these areas regularly.

When we analyze the use of strategies within each season (phases K or F), and compare phases between seasons, we found evidence for a higher fish consumption in 2014 and 2016 than what was found in 2015. During, 2015 fish associated strategies were not used during the K phase whereas 27% and 51% of the trips performed in 2014 and 2016 respectively, performed fish associated strategies and therefore targeting more fish than krill. In addition, during the F phase in 2015, in which an increment on the fish consumption is expected (see section feeding behavior of this chapter), animals showed 88% of the total trips to be related to krill consuming strategies compared to a 42% in 2014 (with no far-lazy-krill strategies observed in this phase in 2014) and only a 13% in 2016. Furthermore, at the K phase, the strategy "Near-Mix-fish" was not utilized in 2015 and was barely used in 2014 (7%) whereas, in 2016, 41% of the trips performed at this phase used this strategy.

Altogether, this highlights that a higher fish consumption was observed in 2014 and an even higher fish consumption was observed in 2016 (even in the K phase in which we expected a reduced consumption of fish) when compared to 2015, in which we found krill consuming strategies used extensively despite the phase in which the trips occurred. All percentages of trips per strategy per phase can be revised in detail in table 5 of Appendix B.

DISCUSSION

With a combination of atmospheric data, characterization/quantification of prey available and consumed, and behavioral data, we were able to identify how breeding female respond behaviorally to interannual environmental variability in an already highly heterogeneous environment. At the edge of their breeding distribution, lactating females have limited possibilities of "working" (diving) harder when krill, the most abundant prey of AFS, is limited (as in 2014 and 2016). Authors have shown these limitations by measuring the female's field metabolic rate from this colony (Costa *et al*., 2000), and have also stated the limitations of behavioral changes in edge colonies from a conceptual point of view (Costa, 2008). However, they have never empirically tested if compensatory strategies are used between already available prey taxa other than changing trip duration, since information of prey species captured is limited to generalized qualitative descriptions, seasonal means, and overall descriptions of behavior with no empirical evidence of the prey captured on each foraging trip. We have obtained this information even from females that we lack of diet estimations, by using the algorithm created in Chapter 2. Females cope with increasing environmental variability by accommodating their already limited foraging strategies used at this location. They increase or reduce, depending on the scenario, the number of times a strategy is used respect to another allowing them to capture

different prey types but not necessarily more prey. In other words, when females are breeding at already highly heterogeneous environments, the only way of coping with even more variability is by modifying the "where" and "what" they capture over 'how much" they target.

Were the years different?

Previous studies have already shown that the 2015-16 ENSO event was one of the strongest on record in the last 50 years (Turner, 2004; Bodart *et al*., 2019). This event is linked with multiple environmental responses such as differences in the mass balance of the Antarctic ice sheet (Bodart *et al*., 2019), the lowest hemisphere spring ice extent ever recorded (Stuecker *et al*., 2017) and long-lasting surface melting of the Ross ice shelf (Nicolas *et al*., 2017). For this, the strongest Southern annular mode (SAM) registered in the last 50 years triggered the lowest ever recorded Antarctic sea ice extent during the spring 2016 (Stuecker *et al*., 2017; Turner *et al*., 2017), dropping from its record high of 12.8 x10^6 km^2 in 2014 to their lowest value of 10.7x 10^6 km^2 of the last 40 years (Parkinson 2019). This has a tremendous impact on the recruitment and abundance of krill (Siebel and Loeb, 1995; Atkinson *et al*., 2004; Loeb *et al*., 2009; Atkinson *et al*., 2019). Consequently, the availability of krill for AFS in the 2016 season was limited. We observed these changes in krill availability from the krill density records of locations south from Cape Shirreff (see the result section) but also reflected in a reduction of krill capture by the fishing industry this year. This is also observed in the differential use of foraging strategies between the seasons used by AFS females (discussed later), but not so much from our on-land atmospheric data. However, we could partially see the transition between a much colder 2014

to a significantly hotter 2016 and the differences in prey consumption: from a more juvenile oriented krill diet in 2014 towards a higher consumption of adult krill by 2016. All together, we identify three different behavioral response to three different seasons that provide different prey availability scenarios and trigger a differential use of four foraging strategies by AFS females breeding at the southernmost edge of their distribution.

Different scenarios, different responses

The season 2014 was characterized by a very cold first half of the season, which directly impacted offspring mass compared to the warmer seasons (2015 and 2016). Effects on pup conditions have been observed due to climatic anomalies in this (Lea *et al*., 2006; Bradshaw *et al*., 2000) and similar species (Gálvez *et al*., 2020). Nevertheless, in our study, pups reach a similar mass by the end of all breeding seasons, despite those initial differences. This is more related to a rapid rate of energy transferred while delivering milk (Sharp *et al*., 2005) rather than changes in the mother's foraging behavior. Females can travel greater distances in difficult years than normal years, extending their trips to sea, but delivering the same overall resources to their offspring once there are back (Staniland *et al*., 2007; Boyd, 1996). Only pups from females spending greater time onshore than others, have been described to reach larger sizes (Doidge and Croxall, 1989). Furthermore, in a similar location, Lea *et al*. (2006) found that pups daily mass gained varied with the extension of the preceding trip, showing that females are more efficient transferring milk in seasons with abundant prey. However, this was concluded from sites with only one prey taxa identified (fish), and it may vary in areas where multiple taxa are consumed. Short-term mass differences seem to impact pup conditions only temporarily but do

not result in significant differences in mass at the end of the breeding season. Therefore, it is not the on-land conditions what would affect pup growth patterns over a large temporal scale but the long-term persistency of extreme variables (e.g. continuous increasing in sea surface temperatures), most likely by modifying prey availability and therefore, mother's energy acquisition and provisioning (Forcada *et al.*, 2005).

Behavioral plasticity is common in this species (Forcada *et al.*, 2008). It is known that they will extend their trips in complex years (Costa *et al.*, 1989; Lea *et al.*, 2006; see also Trillmich *et al.*, 1991 for comparison with other fur seal species) and, when possible, modify their diving activities, diet, and foraging areas, concurrently with changes in their environment and prey availability (Lea *et al.*, 2006). We did not find differences in time hauling out nor trip duration between seasons but we did find different strategies used. For instance, at the beginning of the season 2014, ~27% of the trips included strategies with longer trips to sea. When using mean values of trip duration or from any other foraging proxy to represent seasonal or even monthly behavior, we may be overlooking the combined use of different foraging strategies. Studies have shown that certain decisions are shaped by the success of capturing prey, even in previous instants of a foraging decision (Iwata *et al.*, 2015), unveiling multiple behavioral possibilities in response to changes. Therefore, behavioral plasticity needs to be taken into account by evaluating adjustments in females' foraging strategies since the same individuals can used multiple strategies during one breeding season or when conditions change.

Almost 50% of the krill consumed in 2014 was at a juvenile stage, significantly smaller than the krill consumed during the next two seasons. When consuming krill, AFS would select larger krill whenever possible (Reid and Arnould, 1996). Larger krill was available in 2014 and the

consumption of ~40% of juvenile may be related to how far from the colonies was the large krill found and how less abundant was krill than 2015. Juvenile stages are usually associated to the continental shelf break and the continental shelf itself (Siegel 2005, see also Figure 8 of Appendix B). AFS in this season performed more than 80% of their trips by using foraging strategies that occur between the shelf and the continental break. Behaviorally, small krill sizes would cause AFSs to modify their behavior to increases foraging efficiency. This can be done by 1.- increasing capture attempts of the same prey by increasing dive frequency or spending more time at their foraging locations (Lea *et al*., 2006), and/or 2.- explore other areas in search of other prey items or adult krill. We found no evidence of animals diving harder (e.g. deeper, faster, longer) when we compared dive frequency between years nor within each season, which is in line with previous descriptions of this colony that suggest AFSs females operates at their maximum diving capacity (Costa *et al*., 2000). Instead, our data supports the hypothesis that animals would search for fish in years when krill, the most abundant prey, is less available (Murphy *et al*., 2007; Collins *et al*., 2008; Iwami *et al*., 2011). At the beginning of 2014, we observed the use of more fish-associated foraging strategies (the K phase, in which 27% of the strategies used in 2014 where fish-associated against 0% of them in 2015). This was also true for 2016 when krill availability was limited. Furthermore, in years when krill is more abundant (2015), females may visit far oceanic areas if the reward is greater and more dense krill patches are found as can be observed in a high used of the "far-lazy-krill" strategy of females during the season where more krill density was observed.

The diet data of seasons 2015 and 2016 showed a higher rate of adult krill consumed but only in 2015 we observe a higher use of krill-oriented foraging strategies during the entire breeding season which is consistent with the highest krill density observed of all seasons. The

oceanographic conditions and the low sea ice extent in the previous winter and spring of both 2015 and 2016 season (Stuecker *et al.,* 2017; Turner *et al*., 2017, Parkinson 2019), had a significant impact on krill abundance (Atkinson *et al*., 2019), with very little presence of juvenile stages during 2016. This suggests that finding abundant krill in 2016 was more challenging for females than in 2015, even though adult krill was present in feces. As observed in 2014, this also drove females in 2016 to increase the use of fish-associated strategies at the beginning of the season (K phase, 2016: 50% of the strategies were fish associated). Therefore, although krill remains to be the most important prey item for AFS colonies despite the year, more exclusive consumption occurs only when it is abundant (2015). When krill is not abundant, females will use compensatory strategies increasing consumption of smaller krill (2014) and/or increasing the consumption of fish (2014 and 2016). For this, fish could be playing an important role for this colony when facing additional environmental variability not just progressively during the season as previously reported (Osman *et al*., 2004; Polito and Goebel 2010; Santora, 2013, this study), but also during the first half of those seasons when prey availability is limited.

Krill vs Fish

To cope with difficult years, AFS females adjust their behavior to their prey abundance and distribution (McCafferty *et al*., 1998; Harcourt *et al*., 2002; Lea *et al*., 2006). We recognized that krill is the most abundant prey found despite, in some cases, the large numbers of fish consumed. Siegel, (2005) presents a clear conceptual view on where krill can be found in the WAP during the entire year (see figure 8 of Appendix B). The author shows that during the austral summer, pre-mature stages are likely to be found in the continental shelf and the shelf

break area, whereas adults are usually found in oceanic waters (Siegel 2005). This is why between 30-50% of females' foraging strategies in all years are very likely targeting krill close to the colonies (Near mix krill strategy). It is also consistent with the behavioral differences observed when mostly juvenile (2014), or mostly adult krill (2015, 2016) are consumed. In 2015 and 2016, when we observed more adult krill, females performed, in some cases, almost three times more trips to oceanic waters (Far lazy krill strategy, table 5 Appendix B) than females in 2014, in search of adult krill or fish. When a higher proportion of juvenile krill was observed in the diet (2014), we did not observe this strategy's use at all at the F phase.

Furthermore, the difference between 2015 and 2016 is that, in 2015, females continue the second half of the breeding season using more than 80% of the time krill-targeted strategies, whereas, in 2016, krill-targeted strategies were reduced to 12%, concentrating their effort in targeting mostly fish. Therefore, a reduced krill availability is overcome by either searching for adult krill and/or fish in oceanic waters. As a result, animals would get the necessary energy to survive and breed but with an impact on their own conditions, which is observed in a greater daily weight loss in females operating in complex years (2014-2016) than in 2015 when krill was abundant. Consequently, greater distances and longer trips would result in a higher energy intake (Staniland *et al*., 2007; Boyd 1996), but depending on the strategy, they could be targeting fish or adult krill but not only myctophids as previously reported (Ichii *et al*., 2007; Staniland *et al*., 2007).

Consuming larger quantities of fish when krill availability is limited is a strategy extensively used by marine predators (Murphy *et al*., 2007; Collins *et al*., 2008; Iwami *et al*., 2011). Studies have inferred that females would increase the distance of foraging trips to capture myctophids (Ichii *et al*., 2007; Staniland *et al*., 2007). We observed the same in some cases, such as the first

half of the breeding season in 2014. Here, animals showed increasing use of the long fish strategy (20%), characterized by extended trips to sea to capture fish. However, in 2016 at the same phase, animals increase considerably the "Near mix fish" strategy, which captures a higher proportion of fish but close to the colonies in the same areas than when using the "Near mix krill" strategy. This means that fish was targeted closer to the colonies at the K phase even though myctophid abundance is mostly observed the second half of the breeding season at this location (Santora, 2013). The targeting of myctophids at any time in 2016 (during K or F phase) is a reflection of how low was the abundance of krill that year.

Abundant fish availability earlier in 2016 than in other years remains a plausible explanation of why there was more consumption of fish that season than any other prey, especially since this strategy was sustained until the end of the breeding season. It is possible that fish is present early in the season but not targeted when krill is abundant. Therefore, behavior of AFS is associated with the conditions of krill at this location and the availability and seasonality of fish species in the WAP (Siegel and Piatkowski, 1990; Santora 2013). This would be consistent with our hypothesis proposed in Chapter 1 of this thesis, where we suggest that females have a preference for fish whenever is possible to be captured. However, we lack on-site fish sampling data for these seasons and, although fish density data from areas south from Cape Shirreff suggest similar concentrations of fish available, local understanding of fish populations and the effects that oceanographic events have in Antarctic myctophid dynamics is necessary to test this hypothesis.

Strong episodic krill age classes emerging every few years are responsible for sustaining the krill population (Trathan *et al*., 2007; Hindell *et al*., 2020). The decline of the mean size of krill (Atkinson *et al*., 2004; 2019), the effect of the increasing temperatures with the consequent

decreasing of sea ice extent, and the decrease in krill recruitment, would impact predator's performance (Fraser and Hofmann, 2003). If AFSs can adjust their behavior by increasing predation on myctophids when krill is less available, this would imply an additional stressor over already declining myctophid populations (Klemmedson *et al*., 2020). We have validated that shifting prey is the only mechanism used for individuals living at the edge of their breeding distribution to cope with additional variability. Females have a limited capacity of: diving harder (Costa *et al*., 2000) and follow the projected krill shifts in distribution as other krill dependent predators may do (Hückstädt *et al*., 2020) is very unlikely for AFSs due to their condition as central place foragers. Instead, conceptual models suggest that abandoning their offspring is the next step if extreme events intensified since individual survivorship prevails over the evolutionary pressure of saving the offspring (Costa, 2008). The influence of atmospheric events such as ENSO over Antarctica is increasing (Rahaman *et al*., 2019), and therefore the continuous monitoring of this colonies is critical as it provides more information of novel strategies that we have not seen so far, and may emerge soon in response to the pressure provided by these events over edge colonies.

CONCLUSIONS

Foraging behavior is limited by prey availability at the edge of the AFS breeding distribution. In seasons where krill density is lower (2014) or previous spring conditions lead to a reduction of krill availability in summer (2016), we can see how foraging behavior shifts toward a higher rate of fish capture. This is observed by a higher use of fish-associated foraging strategies, even in stages of the breeding season in which mostly krill should be found (Santora 2013, Polito and Goebel 2010). We did not observe changes in diving behavior, presumably due to the constraints of breeding at their "metabolic ceiling" (Costa *et al*., 2000), been the shifting of prey the only remaining alternative.

This highlights how sensitive AFS are to minor changes in prey availability at this colony, which is concerning with the current projected changes in sea ice extent and temperature that may reduce krill spawning habitats and the already observed reduction of fish populations in the area (Klemmedson *et al*., 2020). Continuous monitoring of AFS behavior in edge colonies provides priceless information of the relationship between Antarctic predators and their prey which is essential to better understand the fragility of this ecosystem.

GENERAL DISCUSSION

The Antarctic fur seal as a model

Marine mammals and seabirds are intensively studied in Antarctica. They are long-lived species capable of integrating environmental information both in space and time, and for this, they are good environmental indicators (Trathan *et al.,* 2007) and are recognized as sentinels for the study of climate change (Costa *et al.,* 2010b). Thus, the information provided by them cannot be replaced by laboratory approaches or using other short-lived species. Antarctic fur seals at Cape Shirreff represent a great model for studying foraging behavior in highly heterogeneous environments. Regardless of their reproductive status, females exhibit a high degree of site fidelity (Bonadonna *et al.,* 2001; Arthur *et al.,* 2015), allowing us to recover instruments from females and reducing the risk of losing instruments. In addition, working with known age animals enabled us to control for age and mass differences, which influence foraging behavior significantly (Bowen *et al.,* 2001; Lea *et al.,* 2009; McDonald *et al.,* 2009). Finally, the breeding colony at Cape Shirreff provides a unique opportunity to study lactating animals at their

maximum field metabolic rate during the breeding period (Costa *et al.,* 2000). Under this scenario, we can assume that individuals would not modify their effort unless limits are pushed, and no alternative strategies exist to survive and reproduce other than trying to reduce the energetic costs of foraging or to increase prey consumed. This would result in unique information that cannot be obtained from individuals of other locations other than those living at the limits of their physiology.

Environmental variability

Otariids are especially sensitive to changes since they have not evolved life history patterns that allow them to cope with resource variation (Costa 1991; 1993; 2007). In AFS, behavioral and population responses to environmental variability have been studied since the 80's (Costa *et al.,* 1989; Boyd *et al.,* 1994; McCafferty *et al.,* 1998; Lea *et al.,* 2006; Lea *et al.,* 2009; Staniland *et al.,* 2010 among others), and behavioral modifications can be summarized in two general strategies:

1.-Modifying the vertical component of foraging: Animals would work harder by exploring deeper areas, extending the time diving, increasing their dive frequency, the time of the day foraging takes place or any other possible diving modification that would allow them to obtain more or better food (e.g. Boyd *et al.,* 1994; Lea *et al.,* 2006; Goldsworthy *et al.,* 2010).

 2.- Modifying the horizontal component: Animals would travel longer distances or extend their trips to sea in response to extreme events (Costa *et al.,* 1989; Boyd *et al.,* 1994; Lea *et al.,* 2006).

These two general modifications in behavior are linked with each species life history and their degree of behavioral plasticity (for instance, see a comparison between pinnipeds facing ENSO in Trillmich *et al.,* 1991). However, the specific strategies used are likely to be related to shifts in the prey targeted in response to changes in the availability of the prey.

Changes in spatial patterns such as modifications in trip duration or distance travelled, are part of a foraging strategies (Boyd *et al.,* 1994), but other variables such as prey consumed are usually inferred. These inferences are made from prey distribution data or qualitative diet estimators presented together with behavioral data. In this thesis, we were able to link quantitative diet data with a large behavioral data set to identify foraging strategies per trip including the percentage of prey targeted, eliminating inferences associated with the prey. This has led us to confirm behavioral modifications driven by the influence of additional atmospheric events already described in previous studies, such as extended trips to sea but also, to identify new empirical information on why those trips are extended and what preys are being captured.

Moreover, we were able to identify non-lactating individuals' behavior for the first time in otariids. Our results suggest that the species' reproductive geographical limits are only given by the constraints of rearing a pup and lactation itself, but not by the species physiological limitations. This is supported with evidence of several juveniles found south from these colonies every austral summer (Santora, 2013), with numbers of individuals increasing every year as far south as Marguerite Bay (figure 6 of Appendix A, Borras-Chavez pers observation). Mothers may also start moving southward along with the projected modifications in krill distribution and whether they could succeed in this task, as other krill dependent species such as crabeaters (Hückstädt *et al.,* 2020), remain to be tested since AFS individuals could be restricted by their

site fidelity (Lunn and Boyd, 1991; Bondonna *et al.,* 2001; Arthur *et al.,* 2015). Alternatively, these reproductive colonies may increase the use of fish-associated strategies switching from krill consumption to a higher consumption of fish, especially if krill continues to contract in the area (Atkinson *et al.,* 2019). This is observed in our data when complex years with less availability of krill were compensated by using fish-associated strategies (Chapter 3).

Describing diet vs quantifying diet

There is a good understanding of AFS diet during the breeding season in several areas of the Southern Ocean (for the WAP, see citations and description in section 4 appendix B. Other locations of the Southern Ocean: Kerguelen island: Cherel *et al.,* 1997; Cherel *et al.,* 2008; Lea *et al.,* 2002 a,b, South Georgia islands: Boyd *et al.,* 1994; Boyd 1999; Iverson *et al.,* 1997a; Brown *et al.,* 1999, Bouvetoya: Biuw *et al.,* 2009). Studies have described AFS diet using multiple approaches, but the diet has never been quantified because the complete development of quantitative tools is relatively recent (see discussion chapter 2) and, in predators in which several taxa compose the diet, quantification gets even harder to accomplished since FA signature values from each prey are also needed. New tools allow us to obtain prey proportional data from FA, using statistical techniques that are used to analyze stable isotope data but with a higher accuracy to reach species-specific diet information (Guerrero and Rogers in prep (a), Guerrero and Rogers in prep (b)).

Our results were obtained from a combination of qualitative and quantitative proxies. Using only scat analysis would have bias our diet estimations since scats information constitutes only

a snapshot of what animals consumed (Bowen 2000, Tollit *et al.,* 2003; Staniland 2002). This bias can be observed in our study, in the mean number of otoliths found in the scats, where, contrary to our behavioral and FA results, we found similar average quantities of otoliths in all seasons. Therefore, the used of multiple proxies both quantitative and qualitative to estimate diet is a more accurate approach to describe diet and foraging strategies.

The quantitative analysis confirmed that at the Cape Shirreff, animals show a combined diet of multiple species (krill or fish), and each prey's proportion consumed would influence the total time invested diving per prey and trip. We showed that females maintain their diving characteristics associated with each prey, and it is only the prey's life history that defines how or where females will dive at this location. In contrast, other studies have shown modifications in diving behavior where AFS females would dive in deeper regions, increase their frequency of dives or increase the percentage of time diving (Boyd *et al.,* 1994; Lea *et al.,* 2006; Goldsworthy *et al.,* 2010). However, at Cape Shirreff, mothers have already increased their effort to a maximum (Costa *et al.,* 2000), which is observed when mothers are compared with non-lactating females (Chapter 1). The only alternative of this colony to obtain the necessary energy for maintenance and reproduction is compensating the lack of one prey, consuming another, making the necessary behavioral modifications to target the new prey.

In Chapter 1, we suggest that AFSs present a preference of fish over krill, with krill been the most consumed prey because is the most abundant prey in the Southern Ocean but not because is the first choice for fur seals. Multiple reasons sustain this hypothesis. First, breeding females in other locations such as the Kerguelen Plateau mostly feed on fish even when krill is present (Lea *et al.,* 2002 a, b, c, Cherel *et al.,* 1997). Second, in other locations females shift prey from

krill to fish under stressful scenarios even if it implies an additional effort (Reid and Arnould 1996). Others despite the presence of krill would change from fish to more energy-rich fish species (Lea *et al.,* 2006). Furthermore, non-lactating animals at Cape Shirreff are investing considerably more time diving when fish is more available than when krill is the most abundant prey. NL females would spend less than 9% of the time diving against more than 20% of L females when krill is abundant (Chapter 1). In contrast, only L females would dive more time to capture krill at this location when krill is abundant.

Moreover, the transition within the breeding season from krill consumption to fish consumption has been historically documented (Reid and Arnould 1996; Iverson *et al.,* 1997a; Osman *et al.,* 2004, Polito and Goebel, 2010; Chapter 3), and it may have to do with the temporal distribution of myctophids (Santora 2013) but is also additional evidence to support the hypothesis that AFS at this location prefer fish. Although this idea needs to be further explored, it opens the possibility that, under the current projection of a decrease in krill recruitment (Atkinson *et al.,* 2019), and its changes in distribution southward and offshore from the AFS current reproductive colonies (Hückstädt *et al.,* 2020), preference for consumption of fish species and compensatory strategies that allow differential consumption of taxa, could benefit this colony. However, this strategy may not be enough if the decline of myctophid fish species in the last decades may affect fish availability in the future (Klemmedson *et al.,* 2020).

Spatial tradeoffs

Studies have suggested that females would go to oceanic waters to forage in distant locations searching for fish (Ichii *et al.,* 2007; Staniland *et al.,* 2007). This has been established only based on fish distribution data but have never been tested on the field. In concordance with previous studies our research found that females would indeed use strategies that involve longer trips to sea in years with a higher variability, but this extension is not necessarily attributed only to fish capture, and they may also extend their trip, presumably, searching for adult krill (Far lazy krill strategy). Our data support the use of strategies oriented to capture more fish or krill using one strategy or the other, but we emphasize that these strategies combine in very similar percentages the capture of both preys and they are only oriented to capture one prey more than the other but usually consuming high percentages of both species.

Furthermore, predators are often found foraging near the continental shelf break, the associated slope, and close to sea mounts (McConnell *et al.,* 1992; Guinet *et al.,* 2001; Goebel *et al.,* 2000, Hückstädt *et al.,* 2020; Hindell *et al.,* 2020; Chapter 3). These areas are considered hotspots of biodiversity due to the inclusion of very nutrient-rich waters (Piñones *et al.,* 2013, Hückstädt *et al.,* 2020), which is why the most used strategies identified in this study involve animals exploring these locations. The use of strategies that involve reaching farther oceanic waters were increased in seasons showing less density of the most important prey: krill. Therefore, extreme events at this location may be forcing females to explore farther and farther areas than early years. Goebel *et al.,* (2000) showed that, out of 11 females targeted in 1998, the maximum distance traveled registered was less than 150 km from the colonies with a mean distance of ~100 km. In contrast, our maximum distance traveled was 774 km, with a maximum distance

registered of 532 km in the season when krill was abundant (2015). The most conservative mean distances registered in our strategies almost double the mean maximum distances described by Goebel *et al.,* (2000). This is concerning since it evidenced the changes in the distribution of krill and/or fish occurring during the last 20 years (Atkinson *et al.,* 2019) and does not only have an impact under intense oceanographic events but also on average distance traveled, which would mandate additional effort and higher energy demand for females of this colony. New measurements of the field metabolic rate of this colony to be compared with those taken at the beginning of 2000 (Costa *et al*., 2000), would reveal if indeed these colonies are pushing their limits even more than described before due to long-term changes in prey distribution and abundance.

Foraging grounds of AFS individuals from Cape Shirreff during winter are found along the Southern coast of Chile associated with the shelf break and pelagic waters of these areas as well as the Patagonian shelf-break and, in some cases, around South Georgia (Arthur *et al.,* 2016). The variety of locations that individuals may visit make winter diet studies very hard to conduct, and therefore winter foraging ecology of AFS is poorly understood. The similarity between the fish and P cluster's FA profile in this study suggests that diet, at least in the previous months before arrival at Cape Shirreff, is composed of fish species. In this thesis, we did not take into account foraging behavior of the very first trips to sea post-partum since it needs to be studied together with AFS diet estimators that could describe feeding behavior in previous seasons (spring and winter) and although we have those values, we lack FA values of the preys captured in previous seasons. As pointed out in Chapter 2, this time of the breeding season is the only time in which fat reserves are used for milk production and, therefore, the only time that these capital breeders may behave as income breeders (Houston *et al.,* 2007). Studying females

foraging behavior at winter, would also provide information to understand why all females studied in this thesis presented similar BCI upon arrival, despite the season studied. Future research should explore the relationship between female initial conditions, first-trip performance and the link of behavior with winter and spring diet.

Machine learning, accuracy, applicability, and improvements

The novelty of successfully determining prey proportions from fatty acids allowed us to use a supervised ML method trained by a data set where the prey captured was known for each trip. The advantage of these methods, such as the RFA used here, is their prediction accuracy, which is essential for its application in long-term data sets (Ladds *et al.,* 2016, Bao and Intille, 2004, chapter 3). Our predictive model showed a 76.2 % accuracy, which is substantial considering that many other factors other than the prey targeted can affect foraging behavior. Furthermore, many dives could be exploratory dives but instead are considered in the decision-making process as feeding dives.

When the algorithm was applied in chapter 3, the time invested diving and capturing each prey was consistent with the prey consumed within each season found from the fatty acid analysis. In addition, it was consistent with the progressive shift of prey consumed from krill to fish that other studies have described only from qualitative diet data (Osman *et al.,* 2004; Polito and Goebel 2010; Tarroux *et al.,* 2016; Chapter 3). Furthermore, the time invested diving was also consistent with targeting fish when krill availability was limited (Murphy *et al.,* 2007; Collins *et al.,* 2008; Iwami *et al.,* 2011). Our approach proved to be successful when applied in a more

extensive data set, opening a door for retrospective analysis on TDR behavioral data that have been accumulated during the last decades (such as the AMLR long term data set among others), especially in prey species where FA profiles are known. Other algorithms indeed proposed similar exciting opportunities (Viviant *et al.,* 2014; Volpov *et al.,* 2016), but so far, they are only capable of identifying capture attempts without recognizing species-specific diving behavior.

Technology is advancing faster than ever before, and the bio-logging industry is not the exception (see later advances in Börger *et al.,* 2020). Accelerometers are the number one instrument for detection and classification of capture attempts (Viviant *et al.,* 2014; Volpov *et al.,* 2015). Its evolution from the initial detections of movement patterns only 15 years ago (Shepard *et al.,* 2008) is promising. Today, new features such as the capability of automatically classifying prey capture attempts remotely (Pucci *et al.,* 2020), should get us close to very effective ways of saving larger amounts of behavioral data while on the field. With an improvement of the battery duration, these new features will convert this data recorder into the new best monitoring instrument of the second half of this century. We did not classify behavior from our accelerometers since we only count with a limited number of them (at the time of this thesis, these instruments were costly), and some of them failed to retrieve the data and were not as representative of the colony's behavior as the TDR data. However, treating TDR's data with machine learning approaches was a successful alternative to explored diving behavior from long-term data sets. Given the large variety of machine learning algorithms, we would follow the recommendation of Ladds *et al.,* (2016) and try additional machine learning tools to see if an improvement of our classification algorithm's predictive accuracy is possible.

Future approaches

Species' adaptative potential can be estimated by understanding the genetic variability that defines behavior (Watt and Dean 2000). This microevolutionary perspective falls short in animal groups such as mammals, in which behavior also depends on learning from facing different scenarios. New tools have been developed lately with which genetic variability within colonies and the entire population can be linked with environmental drivers. Landscape genomics- the discipline that merged population genetics and landscape ecology (Schwartz *et al.,* 2010)- could allow us to understand the genetic relationship between all breeding colonies of the Southern Ocean and the role that environmental drivers have in defining the past and current population distribution and connection with other central place foragers as has been done with penguins lately (Vianna *et al.,* 2020).

Long-term monitoring programs are declining, and along with this, the availability of long-term time series from marine mammal populations. This is a serious problem since short-term series from long-lived species are likely to be statistically underpowered and could be potentially misleading (White, 2019). This would impact our goal of achieving realistic ecosystem models for managing and conserving the Antarctic ecosystem (see sections 1 and 2 of appendix A). Furthermore, the problem is aggravated in areas such as the WAP, considered among the fastest-changing environments of the planet (Gille 2008; Whitehouse *et al.,* 2008). Today, extreme climatic events are more frequent, and there is a high degree of uncertainty about the repercussions over the life history of megafauna in Antarctica, including AFS (Forcada *et al.,* 2008). We believe that the maintenance of long-term monitoring of this colony is crucial to comprehend how AFS, as a species, will respond to the upcoming climatic scenarios and to adequately address ecosystem modeling and conservation measures in the Southern Ocean.

GENERAL CONCLUSIONS

We have successfully measured the simultaneous foraging behavior of lactating and non-lactating female AFS. This constitutes the first work in otariids measuring diving behavior of non-lactating females. Our hypothesis was correct, it is lactation what prevents lactating animals from modifying diving behavior and what drives modifications in spatial behavior to cope with this reproductive event. Contrary to non-lactating females, lactating females perform shorter trips and spend less time hauling-out, two characteristics that allow them to optimize milk provisioning events during the breeding season. Furthermore, the time budget within diving behavior is compromised, with lactating females diving more times per trip but optimizing (reducing) the time spent in the different phases of a dive compared to non-lactating individuals. Extending the time spent diving but reducing the time per dive allows lactating females to increase prey capture attempts and to maintain short trips to sea. There are differences in behavior between L and NL females that are associated to the prey targeted and the additional effort of L females described is more evident when krill is more abundant in the foraging locations than fish.

We generated and validated a predictive algorithm based on fatty acid prey-specific data that allows us to use machine learning tools to describe AFS behavior associated to capturing both fish and krill. Contrary to what was hypothesized, capturing krill at a single-dive scale demands more time within a dive than capturing fish. However, animals may acquire multiple krill per dive event and consequently, a higher prey proportion, than capturing a single krill. We hypothesized correctly that fish is consumed only when krill was less abundant (Chapter 3), and therefore, the consumption of fish is a compensatory strategy presumably in search of an energy-richer prey than krill. This compensatory strategy is used when 1.- fish is available and abundant (usually during the second half of the breeding season) or 2.- krill is less abundant. Validating machine learning tools with diet data is a novel approach that can be implemented retrospectively to evaluate decades of TDR data in this, and potentially, other otariids around the globe.

We successfully applied our machine learning algorithm on a three-year data set to fully characterize foraging females' strategies at the species' southernmost breeding site and identify the differential use of strategies within and between breeding seasons. We identified that strategies suggesting longer trips and that imply foraging in farther areas (oceanic waters) than the regular foraging areas (continental shelf and shelf-break) are more used in years when krill size is different (2014) or less abundant (2016). The intrusion of myctophids into the continental shelf (close to the colonies) during the second half of the breeding season is observed by a significant change in the foraging strategies used (from more krill-associated strategies to more fish-associated strategies). As presented in our hypothesis, the area's highly heterogeneous

conditions leave little room for modifications in diving behavior, as proposed by other authors (Costa, 2008). The only modifications possible are changes in the prey targeted (from more krill to fish), even during months where mostly krill have been described in their diet which is also consistent with our hypothesis. The respective modifications in behavior between contrasting years are usually identified by changes in the strategy used in difficult years but are hard to identify when only the mean values of the different foraging variables are compared between seasons.

Females of this colony are exploring more and more offshore areas than previously reported not just when they are breeding under scenarios highly influenced by extreme atmospheric events but also, in years where krill is abundant. This highlights that long-term changes in krill distribution (i.e. adult krill shifting southward, toward more oceanic waters, and scattering), are constraining the colony. Therefore, as Trillmich *et al.,* (1991) suggested, it is no longer possible to identify what constitutes a "normal" breeding season when it comes to behavioral responses to prey fluctuations caused by intensification of atmospheric events that affect this highly heterogeneous environment.

The projected shift in krill distribution and the decline of Southern Ocean myctophid populations would impose an unprecedented scenario for this colony in the near future. For this, the continuity of a long-term monitoring program of the southernmost breeding colony is of paramount importance if we want to correctly model the future of the species. The secrets of adaptation may be exposed by those living in the fast lane of life.

APPENDIX A. PINNIPEDS FORAGING BEHAVIOR AND THEIR SPATIAL OVERLAP WITH FISHERIES IN THE WESTERN ANTARCTIC PENINSULA[1]

ABSTRACT

Since its establishment in 1982, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has successfully managed fisheries in the Southern Ocean, based on an ecosystem-based approach. In recent decades, the krill fishing fleet has increased its spatial and temporal concentration in certain areas, hence increasing the risk of competition with predators. Antarctic pinnipeds are composed of five species of true seals (phocids) and one species of Fur seal (Otariid). Although they show different diets and foraging behavior, krill and fish are the most important prey items for most species highlighting the need of reviewing the relationship between fisheries and pinniped foraging behavior and distribution, particularly in the Western Antarctic Peninsula (WAP) where our understanding on spatial utilization, niche overlapping and foraging behavior among pinnipeds is recent.

This chapter explores current information available on pinniped foraging behavior and potential overlap with fishing grounds around the WAP. Accounting for changes in the catches, increased environmental variability associated with climate change, the lack of knowledge on pinnipeds winter foraging distribution and information gaps of some pinnipeds (e.g. the Ross seal) in the WAP, are important elements that needs to be considered in the future krill management approach to maintain a sustainable framework of this complex ecosystem.

1.- CCAMLR and the protection of Antarctic marine life

The exploitation of Antarctic marine living resources began in the late 17th century with the first expeditions that sailed down to the Southern Ocean for exploring. After a century of pinnipeds, whales and penguin's over-exploitation the industry shifted focus to other resources, such as fish and krill. The depletion, after a couple of years, of fish species such as marbled rock cod (*Notothenia rossi*) in the early 70s, the mackerel icefish (*Champsocephalus gunnari*) in the late 70s and early 80s (see Tin *et al.,* 2009) and the quick development of the krill fishery with significant catches after a few years, raised concerns that unregulated fisheries could cascade negative impacts on other important members of the Antarctic marine ecosystems (i.e. seals, seabirds, whales and fish). Based on these concerns, in 1980 the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) was established and then entered into force in April 1982 with the aim to protect Antarctic marine life. The convention text stated in Article II that the objective is the conservation of Antarctic marine living resources and specifies that for its purposes, the term "conservation" includes rational use.

The commission is formed by 26 members (25 countries and the European Union) and 10 countries as acceding states. The convention applies to all Antarctic populations of finfish, mollusks, crustaceans and seabirds found south of the Antarctic Convergence (Figure 1). CCAMLR has a decision-making body, the Commission, which is advised by the Scientific Committee, based on the best available science. Hence, managing the fisheries and protecting Antarctic marine living resources based on an ecosystem-based approach, regulated by the agreement and adoption of a comprehensive set of conservation measures (CMs). These CMs are reviewed and developed each year and are grouped into four categories: compliance, general fishery matters, fishery regulation and protected areas. Shortly after its establishment, CCAMLR became a reference for fishery management by moving away from the commonly used single-species approach of fisheries to an ecosystem-based approach following a precautionary principle in its management (Constable, 2011).

Although CCAMLR specifically excludes whales and seals which are the subject of the International Convention for the Regulation of Whaling and the Convention for the Conservation of Antarctic Seals, respectively, marine mammals are protected by specific

conservation measures that are established to minimize incidental mortality (e.g. CM 25-03 "Minimization of the incidental mortality of seabirds and marine mammals in the course of trawl fishing in the Convention Area"[2]).

Currently, the krill fishery is the most important fishery in the convention area. Although, it is still a small fishery compared with other fisheries around the world, its management procedures are critical due to the wider implications for the ecosystem and the key role that Antarctic krill plays on the food web (Atkinson *et al.*, 2012).
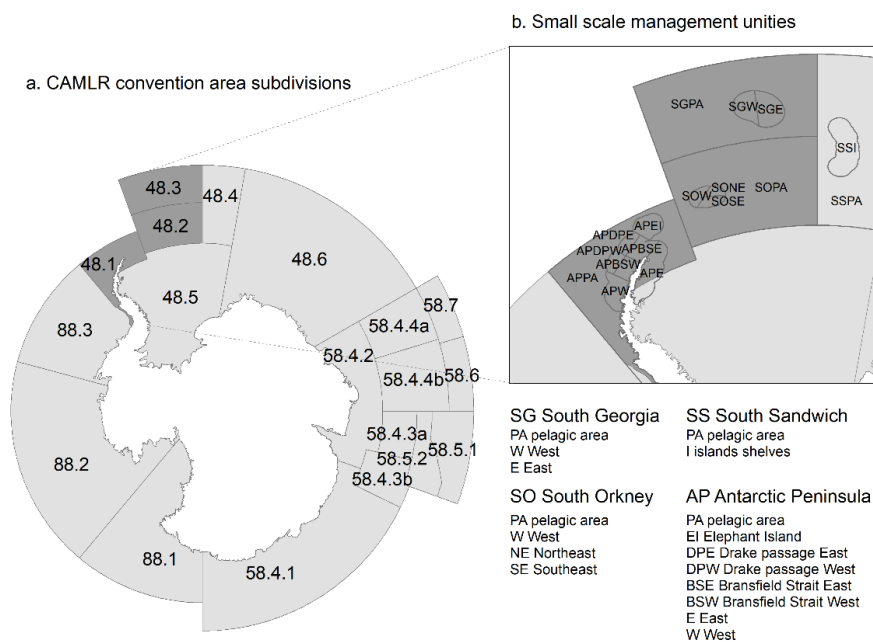
Figure 1. The CCAMLR Area. A. Numbers indicate FAO statistical areas, subareas and subdivisions. Dark-greyed areas show sub-areas within area 48 (subareas 48.1, 48.2 and 48.3) where krill fishery mostly occurs. B. Close up to subareas 48.1, 48.2 and 48.3 and the small-scale management units (SSMUs) within the subareas. These units are devised for spatially subdividing the krill catch limits (SC-CAMLR 2002). SSMUs: 48.1: Antarctic Peninsula East (APE), Antarctic Peninsula West (APW), Bransfield Strait East (APBSE), Bransfield Strait West (APBSW), Drake Passage East (APDPE), Drake Passage West (APDPW), Elephant Island (APEI), Pelagic Area (APPA); SSMUs 48.2: North East (SONE), Pelagic Area (SOPA), South East (SOSE), West (SOW); SSMUs 48.3: East (SGE), Pelagic Area (SGPA), West (SGW); SSMUs 48.4: Pelagic Area (SSPA), Inshore (SSIS).

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[2] See the full list and description of the conservation measures in "Schedule of conservation measures in force", available at www.ccamlr.org

In accordance with CCAMLR's ecosystem approach, in 1989 the Convention established the CCAMLR Ecosystem Monitoring Program (CEMP) to provide information on the effect of fisheries on dependent species (those species that feed on the target species or are impacted by the removal of the targets species from the food web), aiming to i) detect and record significant changes in critical components of the marine ecosystem within the Convention Area, to serve as a basis for the conservation of Antarctic marine living resources, and ii) distinguish between changes due to harvesting of commercial species and changes due to environmental variability, both physical and biological. To accomplish this, CCAMLR selected a series of indicator species including penguins, petrels and the Antarctic fur seal that are monitored using different parameters such as foraging trip duration, offspring growth rates and breeding success. Other krill-dependent species, such as the crabeater seal, have not been included because they live in the pack-ice and so are not amenable to repeated/annual monitoring. In addition, incidental mortality of marine mammals due to the krill fishery are recorded by scientific observers on board, which are part of another successful program established by CCAMLR, the Scheme of International Scientific Observation (SISO). This scheme plays a key role in developing approaches to reducing the impact of fishing on the ecosystem by collecting data on the effectiveness of mitigation measures. Since 2003, CCAMLR has made several efforts in order to develop, improve and implement mitigation methods to reduce incidental mortality of marine mammals (e.g. reporting by observers and the employment of seal-exclusion devices (SEDs)). The adoption of these mitigation methods has greatly reduced seal mortalities, for instance zero mortality of seals recorded between 2008 and 2014; three Antarctic fur seals incidentally captured in 2015 and 2016; and 19 Antarctic fur seals incidentally captured in 2018. Those numbers indicated the success of the mitigation measures applied, as before the adoption of these mitigation methods incidental bycatch of fur seals was considerably higher, i.e., 292 fur seals caught in subarea 48.3 in 2004 and 97 in subarea 48 in 2005 (CCAMLR, 2018).

2. The krill fishery at the West Antarctic Peninsula

The krill fishery is managed as an "Olympic-style fishery" with an opening date (1st of December) and a defined amount of krill allowed for extraction. Members are expected to notify the intention to harvest krill by the 1st of June of the preceding year.

Although the fishery is established in subarea 48 and division 58.4.1 and 58.4.2, fishing is currently conducted in subareas 48.1 to 48.4 (Figure 1). The interim catch limit, known as "trigger level" (CM 51-01[1]) is 620,000 tons, distributed proportionally in subareas 48.1 (25%, 155,000 tons), 48.2 (45% 279,000 tons), 48.3 (45%, 279,000 tons) and 48.4 (15%, 93,000 tons) as stated in CM 51-07[1]. This trigger level represents approximately 1% of the estimated biomass of krill in the region and was decided based on the CCAMLR Survey conducted in 2000 (Constable *et al.,* 2011). The lack of regular large-scale surveys produced controversial points of view about the existing biomass of krill and whether it is stable or decreasing (Cox *et al.,* 2018; Atkinson *et al.,* 2019; Hill *et al.,* 2019). A recent multinational survey conducted in 2019 in area 48 reported preliminary a biomass of 62.6 million tons (SG-ASAM report 2019), However, there is enough evidence pointing out that krill biomass decreased in sectors of the Antarctic Peninsula (Atkinson *et al.,* 2019).

Although catches are relatively low compared to the overall estimated biomass, the fishing fleet has increased its concentration in both spatially and temporally since the mid-2000s (see section below). This could increase potential risk of competition between predators and fisheries, especially in those areas where spatial overlap occurs.

The spatial and temporal dynamics of the exploitation for krill at the WAP is related to the movement of the fleet among the different subareas within the Scotia Arc (area 48), including fishing grounds around the South Orkneys (48.2) and South Georgia (48.3) islands (Figure 1). Antarctic krill catches started with exploratory operations in the 1970s and regular catches started in 1980 (Nicol *et al.,* 2012). Since then, the first relevant period was 1980-1992 when larger catches of 350,000 tons were caught per season, mostly at South Orkneys and South Georgia islands (Figure 2). Later, catches decreased below 150,000 tons per season between 1993-2007. From 2008 onwards, a renewed economic interest has motivated larger catches, peaking in 2018 around 300,000 tons mainly in South Orkneys islands and over new fishing grounds at the WAP. Particularly, the fishing season 2009/10 initiated a new phase of the krill fishery at WAP, going from a mean seasonal catch of approximately 46,500 ± 27,000 tons (period 1980-2009) to closely 155,000 tons per season (the catch limit) between 2010 to 2018 (Figure 2).
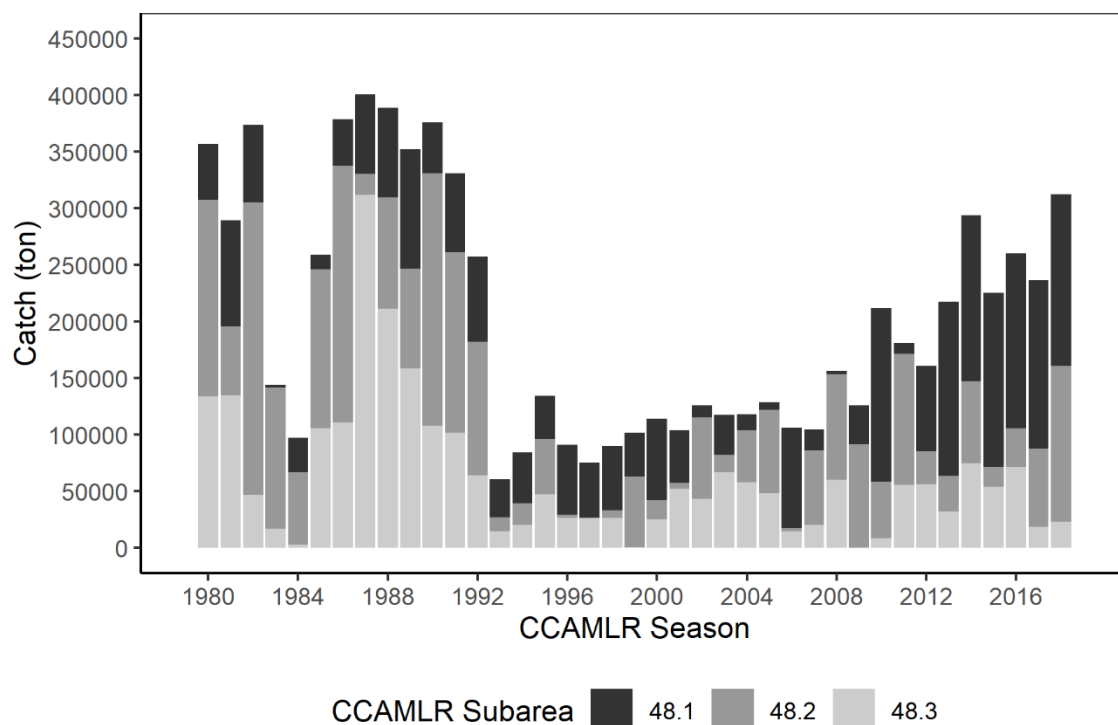
Figure 2. Seasonal catch of the krill fishery in subareas 48.1, 48.2 and 48.3. Data source: CCAMLR Statistical Bulletin 31 (www.ccamlr.org)

2.1 Operational variability

The successful development of new fishing technologies has imposed new scenarios for the krill fishery industry. The fishing dominance of Japan, Russia and Poland during the 1980s - 1990s is today led by Norway, China and Korea. Other members such as Chile and Ukraine have fished intermittently with relatively lower catches compared with the former members. The typical traditional mid-water trawl used for krill harvest has partially been replaced by a continuous mid-water trawl system introduced by Norway, capable of operating uninterruptedly by days or weeks without the need of retrieving the net (Nicol *et al.,* 2012).

2.2 Spatial and temporal variability

Fishing operations at the WAP have experienced significant changes in the spatial and temporal use of the fishing grounds over the last four decades (Figure 3). In 1980s - 1990s, catches were conducted around Elephant Island (APEI) and west off South Shetland islands (Drake Passage side, APDPE and APDPW) (Kawaguchi *et al.*, 2006), however since 2000, and specially in

2010, the fleet moved southward into the Bransfield (APBSE and APBSW) and Gerlache straits (APW) concentrating their catches in specific and well-defined fishing hotspots (Santa Cruz *et al.,* 2018). The temporal dynamic throughout the fishing season is strongly modulated by the presence and persistence of the sea-ice coverage (Kawaguchi *et al.,* 2009). During the 1980s and 1990s, the fishing fleet operated in the Austral summer (December to March) before the sea-ice expanded. Since 2000 the thinning and retreat of sea-ice (Stammerjohn *et al.,* 2008) has allow fishing fleets to explore new and highly productive areas for longer periods, especially in the Bransfield and Gerlache straits, where the fleet is capable to operate until August/September (Figure 4), even exceeding summer catches (Watters *et al.,* 2020). This period is now recognized as the winter fishery (Santa Cruz *et al.,* 2018).
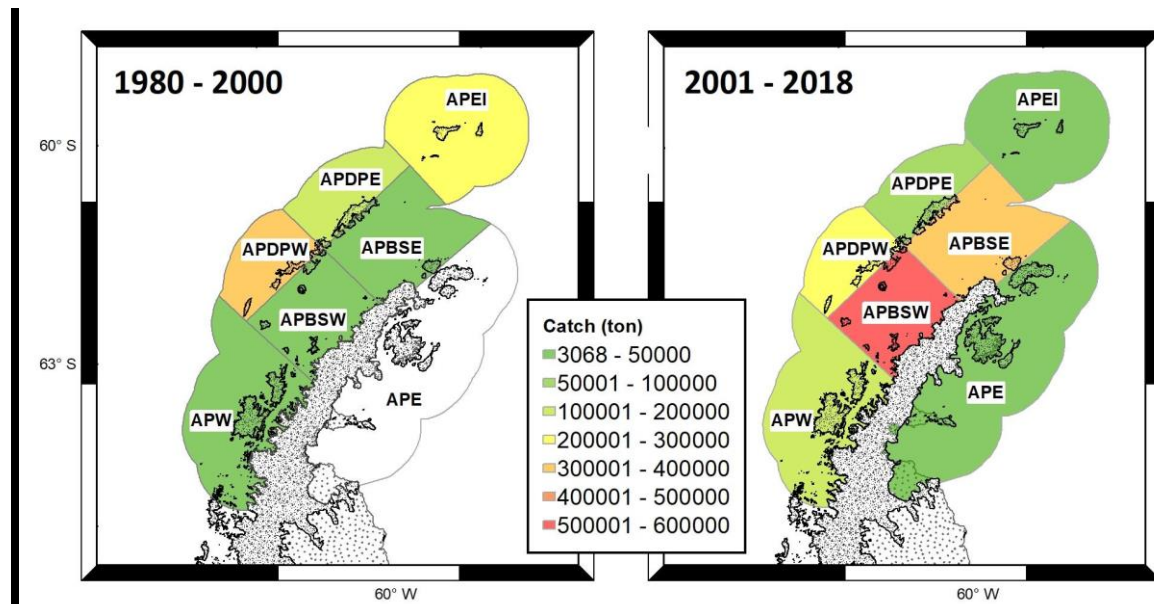
Figure 3. Cumulative catch of the krill fishery among CCAMLR SSMUs for the period 1980 – 2000 and 2001 - 2018. Data source: CCAMLR Statistical Bulletin 31 (www.ccamlr.org).
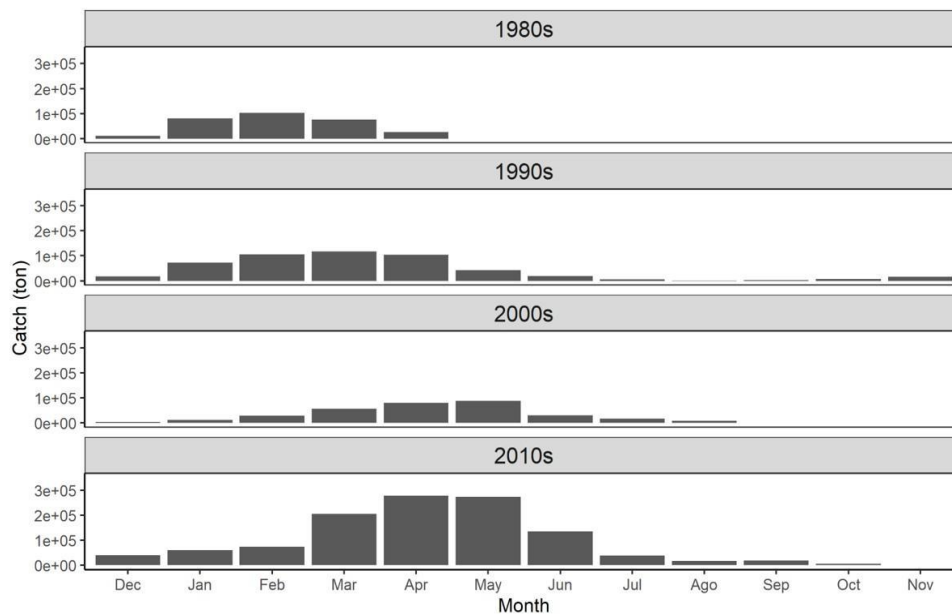
Figure 4. Monthly catches of the krill fishery around the Antarctic Peninsula (subarea 48.1). Data source: CCAMLR Statistical Bulletin volume 31 (www.ccamlr.org).

3. Other fisheries at the WAP

Currently, there are no commercial fisheries operating in the WAP area other than krill fisheries. Due to past overexploitation, finfish fisheries in the WAP were prohibited in 2017. Notothenioids are long-living fishes, whose characteristics and population dynamics (i.e. La Mesa *et al.,* 2004, Hanchet *et al.,* 2015, Riginella *et al.,* 2016) make them particularly sensitive to overexploitation (i.e. Jennings *et al.,* 1998, Dulvy *et al.,* 2003), and recovery from disturbance events could be slow, taking even decades in some species (Jones *et al.,* 2003, Barrera-Oro *et al.,* 2017). CMs were designed to protect fish populations of icefish, myctophids such as *Electrona carlsberg*, all *Dissostichus* spp., notothenids such as *Gobionotothen gibberifrons*, *Lepidonotothen squamifrons*, *Notothenia rossii* and all other finfish species (CM 32-02). Nowadays in order to protect and recover finfish populations the only exception to catch this species in the WAP is through approved scientific research programs (e.g. Arana *et al.,* 2020).

4. Antarctic Pinnipeds Foraging Behavior

Unlike terrestrial mammals, foraging behavior in marine mammals is complex to quantify due to the lack of direct observation. Today, the rapid expansion of technology has helped us to deal with these difficulties (Costa *et al.,* 2010a,b, Harcourt *et al.,* 2019, Börger *et al.,* 2020). This relatively new branch of ecological science is called "Bio-Logging" and is defined as the use of miniaturized electronic instruments attached to animals to register and transmit data related to movement, behavior, physiology and/or the environment associated to an animal (Rutz and Hays 2009, Wilmers *et al.,* 2015). The first instruments elaborated were tested in an Antarctic pinniped species (the Weddell Seal, Kooyman 1967) and ever since, knowledge of foraging behavior in Antarctic pinnipeds has increased exponentially (Hindell *et al.,* 2020). When used together with diet estimators (Banks *et al.,* 2014) we can fully comprehend behavior and physiology on a wide variety of marine species including, Antarctic pinnipeds.

 Six pinniped species are found in Antarctic waters: five phocids (Southern Elephant seal *(Mirounga leonina)*, Crabeater seal (*Lobodon carcinophagus*), Weddell Seal (*Leptonychotes weddellii*), Leopard seal (*Hydrurga lepton*yx), Ross Seal (*Ommatophoca rossii*)) and one otariid, the Antarctic fur seal (*Arctocephalus gazella*). All of them breed almost exclusively in the maritime Antarctic and sub-Antarctic islands. Numbers are impressive. These six species accounts for much of the total world biomass of pinnipeds (Laws 1977, 1985). To sustain these large populations, food characteristics (i.e. abundance, quality and prey distribution) need to match predators' energy requirements, and the strategies to achieve this can only be comprehended in the lights of their foraging behavior (Hindell *et al.,* 2020).

The next section aims to describe the current knowledge on species feeding, behavior, foraging distribution, and ecological niche utilization. Along the text, we will evaluate how past and present fisheries (described in sections 2 and 3) overlap with both diet and foraging spatial distribution of Antarctic pinnipeds. As the other sections of this chapter, this segment focus on waters of the WAP with mention on the foraging diet and distribution of the species outside the peninsula only for the sake of comparison and to provide evidence on the important role that pinnipeds play within the trophic structure of Antarctic ecosystems (Costa and Crocker, 1996).

4.1 Diet and feeding strategies

In early years, Antarctic pinnipeds diet was described only based on scats analysis and stomach content. These diet estimators present a series of biases that prevent quantification of actual prey consumed (Dellinger and Trillmich, 1988, Staniland 2002). In the last twenty years, new tools such as stable isotopes and fatty acid analyses have improved considerably the description and quantification of temporal and spatial feeding behavior on pinnipeds. The information of this section is based on both old and new approaches used during the last decades.

Krill, fish and squid are the three main taxonomic groups targeted by pinnipeds in the WAP. Although these groups differ in relevance, timing and the persistence in the diet among species, all three groups have been described at some point in the diet of all pinnipeds.

The Antarctic krill (*Euphausia superba*) is not only the most important marine fishing resource exploited currently by fishery (sections 1 and 2) but also the central species of the Antarctic food webs (Kock and Shimadzu, 1994, Hofmann and Husreyoglu, 2003) and due to its high abundance and temporal persistence, it is especially important in the WAP (Atkinson *et al.,* 2004). Crabeater seals and Antarctic fur seals are known to feed almost exclusively on krill. This does not mean that they would not eat other prey items (see below) but they are the consumers of the largest amounts of krill in Antarctic waters (Øritsland 1977, Hill *et al.,* 2006, Polito and Goebel, 2010). In addition, krill may play a relevant role on the diet of leopard seals depending on the season and the locations where animals are hauling out.

Fish is the second most important prey taxonomic group for pinnipeds in the Southern Ocean, being highly consumed by elephant and weddell seals (Bradshaw *et al.,* 2003, Heerah *et al.,* 2013, Goetz *et al.,* 2017, Brault *et al.,* 2019). With temporal variation and in a lower proportion, it can also play an important role in the diet of Antarctic fur seals (Polito and Goebel, 2010, Santora 2013, Klemmedson *et al.,* 2020) and leopard seals (Krause *et al.,* 2015). Fish species targeted varied among seal species, but most of the consumption is represented by myctophids and nototheniids (Barrera-Oro 2002).

Fish is the second most important food resource for megafauna throughout the Southern Ocean, but squids and octopus may be as important as fish species in the WAP. Elephant seal foraging behavior suggests an active and recurrent feeding on this prey in deeper waters of the Peninsula (Bradshaw *et al.,* 2003). Although little is known about Ross seals foraging behavior, their teeth

are adapted to capture cephalopods (Thomas and Rogers, 2009) and descriptions in other areas of the continent suggest that squid may be the main prey item of this species (Brault *et al.,* 2019, Southwell *et al.,* 2012).

4.1.1 Antarctic Fur seals (Arctocephalus gazella)

Figure 5. Antarctic Fur Seal. A mother and her offspring. Photo Credits: Renato Borras-Chavez.

As opposed to other pinnipeds, female Antarctic fur seals are found in Antarctic waters in the Austral summer only during the breeding season (Figure 5) but an increased number of juveniles and non-breeding males are found in other areas of the Peninsula (Figure 6) remaining for the rest of the year. The biggest breeding colony of AFS is located at the South Georgia´s islands with millions of animals (54°00'S; 38°02'W, Boyd *et al.,* 1995b). In the WAP to the best of our knowledge, the biggest breeding colony is located at Cape Shirreff Livingston Island (62°28'S; 60°46'W, Figure 6, Hucke-Gaete *et al.,* 2004). During winter, animals would travel long distances to settle and feed in highly productive areas north of the South Shetland Islands (SSI) and consume mostly fish and squid (Polito and Goebel, 2010); however, few studies describe winter diet for colonies in the WAP. Therefore, this section is focused mostly on what we know on female's diet during summer.

More than 80% of AFS diet is composed by krill, making this prey item extremely important during the breeding period (Reid and Arnould, 1996, Casaux *et al.,* 1998, Osman *et al.,* 2004, Polito and Goebel, 2010). The annual consumption of krill at South Georgia alone has been

estimated at almost 4 million tons (Boyd, 2002). In addition, based on scat analysis and stable isotopes, fish and squid are also important (Casaux *et al.,* 1998, Daneri *et al.,* 1999a,b, Casaux *et al.,* 2003, Polito and Goebel, 2010), and their relevance seems to increase as the breeding season progress, incrementing the proportion of fish consumed in the second half of the breeding season (Osman *et al.,* 2004, Polito and Goebel, 2010, Lea *et al.,*,. 2002, Santora 2013, Borras-Chavez in prep). The most consumed myctophid species belong to the genera *Gymnoscopelus* sp. and the species *Electrona antarctica*. A long-term scat analysis has shown that, within the first decade of 2000, there was a higher presence of fish earlier in the season (Goebel Tech report 2008-09) as opposed to the timing of what is currently found in the last decade (Santora 2013, Borras-Chavez in prep). This may have to do with the decline of some mesopelagic species in the last years around the AFS feeding areas (Klemmedson *et al.,* 2020). When quantifying diet from colonies at Cape Shirreff, recent studies suggest that the proportion of fish consumed varies seasonally depending on the environmental variability and the availability of the main prey item; krill, which hold as the main prey item during the entire season (Borras-Chavez in prep). Although it is still unclear, it has been suggested that the progressive increase of fish may be related to the reduction of krill in some areas and the increase of some fish species in late summer (Santora 2013) which would also be driving different foraging strategies in other locations (Goldsworthy *et al.,* 2010). All these variables together would shape the foraging strategies utilized by AFS females in late stages of the breeding season, especially considering that although not as abundant as krill, fish species seems to play a critical role in their diet (Staniland *et al.,* 2007, Cherel *et al.,* 1997, Goldsworthy *et al.,* 1997, Lea *et al.,* 2002b).

Early investigations have demonstrated the existence of sex differences in prey selection. At King George Island, scats analysis showed that AFS males have a higher consumption of myctophid fishes (*Electrona antarctica* and *Gymnoscopelus* sp.) in spring and summer compared to lactating females (Daneri and Coria, 1992, Daneri *et al.,* 2005). This highlights the need for deeper understanding of males and juveniles foraging ecology within the WAP as the number of both groups have increased along the Peninsula (Figure 6) and the Bransfield Strait (Santora and Veit, 2013, Borras-Chavez, personal obs.).

Figure 6. Drone picture of Antarctic fur seal juvenile and subadult males at Marguerite Bay (68.5° S, 68.5° W), Antarctica, 2017. All apparent "dots" on land correspond to juvenile and male individuals hauling out in the surroundings of the Chilean station Carvajal. Animals arrive in this area in the Austral summer- late February. Photo courtesy of Enzo Capurro.

4.1.2 Crabeater Seal (Lobodon carcinophagus)

Figure 7. Crabeater Seal. Teeth adapted to krill consumption. Photo Credit: Renato Borras-Chavez.

Crabeater seals (Figure 7) are one of the most abundant marine mammal species of the world (14-30 million individuals; Southwell *et al.,* 2004, Bengtson *et al.,* 2011). With teeth structure evolved for krill capture, crabeater seals can consume ~63 million tons of krill (Laws, 1977) with some individuals exclusively consuming this resource (revised in Southwell *et al.,* 2012, Hückstädt *et al.,* 2012a, Brault *et al.,* 2019, Hückstädt *et al.,* 2020). Antarctic silverfish (*Pleurogramma antarcticum*) has also been found on crabeater diet (Lowry, 1988) but may correspond only to incidental feeding. The close relationship between crabeater and krill, make this species highly vulnerable to potential negative interactions with the growing of krill fishery activities in the Southern Ocean (section 4.4, Hindell *et al.,* 2020), and the projected environmentally-induced changes of krill distribution that will modify krill spatial availability (Hückstädt *et al.,* 2020).

4.1.3 Southern Elephant seals (Mirounga leonina)

Figure 8. Southern Elephant Seal. A male, a female and a newborn. Foto Credits: Renato Borras-Chavez

The description of the southern elephant seals diet is still a challenge since hard remains are usually too digested for prey identification (Biuw *et al.,* 2007). Stable isotopes and instrumented animals suggest different foraging strategies depending on locations, sex, season and life history (Muelbert *et al.,* 2013, Gallon *et al.,* 2018). In East Antarctica, pelagic feeders would target mostly squid whereas those individuals feeding along the shelf would mostly target fish species (Bradshaw *et al.,* 2003). Other individuals such as those located in the Kergüelen Plateau, consume mainly fish (Cherel *et al.,* 2008). In the WAP, feeding strategies seem to be similar to those described for other areas of Antarctica. Animals feeding close to the shelf break would perform shallow dives (<500m) targeting fish species, whereas the deep divers in oceanic waters are mostly in search of squid (Hückstädt *et al.,* 2012b, Hindell *et al.,* 2016). Although it may sound as a generalist feeding strategy, individuals are very specialists (Hückstädt *et al.,* 2012b) and the prey targeted differs considerably between individuals.

4.1.4 Ross Seal (Ommatophoca rossii)
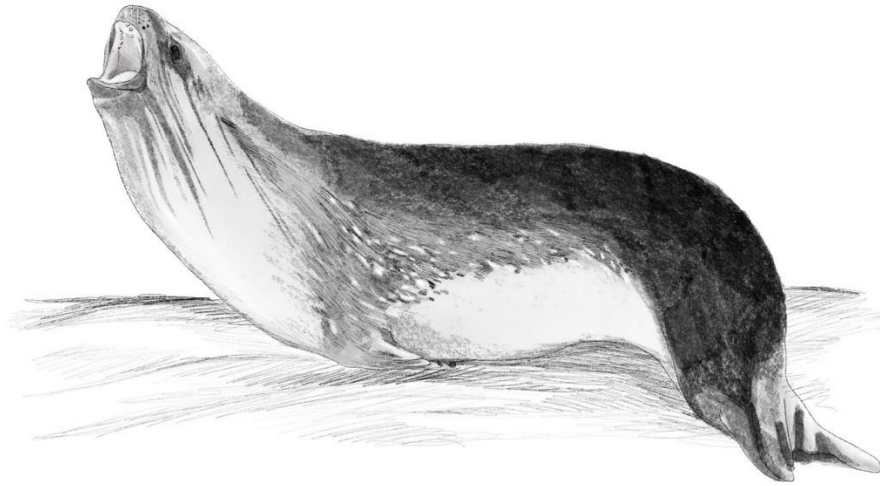
Figure 9. Ross Seal. Is the least known pinniped species in Antarctica. Illustration credits: Alejandra Ramirez.

Ross seal is the most cryptic species of all pinnipeds around the world (King, 1970, Folkens and Reeves, 2002, Thomas and Rogers, 2009), and therefore, knowledge about their foraging behavior is scarce. Squid is considered the most important food item (Southwell *et al.,* 2012, Brault *et al.,* 2019), which is consistent with their adapted teeth for capturing cephalopods (Thomas and Rogers, 2009). Mesopelagic fishes (Myctophids) and mid-water squid species have also been described as important prey items of this species year-round (King 1970, Bengtson and Stewart 1997, Blix and Nordøy 2007). A few descriptions suggested that the fish *Pleurogramma antarcticum* is part of the Ross seal diet (Blix and Nordøy, 2007, Skinner and Klages, 1994). The lack of evidence showing krill consumption by this species and the reduced population numbers estimated around Antarctica (131.000 individuals, Erickson and Handson, 1990) suggest little possibility of overlap between Ross seal and fisheries along the WAP.

4.1.5 Leopard Seals (Hydrurga leptonyx)

Figure 10. Leopard Seal. Photo Credits: Renato Borras-Chavez

Leopard seals are the pinnipeds with the most diverse diet, eating crustaceans, fish, krill, cephalopods, penguins and even other seals (reviewed in Southwell *et al.,* 2012, Schwarz *et al.,* 2013, Krause *et al.,* 2015). Resident female leopard seals are responsible for modulating population growth of Antarctic fur seals in important breeding areas (Boveng *et al.,* 1998, Schwarz *et al.,* 2013, Krause *et al.,* 2020). This is why it has been suggested that leopard seals regulate populations of krill-consuming species, acting as key top-down regulators in Antarctic ecosystems (Scharwz *et al.,* 2013).

Diet of leopard seals vary seasonally around the Antarctic continent (Hall-Aspland *et al.,* 2005, Southwell *et al.,* 2012). Overall, Silverfish, demersal fish and krill are mostly preyed on in winter and spring (Siniff and Stone, 1985; Green and Williams, 1986, Lowry *et al.,* 1988). In summer, animals consume newly weaned crabeater seals (Siniff and Stone, 1985, Siniff 1991), penguins and AFS newborns (Siniff and Stone, 1985, Forcada *et al.,* 2009, Casaux *et al.,* 2009, Schwarz *et al.,* 2013, Krause *et al.,* 2020). In addition, they would opportunistically feed on demersal fish (Casaux *et al.,* 2009, Krause *et al.,* 2015). Krill is also found in the diet of leopard seals during summer in the Peninsula, especially when the number of penguin fledglings and AFS pups are low (Casaux *et al.,* 2009, Borras-Chavez Pers obs). In certain locations, krill can be the most abundant prey item during summer (Casaux *et al.,* 2009). Recently, Krause *et al.,* (2020) suggested that there are sex differences in diet where females would transit to summer diet and therefore energy richer prey more rapidly than males. However, only two males were included in this study and a higher sample size is necessary to draw more accurate conclusions regarding these differences.

4.1.6 Weddell Seal (Leptonychotes weddellii)

Figure 11. Weddell Seal. Photo Credit: Renato Borras-Chavez

Weddell seals are generalists whose diet varies geographically (reviewed in Southwell *et al.,* 2012) and seasonally (Goetz *et al.,* 2017), but is mostly composed by different fish species. While winter diet in East Antarctica is mostly composed of pelagic fish, predominantly *Pleurogramma antarcticum* (Green and Burton, 1987, Heerah *et al.,* 2013) they can change prey when this species is not present or abundant. In the Ross sea, where fish diversity is relatively low, the diet is dominated by Notothenioid species that are consumed by Weddell seals likely based on availability (i.e. *Trematomus* sp., *Notothenia coriiceps* and *Pleurogramma antarcticum*, Burns *et al.,* 1998, Davis *et al.,*1999, Goetz *et al.,* 2017). This is different in the WAP and the Scotia Arc where squid seems to be as important as fish in weddell seals' diet (Lipinski and Woyciechowski, 1981, Clarke and Macleod, 1982, Green and Burton, 1987, Daneri *et al.,* 2012, Casaux *et al.,* 1997; Casseux *et al.,* 2006).

4.2 A note on fish feeding

Ponganis and Stockard (2007) described a frequent and abundant consumption of the economically important Antarctic toothfish (*Dissostichus mawsoni*) by crabeaters in McMurdo based on video recording and visual sight. This has not been described around the WAP but has been suggested as a potential prey for fish-eating seals (Brault *et al.,* 2019). The absence of

toothfish in the fish-eater-seals diet may be because descriptions in the Peninsula and other sites of Antarctica are based on scats and stomach contents, but Antarctic toothfish is hard to identify with these techniques as seals rarely eat the bones (Ainley and Siniff, 2009). In addition, the few descriptions using stable isotopes do not allow discriminating by species and can just suggest toothfish as a potential prey item (Brault *et al.,* 2019). This is also true for other Antarctic seals, such as leopard seals at Cape Shirreff which remove the head of some fish species before eating them (Krause *et al.,* 2015) making estimations from scats at some point, unreliable. Although some authors have mentioned that toothfish is mainly eaten by specialist or older individuals and are not as important as other resources, they may be more important than previously thought, especially in areas where these fisheries still exist such as the Ross Sea (Mormede *et al.,* 2017). The fact that some preys cannot be recognized using certain diet estimators highlight again, the limitations we still face with our current diet analyses and how careful we should be when interpreting diet data. As more and more information we gather that would lead us to identify, at a species level the prey items, we will better understand the true diet of Antarctic pinnipeds.

4.3 Spatial and temporal foraging patterns

Many marine mammals are distributed throughout large geographical scales and Antarctic pinnipeds are not the exception. The Southern Ocean encompasses an area of 31.8 million km^2 and most of the pinniped's species are found almost entirely within this area and along the Circumpolar current (Figure 12). In this section we explored the spatial foraging distribution of Antarctic pinnipeds, with a special focus in the WAP area.
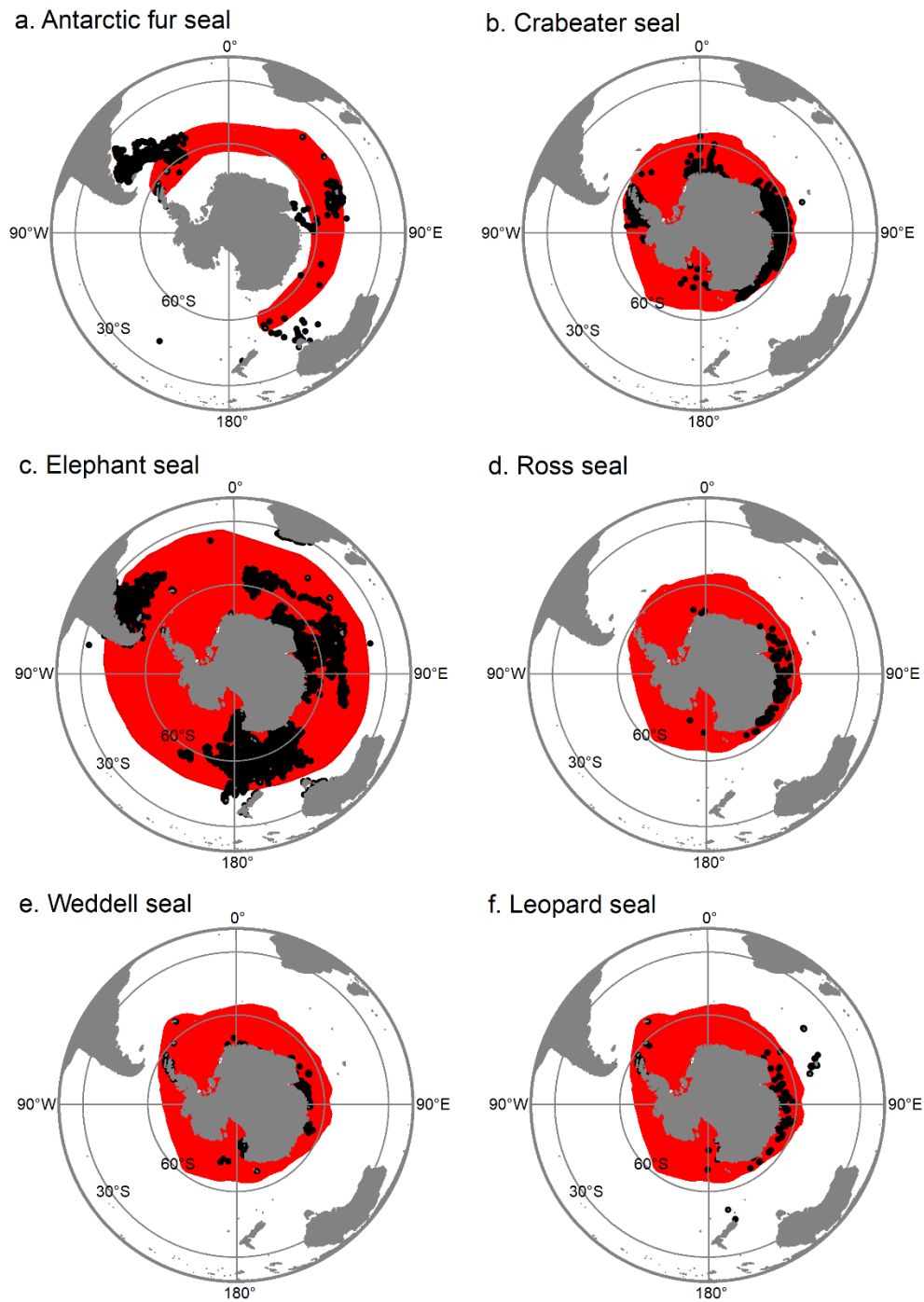
Figure 12. Pinnipeds spatial distribution maps constructed from information available in the International Union for Conservation of Nature (IUCN, 2020). The black dots show occurrence information available from the Ocean Biodiversity Information System (obis.org) and the Antarctic Biodiversity Facility (data.biodiversity.aq). A: Antarctic Fur Seals, B: Crabeater Seal, C.-Elephant Seals, D.-Ross Seal, E.-Weddell Seals and F: Leopard Seal.

4.3.1 Antarctic Fur seals

At Livingston Island, females give birth mostly from the end of November throughout mid-December. AFS are central place foragers that perform multiple trips to sea interspaced by time ashore during the milk provisioning period. Figure 13 shows three trips to sea performed by three different females during the austral summer of 2016 (Dash lines). These trips can last up to 13 days varying among locations (see Lea *et al., 2002a*) averaging 3-4.6 days in the Peninsula (Goebel *et al.,* 2000). Within a trip, animals can travel more than 4000 km while searching prey and eating. However, they will remain within 300 km from the breeding colonies where their offspring are bred (Figure 13, Borras-Chavez *et al.,* in prep). Within this 300 km radius, Goebel *et al.,* 2000 detected three main areas in which foraging takes place: 1. over the continental shelf Break, 2. along the shelf break and 3. in the oceanic region (Figure 13). At the beginning of December, most of the trips occur near the colonies before the shelf break in nearshore habitats. This may have to do with the need of female rapid return after giving birth (Polito and Goebel, 2010) and also, because females still count on the fat reserves from spring foraged prey (Borras-Chavez *et al.,* in prep). From Mid-January to February, visits to the shelf break are more regular especially in the slope of the shelf break and trips toward oceanic waters would increase afterwards. This may have to do with the stationary movement of the polar front which would increase the concentration of fish off both shelf break and oceanic waters (Green *et al.,* 1991, Reid and Arnould, 1996, Ichii *et al.,* 2007) especially in late summer (Santora and Veit, 2013). Most of the females forage at night in concordance with the vertical migration patterns of krill (Croxall *et al.,* 1985) and fish (Collins *et al.,* 2008). Santora and Veit, (2013) also described important feeding areas around Seal and Elephant islands and in late summer, within the Bransfield Strait. It is important to point out that the studies of Santora (2013) and Santora and Veit, (2013) are based on shipboard visual surveys around the SSI and is not possible to differentiate sex of the individuals. This is relevant since we have focused our discussion on breeding females but an increasing number of males and juveniles (Figure 5) are using additional areas around the peninsula. In figure 13, the light orange area represents both the spatial and temporal persistence of animals that may also include males and juveniles (Goebel *et al.,* 2000, Santora and Veit, 2013 and actual data from Borras-Chavez *et al.,* in prep) highlighting the relevance of this area of the Peninsula as feeding grounds also for non-breeding AFS.
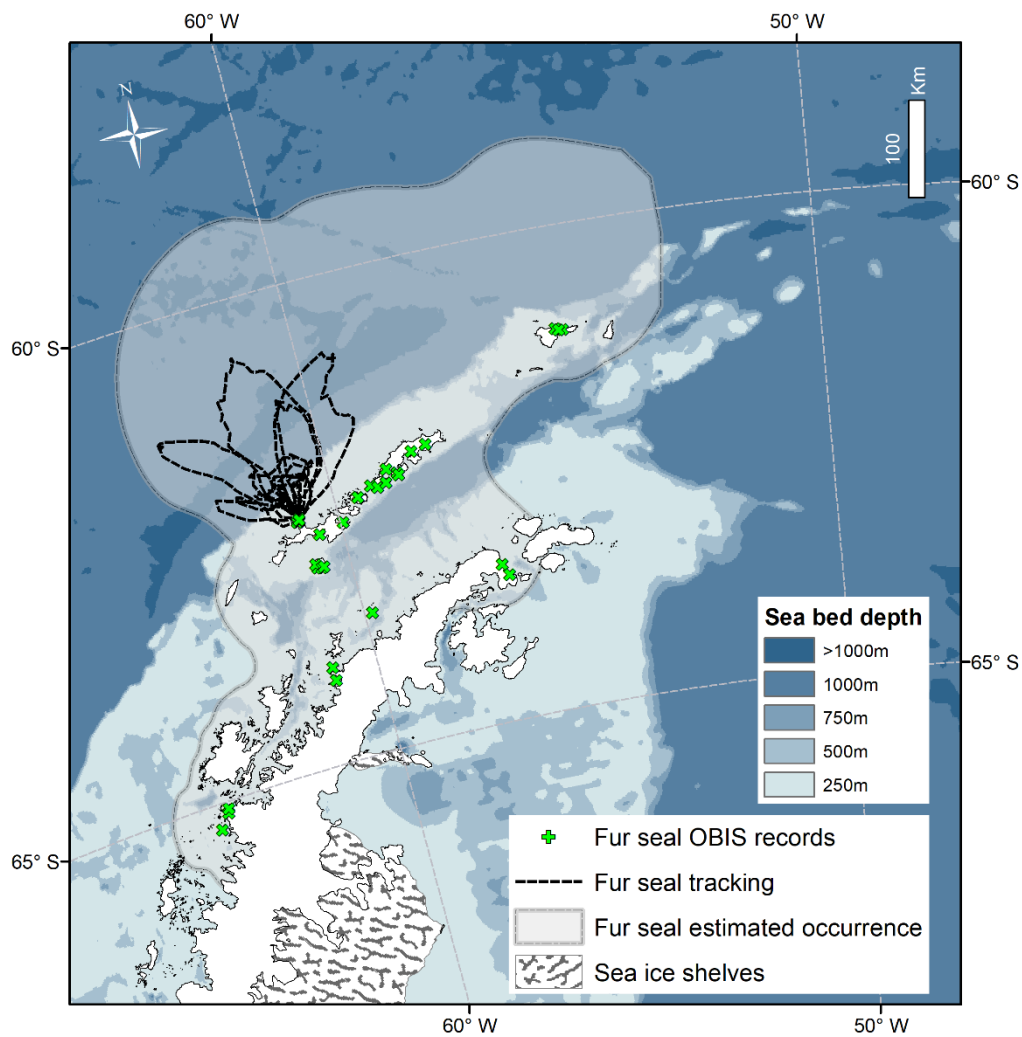
Figure 13. Antarctic fur seal foraging distribution during summer within the WAP. Black dashed lines show three foraging trips to sea performed by three seals during the Austral summer of 2016. The light grey area corresponds to the area where females from the biggest breeding colony at Cape Shirreff, Livingston Island, will forage during the breeding season. This area was drawn based on actual GPS data collected from all trips to sea during three austral summers (2014-2017) from Borras-Chavez (in prep), and a general approximation around Seal and Elephant islands, and the Bransfield strait that represent females and males foraging grounds tracked and described by sea sights in Santora and Veit, (2013) and Santora (2013). Green crosses show records extracted from the Ocean Biodiversity information System (OBIS).

4.3.2 Crabeater Seals

Crabeater seal foraging is one of the greatest examples of how diet drives spatial behavior of a marine predator. Because of their massive consumption of krill throughout the year, crabeater behavior will follow the distribution of krill patches and also respond to their vertical migration patterns (Nachtsheim *et al.,* 2017, Hückstädt *et al.,* 2020 Fig. 14A) not responding to site fidelity associated with a particular colony (Hückstädt *et al.,* 2020). In summer, autumn and the beginning of winter, animals would haul out during daylight feeding mostly during the night (Fraser *et al.,* 1989, Erickson and Hanson 1990, Nordøy, *et al.,* 1995) staying primarily in the upper 50 meters (Bengtson and Stewart, 1992, Nordøy, *et al.,* 1995). On the other hand, in winter, the pattern will drastically change as crabeaters would dive deeper during daylight (Kalinowski and Witek, 1980, Croxall *et al.,* 1985, Fraser *et al.,* 1989), since krill overwinter in deep waters (Gutt and Siegel, 1994). Burns *et al.,* (2004) found that in winter, 55% of the animals tagged in WAP dove deeper than 50 meters and 34% of them deeper than 100 meters. Crabeater seals are tightly associated to sea-ice distribution year-round (Burns *et al.,* 2004, Brault *et al.,* 2019). With such a restrictive relationship between the predator and its prey, the spatial distribution of crabeaters will be driven by the spatial distribution of krill and the clear hotspots identified for krill consumer predators in Antarctica (e.g. Marguerite Bay, Friedlaender *et al.,* 2011, Fig. 14A). A recent study that instrumented animals along the WAP in Crystal Sound, Laubeuf Fjord and Marguerite Bay, showed the relevance of the sector surrounding Marguerite Bay and the Bransfield Strait and predicted that crabeater seals may follow the redistribution of krill southward along the WAP due to warming (Hückstädt *et al.,* 2020), responding to the oceanographic patterns that will define krill distribution along or around the Continental Shelf (Piñones *et al.,* 2013).

4.3.3 Elephant Seals

Elephant seals have a circumpolar foraging distribution with individuals performing incredibly long trips including the entire Peninsula along the Antarctic Polar Front and/or the ice edge (Campagna *et al.,* 2000, Biuw *et al.,* 2007, Bailleul *et al.,* 2008, Hindell *et al.,* 2016, Figure 14B). Animals from the South Shetland Islands would also usually migrate east into the Atlantic sector always within northern waters from the south Scotia ridge (Biuw *et al.,* 2007, Figure 14B). However, those females going west and south in the Peninsula would gain more weight

than those going north. This may have to do with the rich fish hotspots located near the continental Shelf break, since 85% of the instrumented females in the Peninsula forage in continental shelf waters (Figure 14B) from the surrounding waters of King George Island (Borneman *et al.,* 2000) throughout the whole range of the SSI up to Marguerite Bay (Biuw *et al.,* 2007, Hückstädt *et al.,* 2012b, Costa *et al.,* 2010a, Field *et al.,* 2001, McConnell and Fedak, 1996, Costa *et al.,* 2008) including also the deep waters of the Bellingshausen Sea.
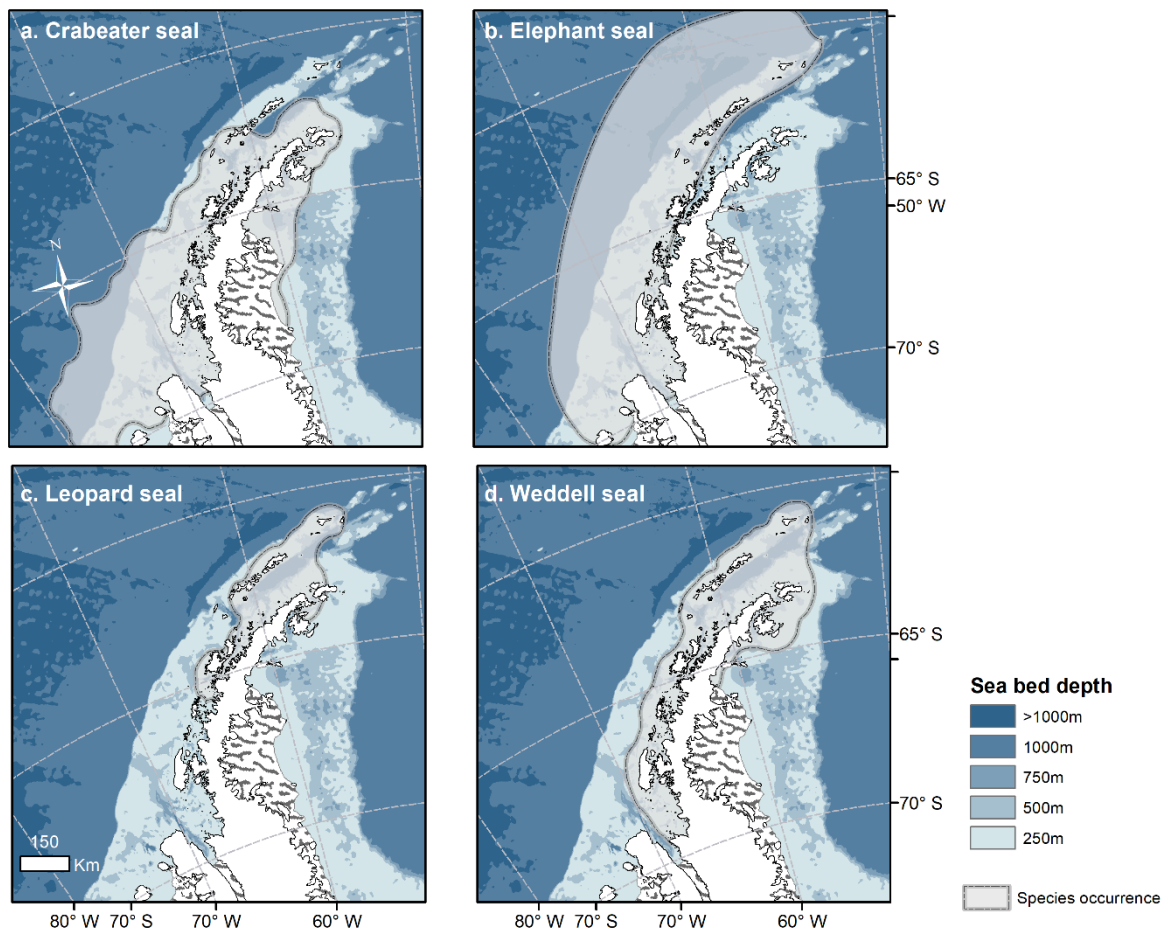
Figure 14. Overall Spatial foraging distribution of seals based on current literature geolocation descriptions plus data from the Ocean Biodiversity Information System (obis.org) and the Antarctic Biodiversity Facility (data.biodiversity.aq). A.-Elephant seals (Biuw *et al.,* 2007, Costa *et al.,* 2010a, Hückstädt *et al.,* 2012b), B.- Crabeater seals (Burns *et al.,* 2004, Hückstädt *et al.,* 2020 and Borras-Chavez pers. Obs.), C.-Leopard Seals (Krause *et al.,* 2015, Costa *et al.,* in progress), D.-Weddell Seals (Goetz *et al.,* 2017, Hindell *et al.,* 2020).
4.3.4 Ross Seal

Ross seals have a circumpolar distribution and spend more than 78% of their time in open waters (Arcalís-Planas *et al.,* 2015) making it harder to recover hard remains or even perform captures for further behavioral descriptions. To the best of our knowledge, no animals have ever

been instrumented in the WAP. Therefore, our limited knowledge is based on other locations in Antarctica. In East Antarctica, animals would dive on average, 110 m, and the deeper dives would reach 212 m (Bengtson and Stewart, 1997) which is consistent with the diet found of fish and mid water squids. Unfortunately, no information on spatial distribution has been published so far for the WAP.

4.3.5 Leopard Seals

Most of what is known on leopard seals spatial foraging distribution in the WAP comes from instrumented animals from Livingston Island (Krause *et al.,* 2016, Costa *et al.,*,. in progress, Fig. 14C). Leopard seal population in the WAP has steadily increased in the last 30 years by more than two orders of magnitude from what have been reported by regional surveys (Krause *et al.,* 2016). Consequently, this has had a huge impact in AFS colonies due to the high rates of offspring predation driven mostly by resident leopard seals (Schwartz *et al.,* 2013, Krause *et al.,* 2015, Krause *et al.,* 2020, Costa *et al.,* in progress). The reasons for this exponential increase of leopard seals in the area are still unclear, but pack ice habitat reduction in southern areas of the WAP seems to be the main reason (Forcada *et al.,* 2012, Massom and Stammerjohn, 2010). The availability of energetically rich prey (i.e. AFS pups) and abundant penguin colonies makes the northern WAP ideal for summer foraging. The foraging of these prey takes place on the surface, which is consistent with the only few instrumented animals that have been described in the Peninsula during summer, where shallow dives (<30 m deep) represent 90% of the dives (Krause *et al.,* 2015, 2016). Long-term bio-logging have been used recently (Costa *et al.,* in progress) and preliminary results suggest that resident females will move a few hundred meters around their haul out areas during the whole year and only a few animals would go to the northern islands of the peninsula (Figure 14C, Daniel Costa, Pers. Comm.).

4.3.6 Weddell Seals

Weddell seals would follow their prey chasing them to incredible depths below 700 m targeting both benthic and pelagic preys (Testa, 1994, Lake *et al.,* 2006). Animals from McMurdo Sound, Ross Sea, would travel in winter up north diving 125 meters deep in search of pelagic prey (Goetz *et al.,* 2017). Others would perform shallow dives during winter following the vertical migration of fish species (Heerah *et al.,* 2013). Their foraging behavior suggests they have the

ability of traveling long distances along the WAP searching for fish and therefore expanding its foraging grounds using most of the shelf break along the Peninsula (Fig. 14D) but also deep waters in search of octopus (Daneri *et al.,* 2012). The exact areas where Weddell seals are foraging in the WAP have been generally revised (Hindell *et al.,* 2020) but not in detail within the WAP. Animals from Livingston Island have been tagged but results have not been published yet (Michael Goebel, Pers. Com). Further information on Weddell seal foraging spatial distribution is needed along the WAP as most information within this chapter is only based on diving behavior and diet data.

4.4. Pinnipeds and Krill Fisheries overlap

As mentioned in section 2, Antarctic fisheries in the WAP are currently focused on one resource: krill. If we consider the spatial foraging distribution of pinnipeds described in section 4 (see also Figures 13 and 14), an important overlap occurs between the fishery and three pinniped species that rely on krill (i.e. specialists: Antarctic fur seals and Crabeater seals and the generalist Leopard seal). However, it is worth noting that, as suggested by Hinke *et al.* (2017), this is a "functional" overlap where species are more likely to be impacted by interaction with fisheries due to *potential* competition than *actual* competition, in other words, affected by the removal of krill biomass that, without fishing activities, would have been available for them. It is still complex to quantify the actual competition for resources between these species and krill fishery but we have enough evidence from spatial data to suggest that krill fleet are disproportionately concentrated in areas of ecological significance throughout the Southern Ocean (Santa Cruz *et al.,* 2018, Hindell *et al.,* 2020), potentially affecting krill predator populations (Hinke *et al.,* 2017, Watters *et al.,* 2020) Therefore, we focus this section on those species relying on krill and, hence, are potentially interacting with krill fishery. We do this by evaluating the evidence of this interaction provided by spatial data and ecosystem modeling of this interaction.

Perhaps the best scientific collective effort to evaluate the overlap between Antarctic predators and fisheries is the recent work of Hindell *et al.* (2020). Using spatial data, and more than 4,000 tracks of 17 birds and 5 marine mammal species, they construct habitat selection models to identify "areas of ecological significance" (AESs) around the Southern Ocean. This research confirms what can be seen in Figure 14 and also discussed in previous sections; 89% of the

areas below 60° latitude, including the WAP and within 200 km of the continental shelf, following much of the Scotia Sea and the surrounding waters are the most utilized areas for this and other krill predators (Hindell *et al.,* 2020). The study includes most of the pinniped species found in Antarctic water but caution must be taken in making local (related to the WAP) conclusions from regional evaluations since, as discussed in section 4.3, there is a lack of spatial information of individuals from the WAP, mainly Weddell and leopard seals, and definition of relevant areas for those species is based on simulated spatial data from the limited existent data. Therefore, it is necessary to revise local research around the WAP on the interaction between fisheries and spatial data of these species.

Figure 15 shows the areas where krill fisheries currently occur within the WAP, highlighting (red hatch area) those fishing spots where fleet activities have been highly concentrated but also (based on Section 4) where occurrence of krill-consumer pinnipeds (AFS, Crabeaters and Leopard seals) is higher. These areas are not the only areas where fishery may overlap with pinniped foraging grounds, they represent our current knowledge based on tracking and diving pinniped data and the most relevant areas where krill fisheries take place. Predators focus their effort in areas of the Antarctic Peninsula within the 200 km of the continental shelf (Santora and Veit, 2013, Nowacek *et al.,* 2011, Hindell *et al.,* 2020, Hückstädt *et al.,* 2020) which historically have also been the fishing hotspots of krill harvest (Figure 3).

Hinke *et al.,* (2017) found vertical overlap (krill is caught within the same depth as where AFS capture their prey) and spatio-temporal overlap of krill fishery and AFS foraging grounds in the Peninsula. In the past, fishery was concentrated during summer in areas APDPW and APEI (section 2 Figures 2 and 15), where AFS breeding females tend to concentrate their foraging activities (Goebel *et al.,* 2000, Santora, 2013, Santora and Veit, 2013). In the last few years, krill catches have concentrated mostly within the Bransfield Strait (APBSW and APPSE, section 2) through autumn and winter (Nicol *et al.,* 2012, Santa Cruz *et al.,* 2018). This again is consistent with what has been reported on the spatial foraging behavior of AFS individuals within the strait, with a clear increase of presence of AFS animals at the same timeframe that fleets are fully operative along the Bransfield (Santora and Veit, 2013). Hückstädt *et al.,* (2020) show the high use of the continental shelf particularly areas APBSW and APBSE by crabeaters showing evident overlap with fisheries in this area. In addition, the Bransfield Strait is considered a corridor between the Peninsula and the East Scotia Sea for several species (Biuw *et al.,* 2007, Hindell *et al.,* 2020, Section 4.2, Figure 14). Therefore, the increase in the intensity

of krill fisheries in the Bransfield Strait in the last few years (Santa Cruz *et al.,* 2018), potentially increases the overlap between fishery and pinnipeds foraging activities.

Although there is no research on direct competitive interaction between seals and fisheries in the WAP, some conclusions can be drawn from recent publications (Hindell *et al.,* 2020). The number of leopard seals have increased in both Livingston island (Krause *et al.,* 2016, Krause *et al.,* 2020) and the waters around the Bransfield Strait (Borras-Chavez pers. Obs O'Higgins Base). Therefore, the overlap of fishery at least in APDPW, APBSW and APPSE could affect this species if future catches remain concentrated in these areas, especially in years of low productivity, as it has been recently demonstrated for penguin species (Watters *et al.,* 2020). In the APEI region, krill fishing activities have been reduced (Figure 3, Santa Cruz *et al.,* 2018) which may have benefited especially those animals in transit toward northern waters for the winter. Crabeaters would remain close to waters where they haul out such as those animals from Marguerite Bay (Burns *et al.,* 2004, Hückstädt *et al.,* 2020), and, although several animals are seen in the vicinities of Livingston Islands, the lack of spatial distribution information from the Northern islands of the Peninsula makes hard to generate an overall estimation of the influence that krill fisheries can have on this species in the tip of the Peninsula. To this date, we can only conclude that fisheries within APDPW may have a direct effect on animals hauling out around this area (figure 14) but it is clear that more research is needed in order to fully understand the implications of the overlap between fisheries and seals in these areas.
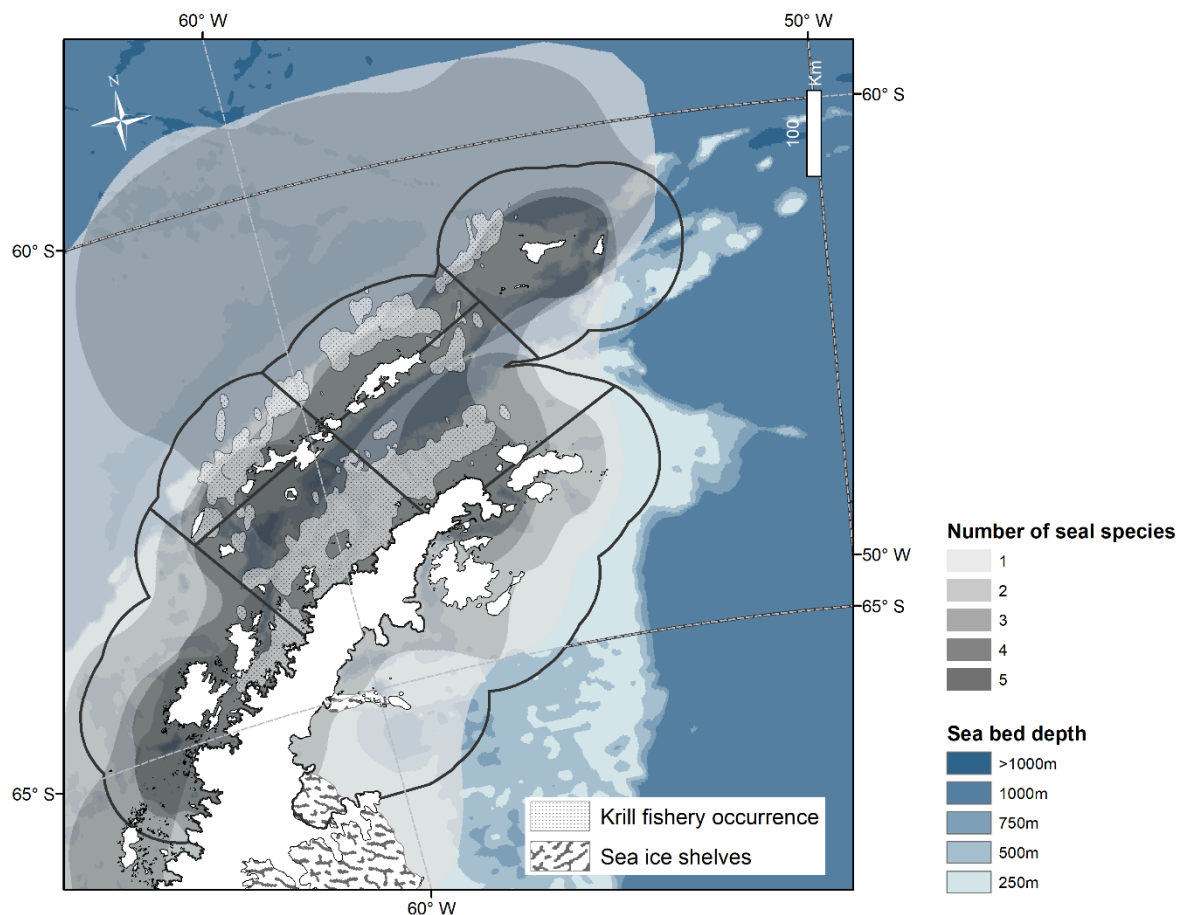
Figure 15. Spatial overlap between krill fisheries and pinnipeds. The grey scale represents the number of species that can be found along the WAP. The black line is the contour of the sum of the SSMUS where catches take place. The dash areas represent the concentration of krill fleet activities.

4.5 Modeling spatial interaction

The CCAMLR precautionary approach taken in the management of krill fisheries (see section 1) has proved to be successful for many decades when data on prey biomass consumed by krill-predators was limited and the understanding of fisheries-predator interactions could not be fully understood (Boyd *et al.,* 2001, Reid *et al.,* 2005). When evaluating the efficiency of current measures, gaps are found and explained by the complexity of krill life history (e.g., recruitment, see Reiss *et al.,* 2008) and the physical and oceanographic variabilities that shape krill distribution, i.e., flux, climatic variability, bathymetric conditions, transport and currents among others (Murphy *et al.,* 1998, Forcada *et al.,* 2009, Santora and Veit, 2013, Piñones *et al.,* 2013). Some of the major caveats for fully understanding predator's behavior along the WAP are their high mobility and technical limitations for following or sampling in certain areas and times of

the year. The lack of such information had forced CCAMLR to set precautionary limits to krill fishery as a small proportion of the *target species* (Constable *et al.,* 2000), but does not take into account whether these limits are precautionary for the *krill-consumer species* leading to inaccurate calculation of those limits (Watters *et al.,* 2020). Furthermore, precautionary limits are *regional* and not *local* and while the fleet are respecting those limits, their regional catch limit is achieved within very specific and narrow areas of the WAP (see section 3 and figure 3) that match also the most used areas by krill predators. Actually, Watters *et al.,* (2020) point out that this regional approach and the concentration of fishing effort both in time and location also increase the vulnerability of predators, being not precautionary at all for the consumers. Local and seasonal abundance surveys would help to set maximum catch limits in line of what predators are consuming in these conflictive areas, however, this could only be possible to conceive if we improve our understanding on foraging behavior of predators both locally and regionally. Fortunately, CCAMLR has now acknowledged the need for the adoption of a new approach that takes into account these variables as well as current environmental changes occurring in the WAP (CCAMLR 2019).

Modeling has helped tremendously improving the ecosystem-based management approach in the region by dealing better with uncertainty (Watters *et al.,* 2013) and incorporating the spatial data available of Antarctic predators (Hinke *et al.,* 2017, Watters *et al.,* 2020, Hindell *et al.,* 2020). They have also included additional variables that may act synergistically with fisheries such as climate change (Dahood *et al.,* 2019, Klein *et al.,* 2018, Hindell *et al.,* 2020) which will impact krill populations and alter the food web (Atkinson *et al.,* 2004, Ducklow *et al.,* 2007, Lynch *et al.,* 2012). Models might not be an exact representation of the ecosystem but if they are fed with more and better empirical data, they could be an accurate picture of the ecosystem and a powerful tool for management and conservation planning.

With limited empirical evidence, risk assessment has also been another great approach that may help CCAMLR to progress in decisions such as the implementation of Marine Protected Areas (MPAs) for the conservation of highly ecologically relevant areas (Hinke *et al.,* 2017, Krüger *et al.,* 2017, Hays *et al.,* 2019, Heerah *et al.,* 2019). The limited percentage of coverage that MPAs have in Antarctica (0.04% of the world oceans, UNEP- WCMC and IUCN 2020) could be the biggest problem for the conservation of the Southern Ocean. Risk assessment have shown that MPAs are located in areas less suitable for megafaunal biodiversity than those mostly use for predators (Brooks *et al.,* 2020, Hindell *et al.,* 2020) and the most suitable habitat remain

unprotected and overlapping with areas where fisheries are growing (Trathan *et al.,* 2018, Santa Cruz *et al.,* 2018, section 3, Figure 15). Currently, new proposed MPAs are more in line with protecting priority areas of conservation (Sundblad *et al.,* 2011) but have not yet been implemented due to the complex system of administration and decision-making in Antarctica (see section 1). CCAMLR has recognized these caveats and scientist are doing a remarkable effort to make available a strong body of knowledge to advance on the necessary restriction and changes that future fisheries need to reconsider (CCAMLR 2019) in lights of more effective MPAs and the protection and conservation of marine life including, among them, the pinniped species of the Southern Ocean.

5. Conclusions

Fisheries are likely to continue growing since economic pressures for the extraction of Antarctic marine resources are increasing (Kock *et al.,* 2007, Nicol *et al.,* 2012, Chown *et al.,* 2019). Even though, there is a significant overlap between fishing hotspots and foraging areas of pinnipeds, currently there is no evidence of directs detrimental effect from fisheries on pinnipeds and the summarized data presented here is limited to the animal track data available and the spatial and temporal overlap which show functional overlap (i.e indirect competition) between fisheries and pinnipeds foraging locations. However, new evidence has shown how predators follow (and will follow) krill distribution, expanding their range away from coastal areas and to southern sectors of the WAP (Hückstädt *et al.,* 2020) just like fisheries are doing it too (Santa Cruz *et al.,* 2018, Hindell *et al.,* 2020). For this, it is critical to reinforce the need of maintaining long-term monitoring of predator populations, krill stocks/biomass estimators and research on spatial behavior in individuals inhabiting this area. In this regard, CCAMLR has now started to develop a new preferred management approach that includes different components including krill biomass and stock estimates as well as risk assessments. This certainly will constitute a huge step into the right direction to strengthen the conservation of Antarctic marine living resources and with this, the krill dependent predators in such a fragile environment.

APPENDIX B. ADDITIONAL METHODS AND RESULTS

Chapter 1

Addition Results
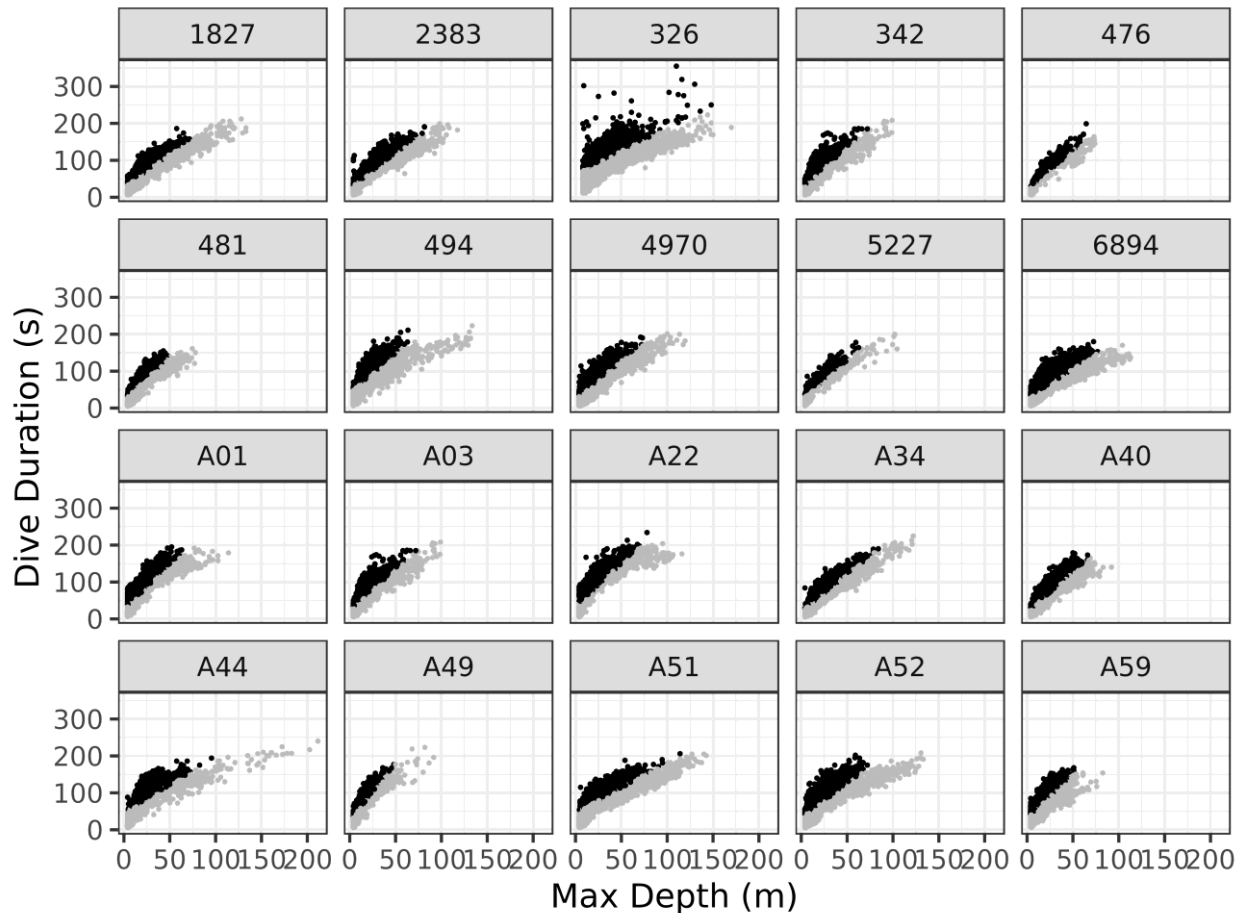
Figure 1. Residuals of the relationship between Dive duration (y axis) and Maximum depth (x axis) for each female of the study: Non-lactating females (NL; 326, 494, 4970,342, A03) and Lactating females (L: the remaining). Here, each female per group is presented individually on each graph but the linear mixed-effect model (LMM) presented in the study was fitted using the identity of each female as the random factor to account for individual behavioral variability and maximum depth as the random slope term since the duration-depth relationship may vary across females. With this, positive (Grey, longer than predicted) and negative (Black, shorter than predicted) dive residuals are shown per female and no significant differences between groups were found (X2(1)= 0.0017, P= 0.9668).

Chapter 2

Additional Results
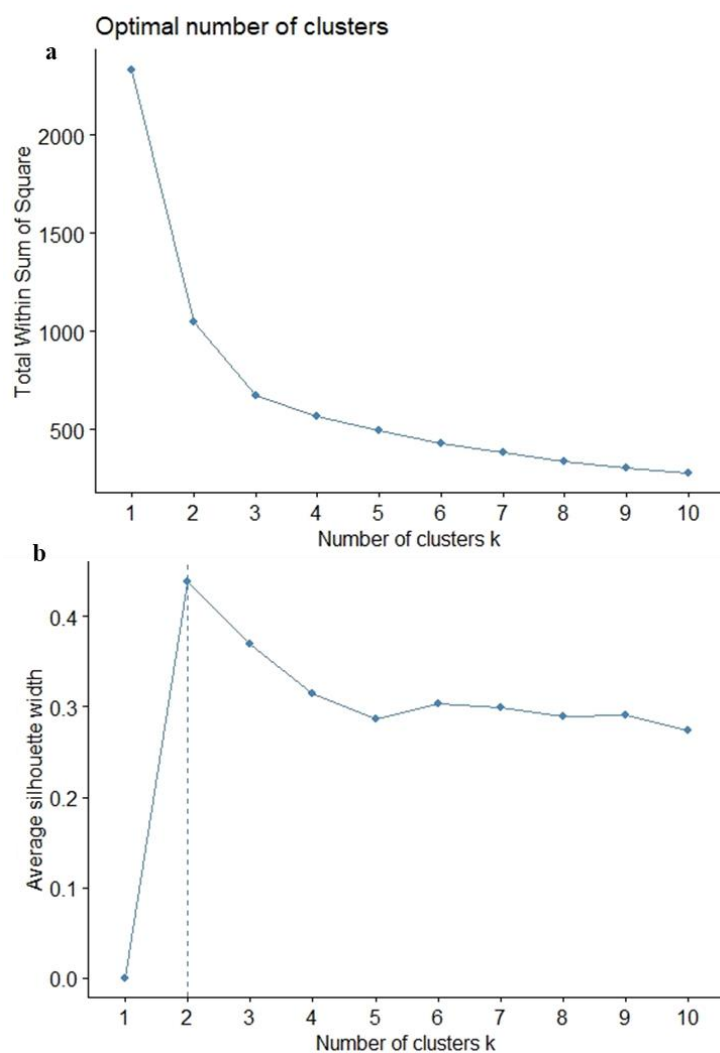
Figure 2. Elbo (a) and Silhouette (b) methods to determined optimal number of clusters from fatty acid data. The method was implemented with all fatty acid samples obtained based on the differences between fatty acid composition and prey proportional data.

Chapter 3

Additional Methods

Results of the linear regression analysis between maximum distance to colonies and trip duration from females carrying GPS sensors. The resulting formula was later used to predict maximum distance to colonies in trips and females that were not carrying GPS sensors.

lm(formula = MaxDistancetoColony_km ~ tripdur)

Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-21.771	16.051	-1.356	0.179
tripdur	71.072	4.322	16.444	<2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 39.58 on 78 degrees of freedom

Multiple R-squared: 0.7761, Adjusted R-squared: 0.7732

F-statistic: 270.4 on 1 and 78 DF, p-value: < 2.2e-16
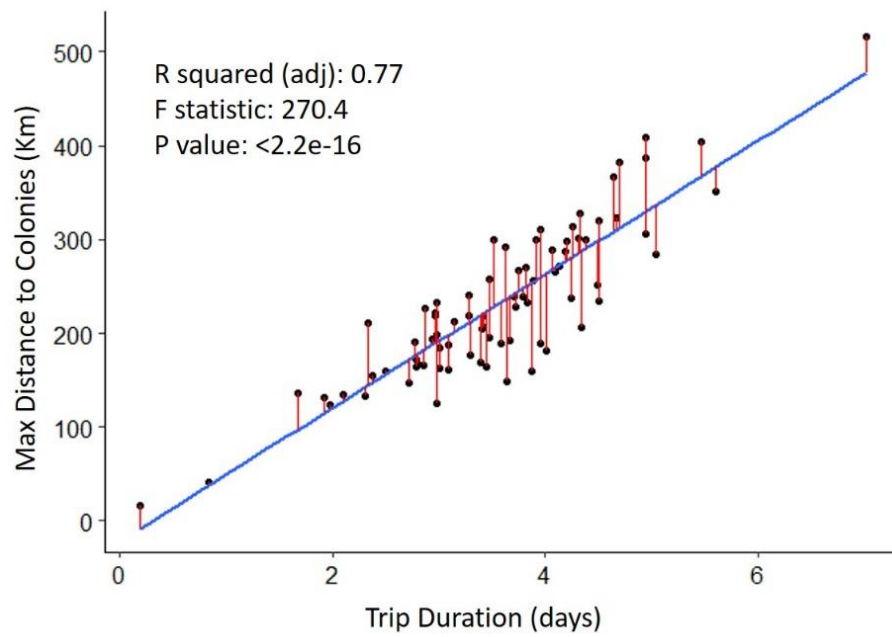
Figure 3. Regression analysis between maximum distance to colonies (Km) and trip duration (days) of all trips performed by Antarctic fur seal females carrying GPS sensor (20 females). The resulting equation used to predict maximum distance in trip data of females with no GPS was: Max distance to colonies = -21.7 + 71.07*Trip Duration.

Additional results
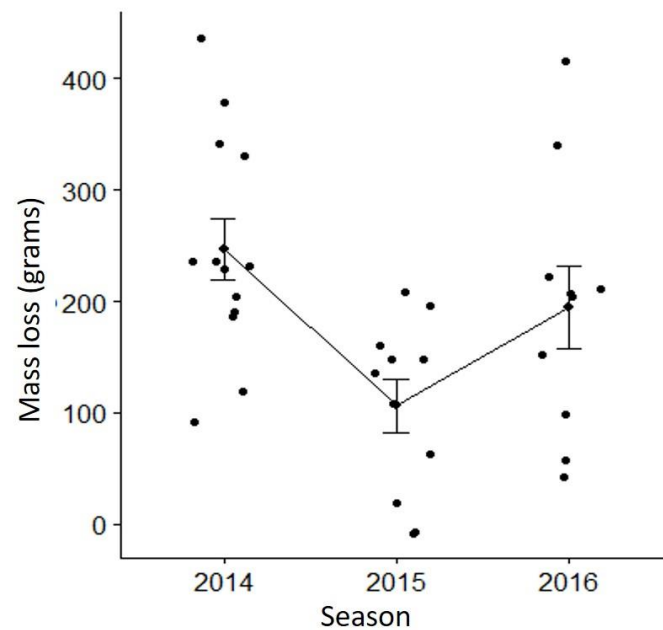
Figure 4: Mass balance of all female Antarctic fur seal females included in chapter 3. Because capture days differed between females, mass loss was calculated subtracting the final mass from the initial mass and then divided by the number of days between the initial and final measure per female.

Table 1 Antarctic fur seal females morphometric measures and Body condition Index (BCI)

Season	Female ID	Female Initial Mass (Kg)	Total Length (Cm)	Body Condition Index (BCI)*
2014	1701	51.8	131	0.40
	288	54.6	130	0.42
	345	56.3	129	0.44
	A17	57.8	134	0.43
	A16	57.2	137	0.42
	486	61.2	133	0.46
	A27	51.8	127	0.41
	A20	54.4	136	0.40
	A21	47.2	122	0.39
	A28	48.4	132	0.37
	1611	53.8	132	0.41
	A22	58.6	138	0.42
	A23	56.1	136	0.41
	274	**na**	**na**	**na**
	451	**na**	**na**	**na**
2015	488	51.6	129	0.40
	489	54.8	135	0.41
	1701b	46	127	0.36
	476	57	132	0.43
	A35	55	133	0.41
	385	49.8	129	0.39
	5227	46.4	123	0.38
	A37	35.8	122	0.29
	4970	44.6	123	0.36
	1827	50.2	128	0.39
	A06	57.8	139	0.42
	A34	51	124	0.41
	A40	59.4	137	0.43
	2383	52.8	127	0.42
2016	6894	46.8	124	0.38
	A01	57.4	131	0.44
	A22b	59.8	140	0.43
	A44	49.2	131	0.38
	A49	54.8	137	0.40
	A51	48	135	0.36
	A52	55.2	134	0.41
	A58	48	128	0.38
	A59	47.6	130	0.37
	A47	46.6	126	0.37
	481	54.8	131	0.42
	A54	51.6	131	0.39

* Body condition index (BCI) was calculated by dividing Female's initial Mass by total length.
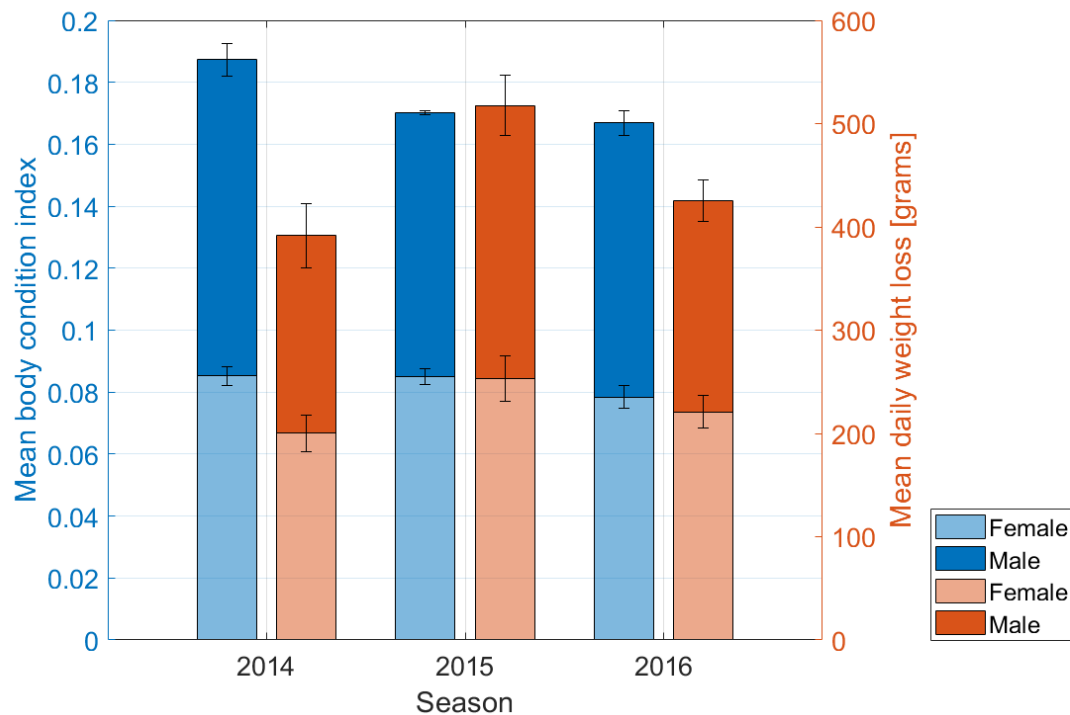
Figure 5. Pups mean body condition indexes (BCI, blue tones) and mean daily weight loss (grams, presented in red tones) of the studied pups separated in females (light color) and males (plain color).

Table 2. Mean morphometric measures of all studied pups for all three seasons

Season	Sex	N° of pups	Mean Mass (Kg)	Mean Length (cm)	Mean Body condition Index (BCI)	Daily Weight Loss (grams/day)
2014	F	9	5.28 ± 0.62	62 ± 2.87	0.085 ± 0.01	200.06 ± 53.61
	M	4	6.75 ± 0.75	66 ± 2.45	0.10 ± 0.01	191.61 ± 61.93
2015	F	10	5.25 ± 0.64	61.7 ± 4.42	0.085 ± 0.01	252.96 ± 69.71
	M	4	5.57 ± 0.38	65.5 ± 5.19	0.085 ± 0.001	264.71 ± 59.04
2016	F	6	4.86 ± 0.52	62.08 ± 2.62	0.078 ± 0.01	220.90 ± 38.50
	M	6	5.67 ± 0.89	63.83 ± 3.82	0.078 ± 0.01	204.21 ± 49.06

Table 3. Post hoc Tukey test comparison of mean mass between seasons on female and male pups at 30, 45, 60 and 70 days after median pup parturition date (MPPD).

Days after MPPD	Sex	Seasons contrasted	p-values
30	F	2014-2015	**0.0086***
		2014-2016	**0.0075***
		2015-2016	0.9959
	M	2014-2015	**0.0103***
		2014-2016	**0.0227***
		2015-2016	0.932
45	F	2014-2015	**0.0003***
		2014-2016	0.4466
		2015-2016	**0.0209***
	M	2014-2015	**0.0124***
		2014-2016	0.2675
		2015-2016	0.4
60	F	2014-2015	0.97
		2014-2016	0.4569
		2015-2016	0.6209
	M	2014-2015	0.1577
		2014-2016	0.2712
		2015-2016	0.9387
75	F	2014-2015	0.4787
		2014-2016	0.7165
		2015-2016	0.9511
	M	2014-2015	0.972
		2014-2016	0.9306
		2015-2016	0.9939

Significant p values were obtained using a confidence level of 0.95 and highlight in bold and with asterisk (*). M=Male, F=Female.
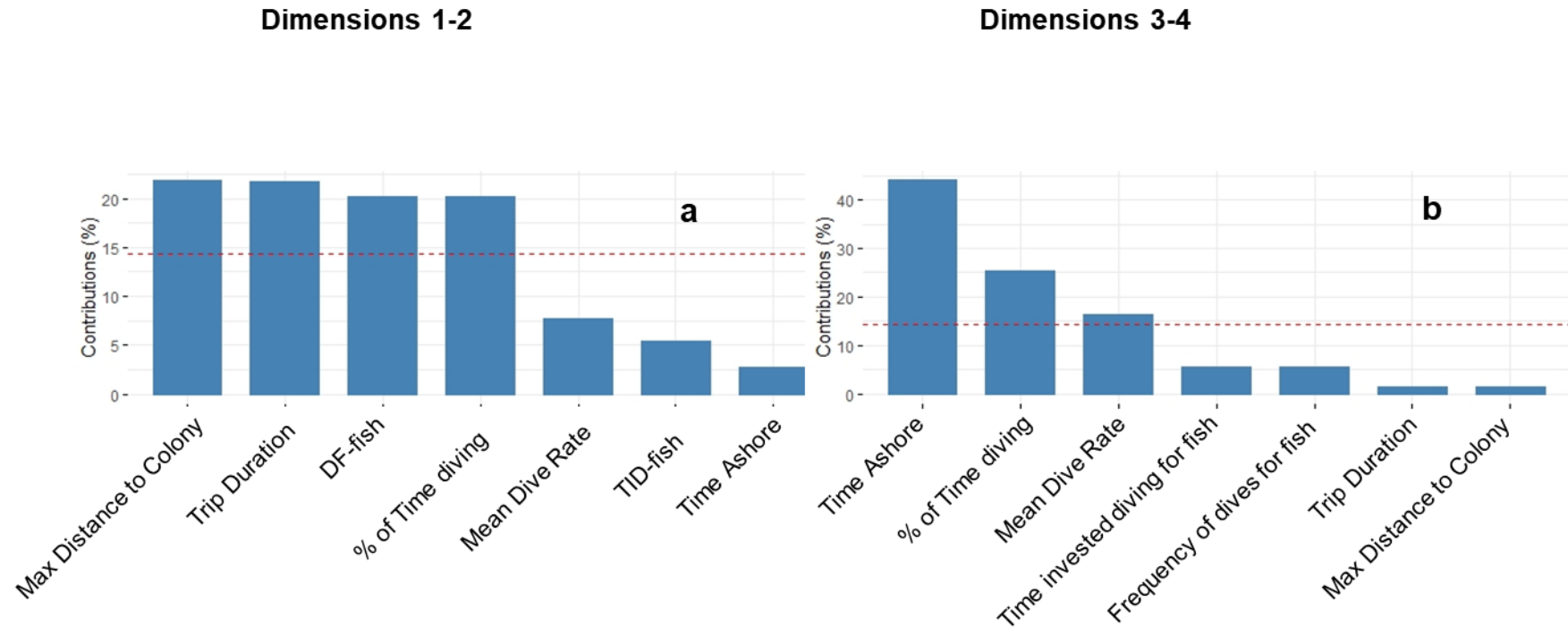
Figure 6. Contribution of each variable (%) to the variance explained by the four most important dimensions of the Principal component analysis performed for the determination of foraging strategies. The red dotted line indicates the percentage that each variable should contribute to the dimensions represented per graph (a.- dimensions 1 and 2 and b.- dimensions 3 and 4) to have equal percentage of variance explained by all variables. All variables showing percentual values above this line were later considered to define foraging strategies.
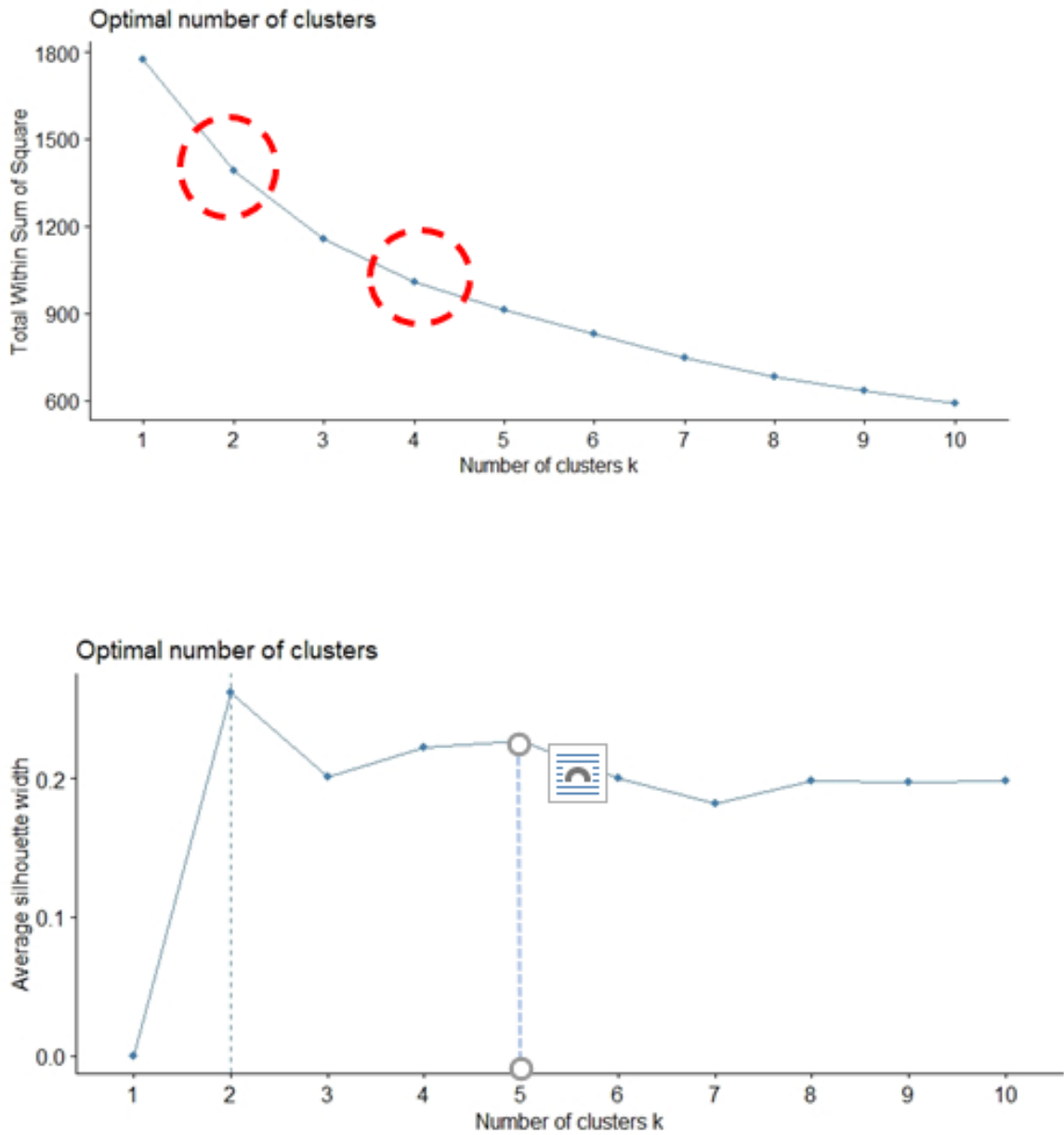
Figure 7. Optimal number of clusters results from the Elbo (upper graph) and silhouette (lower graph) methods after performing an agglomerative hierarchical analysis of all diving variables used for the determination of foraging strategies. The Elbo method suggests either two or four clusters (red dotted circles) whereas the Silhouette method suggests two or, less likely, five clusters.

Table 4. Prey percentages of krill and Fish consumed per foraging strategy.

Strategy	Sample Size	Mean Percentage Krill	Mean Percentage Fish
Long-Fish	9	24.4 ± 27	75.6 ± 24
Near-Mix-Fish	7	31.4 ± 24	68.2 ± 24
Near-Mix-Krill	7	62.2 ± 37	37.8 ± 37
Far-Lazy- Krill	9	66.8 ± 36	33.2 ± 36

Table 5. Percentage of trips using each strategy out of the total amount of trips per phase for all three breeding seasons (2014, 2015 and 2016).

Season	Phase	Strategy	Number of trips	Percentage of trips (%)
2014	**K**	Long-Fish	14	20
		Near-Mix-Fish	5	7.1
		Near-Mix-Krill	40	57.1
		Far-Lazy-Krill	11	15.8
	F	Long-Fish	7	36.8
		Near-Mix-Fish	4	21
		Near-Mix-Krill	8	42.2
2015	**K**	Near-Mix-Krill	34	54.8
		Far-Lazy-Krill	28	45.2
	F	Long-Fish	2	4.1
		Near-Mix-Fish	4	8.2
		Near-Mix-Krill	31	63.3
		Far-Lazy-Krill	12	24.4
2016	**K**	Long-Fish	6	9.3

	Near-Mix-Fish	27	41.5
	Near-Mix-Krill	25	38.5
	Far-Lazy-Krill	7	10.7
F	Long-Fish	10	62.5
	Near-Mix-Fish	4	25
	Near-Mix-Krill	1	6.2
	Far-Lazy-Krill	1	6.3
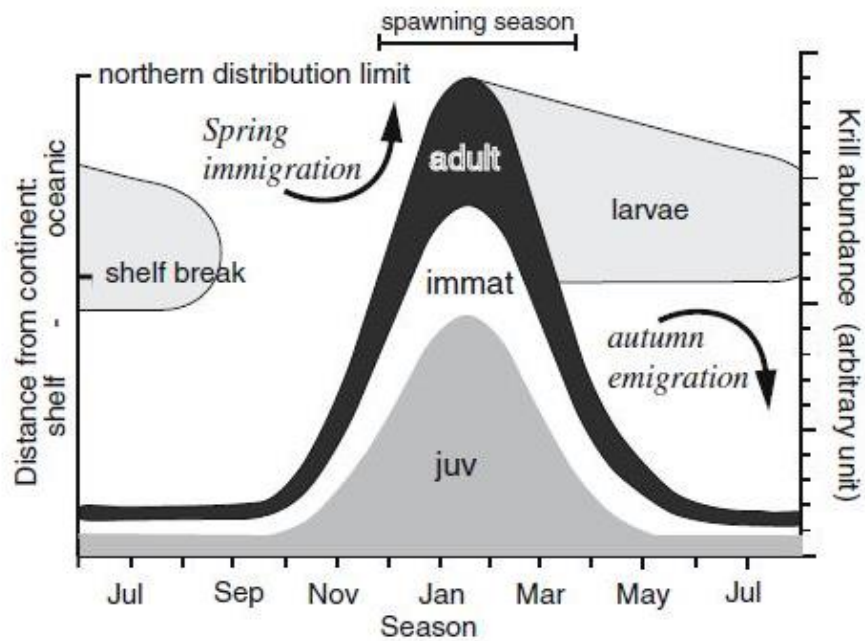
Figure 8. Conceptual view of seasonal and spatial variation of krill at different size classes and maturity stages along the Antarctic peninsula (figure extracted from Siegel, 2005).

REFERENCES

Abrahms, B., Hazen, E. L., Bograd, S. J., Brashares, J. S., Robinson, P. W., Scales, K. L., ... & Costa, D. P. (2018). Climate mediates the success of migration strategies in a marine predator. Ecology letters, 21(1), 63-71.

Ainley, D. G., & Siniff, D. B. (2009). The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. Antarctic Science, 21(4), 317-327.

Arana, P. M., Jones, C. D., Alegría, N. A., Sarralde, R., & Rolleri, R. (2020). Antarctic demersal finfish around the Elephant and the South Orkney islands: distribution, abundance and biological characteristics. Latin american journal of aquatic research, 48(2), 304-322.

Arcalís-Planas, A., Sveegaard, S., Karlsson, O., Harding, K. C., Wåhlin, A., Harkonen, T., & Teilmann, J. (2015). Limited use of sea ice by the Ross seal (Ommatophoca rossii), in Amundsen Sea, Antarctica, using telemetry and remote sensing data. Polar Biology, 38(4), 445-461.

Arnold, S. J. (1981). Behavioral variation in natural populations. II. The inheritance of a feeding response in crosses between geographic races of the garter snake, Thamnophis elegans. Evolution, 510-515.

Arnould, J. P., & Boyd, I. L. (1995). Temporal production patterns of milk in Antarctic fur seals (Arctocephalus gazella). Journal of Zoology, 237(1), 1-12.

Arnould, J. P., Boyd, I. L., & Speakman, J. R. (1996). The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. Journal of Zoology, 239(4), 769-782.

Arnould, J. P. (1997). Lactation and the cost of pup-rearing in Antarctic fur seals. Marine Mammal Science, 13(3), 516-526.

Arnould, J. P., & Hindell, M. A. (2001). Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (Arctocephalus pusillus doriferus). Canadian Journal of Zoology, 79(1), 35-48.

Arthur, B., Hindell, M., Bester, M., Trathan, P., Jonsen, I., Staniland, I., ... & Lea, M. A. (2015). Return customers: Foraging site fidelity and the effect of environmental variability in wide-ranging Antarctic fur seals. PloS one, 10(3), e0120888.

Arthur, B., Hindell, M., Bester, M. N., Oosthuizen, W. C., Wege, M., & Lea, M. A. (2016). South for the winter? Within-dive foraging effort reveals the trade-offs between divergent foraging strategies in a free-ranging predator. Functional Ecology, 30(10), 1623-1637.

Atkinson, A., Siegel, V., Pakhomov, E., & Rothery, P. (2004). Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature, 432(7013), 100-103.

Atkinson, A., Hill, S.L., Pakhomov, E.A., Siegel, V., Reiss, C.S., Loeb, V.J., Steinberg, D.K., Schmidt, K., Tarling, G.A., Gerrish, L., Sailley, S.F., (2019). Krill (Euphausia superba) distribution contracts southward during rapid regional warming. Nat. Clim. Chang. 9, 142–147.

Austin, D., Bowen, W. D., McMillan, J. I., & Iverson, S. J. (2006). Linking movement, diving, and habitat to foraging success in a large marine predator. Ecology, 87(12), 3095-3108.

Bailleul, F., Pinaud, D., Hindell, M., Charrassin, J. B., & Guinet, C. (2008). Assessment of scale-dependent foraging behavior in southern elephant seals incorporating the vertical dimension: a development of the First Passage Time method. Journal of Animal Ecology, 77(5), 948-957.

Banks, J., Lea, M. A., Wall, S., McMahon, C. R., & Hindell, M. A. (2014). Combining bio-logging and fatty acid signature analysis indicates spatio-temporal variation in the diet of the

southern elephant seal, Mirounga leonina. Journal of experimental marine biology and ecology, 450, 79-90.

Barrera-Oro, E. (2002). The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. Antarctic Science, 14(4), 293-309.

Barrera-Oro, E., Marschoff, E., & Ainley, D. (2017). Changing status of three notothenioid fish at the South Shetland Islands (1983–2016) after impacts of the 1970–80s commercial fishery. Polar Biology, 40(10), 2047-2054.

Barton, K. (2010). MuMIn: multi-model inference. 2017. R package version, 1(1).

Bastille-Rousseau, G., Fortin, D., & Dussault, C. (2010). Inference from habitat-selection analysis depends on foraging strategies. Journal of Animal Ecology, 79(6), 1157-1163.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823. doi: 10.18637/jss.v067.i01

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., ... & Green, P. (2018). Package 'lme4'. Version, 1, 17.

Bateson, M., & Kacelnik, A. (1998). Risk-sensitive foraging: decision making in variable environments. Cognitive ecology: The evolutionary ecology of information processing and decision making, 297-341.

Battaile, B. C., Sakamoto, K. Q., Nordstrom, C. A., Rosen, D. A., & Trites, A. W. (2015). Accelerometers identify new behaviors and show little difference in the activity budgets of lactating northern fur seals (Callorhinus ursinus) between breeding islands and foraging habitats in the Eastern Bering Sea. PLoS One, 10(3), e0118761.

Beauplet, G., Guinet, C., & Arnould, J. P. (2003). Body composition changes, metabolic fuel use, and energy expenditure during extended fasting in subantarctic fur seal (Arctocephalus tropicalis) pups at Amsterdam Island. Physiological and Biochemical Zoology, 76(2), 262-270.

Beauplet, G., Dubroca, L., Guinet, C., Cherel, Y., Dabin, W., Gagne, C., & Hindell, M. (2004). Foraging ecology of subantarctic fur seals Arctocephalus tropicalis breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. *Marine Ecology Progress Series*, *273*, 211-225.

Bengtson, J. L., & Stewart, B. S. (1992). Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. Polar Biology, 12(6-7), 635-644.

Bengtson, J. L., & Stewart, B. S. (1997). Diving patterns of a Ross seal (Ommatophoca rossii) near the eastern coast of the Antarctic Peninsula. Polar Biology, 18(3), 214-218.

Bengtson, J. L., Laake, J. L., Boveng, P. L., Cameron, M. F., Hanson, M. B., & Stewart, B. S. (2011). Distribution, density, and abundance of pack-ice seals in the Amundsen and Ross Seas, Antarctica. Deep Sea Research Part II: Topical Studies in Oceanography, 58(9-10), 1261-1276.

Berthold, M. R., Cebron, N., Dill, F., Di Fatta, G., Gabriel, T. R., Georg, F., ... & Wiswedel, B. (2009). Technical Report Knime: The Konstanz Information Miner.

Bestley, S., Jonsen, I. D., Hindell, M. A., Harcourt, R. G., & Gales, N. J. (2015). Taking animal tracking to new depths: synthesizing horizontal–vertical movement relationships for four marine predators. Ecology, 96(2), 417-427.

Bidder, O. R., Campbell, H. A., Gómez-Laich, A., Urgé, P., Walker, J., Cai, Y., ... & Wilson, R. P. (2014). Love thy neighbour: automatic animal behavioural classification of acceleration data using the k-nearest neighbour algorithm. PloS one, 9(2), e88609.

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J. B., ... & Tremblay, Y. (2007). Variations in behavior and condition of a Southern Ocean top predator in relation to in

situ oceanographic conditions. Proceedings of the National Academy of Sciences, 104(34), 13705-13710.

Biuw, M., Krafft, B. A., Hofmeyr, G. G., Lydersen, C., & Kovacs, K. M. (2009). Time budgets and at-sea behaviour of lactating female Antarctic fur seals Arctocephalus gazella at Bouvetøya. Marine Ecology Progress Series, 385, 271-284.

Blanchard, J. W. (2011). Inference on the diet composition of predators using fatty acid signatures: an application of Bayesian inference on linear mixing models.

Blix, A. S., & Nordøy, E. S. (2007). Ross seal (Ommatophoca rossii) annual distribution, diving behavior, breeding and moulting, off Queen Maud Land, Antarctica. Polar Biology, 30(11), 1449-1458.

Bodart, J. A., & Bingham, R. J. (2019). The Impact of the Extreme 2015–2016 El Niño on the Mass Balance of the Antarctic Ice Sheet. Geophysical Research Letters, 46(23), 13862-13871.

Bograd, S. J., Block, B. A., Costa, D. P., & Godley, B. J. (2010). Biologging technologies: new tools for conservation. Introduction. Endangered Species Research, 10, 1-7.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. The American Naturalist, 161(1), 1-28.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., ... & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. Trends in ecology & evolution, 26(4), 183-192.

Bonadonna, F., Lea, M. A., & Guinet, C. (2000). Foraging routes of Antarctic fur seals (Arctocephalus gazella) investigated by the concurrent use of satellite tracking and time-depth recorders. Polar Biology, 23(3), 149-159.

Bonadonna, F., Lea, M. A., Dehorter, O., & Guinet, C. (2001). Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal Arctocephalus gazella. Marine Ecology Progress Series, 223, 287-297.

Böning, C. W., Dispert, A., Visbeck, M., Rintoul, S. R., & Schwarzkopf, F. U. (2008). The response of the Antarctic Circumpolar Current to recent climate change. Nature Geoscience, 1(12), 864-869.

Bonner, W. N. (1984). Lactation strategies in pinnipeds: Problems for a marine mammalian group. Symp. Zool. Soc. Lond. 51, 253–272.

Börger, L., Bijleveld, A. I., Fayet, A. L., Machovsky-Capuska, G. E., Patrick, S. C., Street, G. M., & Vander Wal, E. (2020). Biologging special feature. Journal of Animal Ecology, 89(1), 6-15.

Bornemann, H., Kreyscher, M., Ramdohr, S., Martin, T., Carlini, A., Sellmann, L., & Plötz, J. (2000). Southern elephant seal movements and Antarctic sea ice. Antarctic Science, 12(1), 3-15.

Borras-Chavez, R., Goebel, M. E., Villegas-Amtmann S., Hückstädt, L. A., Costa D. P., Budge, S. M., Guerrero, A., Fariña J. M. & Bozinovic F. (in prep). Linking prey targeted and behavior by using diet and Machine Learning tools in an ocean predator.

Borras-Chavez (2018). Bio-logging: Revelando conductas ocultas. Boletín Antártico Chileno, 37 (1 y 2), 74-76.

Bourque, J., Atwood, T. C., Divoky, G. J., Stewart, C., & McKinney, M. A. (2020). Fatty acid-based diet estimates suggest ringed seal remain the main prey of southern Beaufort Sea polar bears despite recent use of onshore food resources. Ecology and Evolution, 10(4), 2093-2103.

Boveng, P. L., Hiruki, L. M., Schwartz, M. K., & Bengtson, J. L. (1998). Population growth of Antarctic fur seals: limitation by a top predator, the leopard seal?. Ecology, 79(8), 2863-2877.

Bowen, W. D. (2000). Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. Canadian Journal of Fisheries and Aquatic Sciences, 57(5), 898-905.

Bowen, W. D., Iverson, S. J., Boness, D. J., & Oftedal, O. T. (2001). Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. Functional Ecology, 325-334.

Boyd, I. L., Lunn, N. J., & Barton, T. (1991). Time budgets and foraging characteristics of lactating Antarctic fur seals. The Journal of Animal Ecology, 577-592.

Boyd, I. L., & Croxall, J. P. (1992). Diving behaviour of lactating Antarctic fur seals. Canadian Journal of Zoology, 70(5), 919-928.

Boyd, I. L., Arnould, J. P., Barton, T., & Croxall, J. P. (1994). Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. Journal of Animal Ecology, 703-713.

Boyd, I. L., Reid, K., & Bevan, R. M. (1995a). Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. Animal Behaviour, 50(3), 769-784.

Boyd, I. L., Croxall, J. P., Lunn, N. J., & Reid, K. (1995b). Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. Journal of Animal Ecology, 505-518.

Boyd, I. L. (1996). Temporal scales of foraging in a marine predator. *Ecology*, *77*(2), 426-434.

Boyd, I. L., McCafferty, D. J., & Walker, T. R. (1997). Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. Behavioral Ecology and Sociobiology, 40(3), 135-144.

Boyd, I. L. (1998). Time and energy constraints in pinniped lactation. The American Naturalist, 152(5), 717-728.

Boyd, I. L. (1999). Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. Behavioral Ecology, 10(2), 198-208.

Boyd, I. L., Murray, A. W.A. (2001). Monitoring a marine ecosystem using responses of upper trophic level predators. J Anim Ecol, 70: 747-760.

Boyd, I. L. (2002). Integrated environment-prey-predator interactions off South Georgia: implications for management of fisheries. Aquatic Conservation: Marine and Freshwater Ecosystems, 12(1), 119-126.

Bozinovic, F., & Pörtner, H. O. (2015). Physiological ecology meets climate change. Ecology and evolution, 5(5), 1025-1030.

Bracegirdle, T. J., Connolley, W. M., & Turner, J. (2008). Antarctic climate change over the twenty first century. Journal of Geophysical Research: Atmospheres, 113(D3).

Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. Proceedings of the Royal Society B: Biological Sciences, 284(1855), 20170449.

Bradshaw, C. J., Davis, L. S., Lalas, C., & Harcourt, R. G. (2000). Geographic and temporal variation in the condition of pups of the New Zealand fur seal (Arctocephalus forsteri): evidence for density dependence and differences in the marine environment. Journal of Zoology, 252(1), 41-51.

Bradshaw, C. J., Hindell, M. A., Best, N. J., Phillips, K. L., Wilson, G., & Nichols, P. D. (2003). You are what you eat: describing the foraging ecology of southern elephant seals (Mirounga leonina) using blubber fatty acids. Proceedings of the Royal Society of London. Series B: Biological Sciences, 270(1521), 1283-1292.

Brault, E. K., Koch, P. L., Costa, D. P., McCarthy, M. D., Hückstädt, L. A., Goetz, K. T., ... & Harkonen, T. (2019). Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. Marine Ecology Progress Series, 611, 1-18.

Breiman, L. (2001). Random Forests. Mach. Learn. 45, 5–32.

Brewster, L. R., Dale, J. J., Guttridge, T. L., Gruber, S. H., Hansell, A. C., Elliott, M., ... & Gleiss, A. C. (2018). Development and application of a machine learning algorithm for classification of elasmobranch behaviour from accelerometry data. Marine biology, 165(4), 62.

Brooks, C. M., Crowder, L. B., Österblom, H., & Strong, A. L. (2020). Reaching consensus for conserving the global commons: The case of the Ross Sea, Antarctica. Conservation Letters, 13(1), e12676.

Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics. Functional Ecology, 24(1), 28-34.

Brown, D. J., Boyd, I. L., Cripps, G. C., & Butler, P. J. (1999). Fatty acid signature analysis from the milk of Antarctic fur seals and Southern elephant seals from South Georgia: implications for diet determination. Marine Ecology Progress Series, 187, 251-263.

Budge, S. M., Iverson, S. J., & Koopman, H. N. (2006). Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Marine Mammal Science, 22(4), 759-801.

Burns, J. M., Trumble, S. J., Castellini, M. A., & Testa, J. W. (1998). The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biology, 19(4), 272-282.

Burns, J. M., Costa, D. P., Fedak, M. A., Hindell, M. A., Bradshaw, C. J., Gales, N. J., ... & Crocker, D. E. (2004). Winter habitat use and foraging behavior of crabeater seals along the

Western Antarctic Peninsula. Deep Sea Research Part II: Topical Studies in Oceanography, 51(17-19), 2279-2303.

Burns, J. M., Hindell, M. A., Bradshaw, C. J., & Costa, D. P. (2008). Fine-scale habitat selection of crabeater seals as determined by diving behavior. Deep Sea Research Part II: Topical Studies in Oceanography, 55(3-4), 500-514.

Campagna, C., Rivas, A. L., & Marin, M. R. (2000). Temperature and depth profiles recorded during dives of elephant seals reflect distinct ocean environments. Journal of Marine Systems, 24(3-4), 299-312.

Carroll, G., Slip, D., Jonsen, I., & Harcourt, R. (2014). Supervised accelerometry analysis can identify prey capture by penguins at sea. Journal of Experimental Biology, 217(24), 4295-4302.

Casaux, R., Baroni, A., & Carlini, A. (1997). The diet of the Weddell seal Leptonychotes weddelli at Harmony Point, South Shetland Islands. Polar Biology, 18(6), 371-375.

Casaux, R., Baroni, A., & Carlini, A. (1998). The diet of the Antarctic fur seal Arctocephalus gazella at Harmony Point, Nelson Island, South Shetland Islands. Polar Biology, 20(6), 424-428.

Casaux, R., Baroni, A., & Ramon, A. (2003). Diet of antarctic fur seals Arctocephalus gazella at the Danco Coast, Antarctic Peninsula. Polar Biology, 26(1), 49-54.

Casaux, R., Baroni, A., & Ramon, A. (2006). The diet of the Weddell seal Leptonychotes weddellii at the Danco Coast, Antarctic Peninsula. Polar Biology, 29(4), 257-262.

Casaux, R., Baroni, A., Ramón, A., Carlini, A., Bertolin, M., & DiPrinzio, C. Y. (2009). Diet of the leopard seal Hydrurga leptonyx at the Danco Coast, Antarctic Peninsula. Polar Biology, 32(2), 307-310.

Cayford, J. T., & Goss-Custard, J. D. (1990). Seasonal changes in the size selection of mussels, Mytilus edulis, by oystercatchers, Haematopus ostralegus: an optimality approach. Animal Behaviour, 40(4), 609-624.

CCAMLR (2019). Report of the thirty-eighth meeting of the scientific committee. CCAMLR, Hobart, 598 pp.

CCAMLR (2018). Krill Fishery Report 2018. Available in www.ccamlr.org

CCAMLR (2020). Fishery Report: Euphasia superba in Area 48. Available in www.ccamlr.org

Cherel, Y., Guinet, C., & Tremblay, Y. (1997). Fish prey of Antarctic fur seals Arctocephalus gazella at Ile de Croy, Kerguelen. Polar Biology, 17(1), 87-90.

Cherel, Y., Ducatez, S., Fontaine, C., Richard, P., & Guinet, C. (2008). Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. Marine Ecology Progress Series, 370, 239-247.

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I. M., Travis, J. M., & Scott, B. E. (2016). The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. Ecology and evolution, 6(3), 727-741.

Chown, S. L., & Brooks, C. M. (2019). The state and future of Antarctic environments in a global context. Annual Review of Environment and Resources, 44, 1-30.

Cianchetti-Benedetti, M., Catoni, C., Kato, A., Massa, B., & Quillfeldt, P. (2017). A new algorithm for the identification of dives reveals the foraging ecology of a shallow-diving seabird using accelerometer data. Marine Biology, 164(4), 77.

Clarke, M. R., & Macleod, N. (1982). Cephalopod remains in the stomachs of eight Weddell seals. BAS Bulletins, (57), 33-40.

Clarke, A., Murphy, E. J., Meredith, M. P., King, J. C., Peck, L. S., Barnes, D. K., & Smith, R. C. (2007). Climate change and the marine ecosystem of the western Antarctic Peninsula. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1477), 149-166.

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. Nature, 337(6204), 260-262.

Collins, M. A., Xavier, J. C., Johnston, N. M., North, A. W., Enderlein, P., Tarling, G. A., ... & Cunningham, N. J. (2008). Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. Polar Biology, 31(7), 837-851.

Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I., & Miller, D. (2000). Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES Journal of marine Science, 57(3), 778-791.

Constable, A. J. (2011). Lessons from CCAMLR on the implementation of the ecosystem approach to managing fisheries. Fish and Fisheries, 12(2), 138-151.

Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K., ... & Davidson, A. T. (2014). Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Global change biology*, *20*(10), 3004-3025.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., & Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. Trends in ecology & evolution, 19(6), 334-343.

Costa, D. P., & Gentry, R. L. (1986). Free-ranging energetics of northern fur seals. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, NJ, 79-101.

Costa, D. P., Boeuf, B. L., Huntley, A. C., & Ortiz, C. L. (1986). The energetics of lactation in the northern elephant seal, Mirounga angustirostris. Journal of Zoology, 209(1), 21-33.

Costa, D. P., & Trillmich, F. (1988). Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (Arctocephalus gazella) and Galapagos fur seals (Arctocephalus galapagoensis). Physiological Zoology, 61(2), 160-169.

Costa, D. P., Croxall, J. P., & Duck, C. D. (1989). Foraging energetics of antarctic fur seals in relation to changes in prey availability. Ecology, 70(3), 596-606.

Costa, D. P. (1991). Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. American Zoologist, 31(1), 111-130.

Costa, D. P. (1993). The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. In Symp Zool Soc Lond (Vol. 66, pp. 293-314).

Costa, D. P., & Crocker, D. E. (1996). Marine mammals of the Southern Ocean. Foundations for Ecological Research West of the Antarctic Peninsula, Antarctic Research Series.

Costa, D. P., Goebel, M. E., & Sterling, J. T. (2000). Foraging energetics and diving behavior of the Antarctic fur seal, Arctocephalus gazella, at Cape Shirreff, Livingston Island. Antarctic ecosystems: models for wider ecological understanding. New Zealand Natural Sciences, Christchurch, 77-84.

Costa, D. P., & Gales, N. J. (2003). Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, Neophoca cinerea. Ecological Monographs, 73(1), 27-43.

Costa, D. P., Kuhn, C. E., Weise, M. J., Shaffer, S. A., & Arnould, J. P. (2004, December). When does physiology limit the foraging behaviour of freely diving mammals? In International congress series (Vol. 1275, pp. 359-366). Elsevier.

Costa, D. P. (2008). A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. Aquat Conserv Mar Freshw Ecosyst 17:S44–S52.

Costa, D. P., Klinck, J. M., Hofmann, E. E., Dinniman, M. S., & Burns, J. M. (2008). Upper ocean variability in west Antarctic Peninsula continental shelf waters as measured using instrumented seals. Deep Sea Research Part II: Topical Studies in Oceanography, 55(3-4), 323-337.

Costa, D. P. (2009). Energetics. In *Encyclopedia of marine mammals* (pp. 383-391). Academic Press.

Costa, D. P., Block, B. A., Bograd, S., Fedak, M. A., and Gunn, J. S. (2010a). TOPP as a marine life observatory: using electronic tags to monitor the movements, behavior and habitats of marine vertebrates. Proc. OceanObs 9, 21–25. doi: 10.5270/OceanObs09.cwp.19

Costa, D. P., Hückstädt, L. A., Crocker, D. E., McDonald, B. I., Goebel, M. E., & Fedak, M. A. (2010b). Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. Integrative and Comparative Biology, 50(6), 1018-1030.

Costa, D. P., Robinson, P. W., Arnould, J. P., Harrison, A. L., Simmons, S. E., Hassrick, J. L., ... & Crocker, D. E. (2010c). Accuracy of ARGOS locations of pinnipeds at-sea estimated using Fastloc GPS. PloS one, 5(1), e8677.

Cox, M.J., Candy, S., de la Mare, W.K., Nicol, S., Kawaguchi, S., Gales, N., 2018. No evidence for a decline in the density of Antarctic krill Euphausia superba Dana, 1850, in the Southwest Atlantic sector between 1976 and 2016. J. Crustac. Biol. 38, 656–661. https://doi.org/10.1093/jcbiol/ruy072

Crocker, D. E., Gales, N. J., & Costa, D. P. (2001). Swimming speed and foraging strategies of New Zealand sea lions (Phocarctos hookeri). Journal of Zoology, 254(2), 267-277.

Croxall, J. P., Everson, I., Kooyman, G. L., Ricketts, C., & Davis, R. W. (1985). Fur seal diving behavior in relation to vertical distribution of krill. The Journal of Animal Ecology, 1-8.

Dahood, A., Watters, G. M., & de Mutsert, K. (2019). Using sea-ice to calibrate a dynamic trophic model for the Western Antarctic Peninsula. PloS one, 14(4).

Daly, K. L. (2004). Overwintering growth and development of larval Euphausia superba: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. Deep Sea Research Part II: Topical Studies in Oceanography, 51(17-19), 2139-2168.

Daneri, G. A., & Coria, N. R. (1992). The diet of Antarctic fur seals, Arctocephalus gazella, during the summer-autumn period at Mossman Peninsula, Laurie Island (South Orkneys). Polar Biology, 11(8), 565-566.

Daneri, G. A., & Carlini, A. R. (1999a). Spring and summer predation on fish by the Antarctic fur seal, Arctocephalus gazella, at King George Island, South Shetland Islands. Canadian Journal of Zoology, 77(7), 1157-1160.

Daneri, G. A., Piatkowski, U., Coria, N. R., & Carlini, A. R. (1999b). Predation on cephalopods by Antarctic fur seals, Arctocephalus gazella, at two localities of the Scotia Arc, Antarctica. Polar Biology, 21(1), 59-63.

Daneri, G. A., Carlini, A. R., Hernandez, C. M., & Harrington, A. (2005). The diet of Antarctic fur seals, Arctocephalus gazella, at King George Island, during the summer–autumn period. Polar Biology, 28(4), 329-333.

Daneri, G. A., Carlini, A. R., Negri, A., Allcock, A. L., & Corbalán, A. (2012). Predation on cephalopods by Weddell seals, Leptonychotes weddellii, at Hope Bay, Antarctic Peninsula. Polar biology, 35(4), 585-592.

Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., ... & Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. Science, 283(5404), 993-996.

Davidson, A. D., Boyer, A. G., Kim, H., Pompa-Mansilla, S., Hamilton, M. J., Costa, D. P., ... & Brown, J. H. (2012). Drivers and hotspots of extinction risk in marine mammals. Proceedings of the National Academy of Sciences, 109(9), 3395-3400.

Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2003). Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Marine Ecology Progress Series, 256, 229-242.

Dellinger, T., & Trillmich, F. (1988). Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable?. Canadian Journal of Zoology, 66(8), 1865-1870.

Dill, L. M. (1983). Adaptive flexibility in the foraging behavior of fishes. Canadian Journal of Fisheries and Aquatic Sciences, 40(4), 398-408.

Doidge, D. W., & Croxall, J. P. (1989). Factors affecting weaning weight in Antarctic fur seals Arctocephalus gazella at South Georgia. Polar Biology, 9(3), 155-160.

Donohue MJ, Costa DP, Goebel E, Antonelis GA, Baker JD (2002). Milk intake and energy expenditure of free-ranging northern fur seal, Callorhinus ursinus, pups. Physiological and Biochemical Zoology, 75(1): 3-18. doi: 10.1086/338284

Ducklow, H. W., Baker K., Martinson, D. G., Quetin, L. B., *et al*. (2007). Marine pelagic ecosystems: The West Antarctic Peninsula. Philos Trans R Soc B-Biol Sci, 362(1477):67–94.

Dulvy, N.K., Sadovy, Y., Reynolds, J.D. (2003). Extinction vulnerability in marine populations. Fish and Fisheries, 4: 25-64

Erickson, A. W., & Hanson, M. B. (1990). Continental estimates and population trends of Antarctic ice seals. In Antarctic Ecosystems (pp. 253-264). Springer, Berlin, Heidelberg.

Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors (2011). Ocean Base map credits.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., ... & Forester, J. (2013). Spatial memory and animal movement. Ecology letters, 16(10), 1316-1329.

Fahlman, A., Svärd, C., Rosen, D. A., Jones, D. R., & Trites, A. W. (2008). Metabolic costs of foraging and the management of O2 and CO2 stores in Steller sea lions. Journal of Experimental Biology, 211(22), 3573-3580.

Fedak, M. A., & Anderson, S. S. (1982). The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (Halichoerus grypus). Journal of Zoology, 198(4), 473-479.

Fedak, M. A., Lovell, P., & Grant, S. M. (2001). Two Approaches to compressing and interpreting Time-Depth information collected by time-Depth recorders and satellite-linked data recorders. Marine Mammal Science, 17(1), 94-110.

Feldkamp, S. D., DeLong, R. L., & Antonelis, G. A. (1991). Effects of El Niño 1983 on the foraging patterns of California sea lions (Zalophus californianus) near San Miguel Island, California. In *Pinnipeds and El Niño* (pp. 146-155). Springer, Berlin, Heidelberg.

Fendt, M., Parsons, M. H., Apfelbach, R., Carthey, A. J., Dickman, C. R., Endres, T., ... & Kreutzmann, J. C. (2020). Context and trade-offs characterize real-world threat detection systems: A review and comprehensive framework to improve research practice and resolve the translational crisis. Neuroscience & Biobehavioral Reviews.

Festa-Bianchet, M. (1988). Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia, 75(4), 580-586.

Field, I., Hindell, M., Slip, D., & Michael, K. (2001). Foraging strategies of southern elephant seals (Mirounga leonina) in relation to frontal zones and water masses. Antarctic Science, 13(4), 371-379.

Forcada, J., Trathan, P. N., Reid, K., & Murphy, E. J. (2005). The effects of global climate variability in pup production of Antarctic fur seals. *Ecology*, *86*(9), 2408-2417.

Forcada, J., Trathan, P. N., Reid, K., Murphy, E. J., & Croxall, J. P. (2006). Contrasting population. changes in sympatric penguin species in association with climate warming. Global Change Biology, 12(3), 411-423.

Forcada, J., Trathan, P. N., & Murphy, E. J. (2008). Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, *14*(11), 2473-2488.

Forcada, J., & Trathan, P. N. (2009). Penguin responses to climate change in the Southern Ocean. *Global Change Biology*, *15*(7), 1618-1630.

Forcada, J., Malone, D., Royle, J. A., & Staniland, I. J. (2009). Modelling predation by transient leopard seals for an ecosystem-based management of Southern Ocean fisheries. Ecological Modelling, 220(12), 1513-1521.

Forcada, J., Trathan, P. N., Boveng, P. L., Boyd, I. L., Burns, J. M., Costa, D. P., ... & Southwell, C. J. (2012). Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. Biological Conservation, 149(1), 40-50.

Francis, J., Boness, D., & Ochoa-Acuña, H. (1998). A protracted foraging and attendance cycle in female Juan Fernandez fur seals. *Marine Mammal Science*, *14*(3), 552-574.

Fraser, W. R., & Hofmann, E. E. (2003). A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, *265*, 1-15.

Fraser, W. R., Pitman, R. L., & Ainley, D. G. (1989). Seabird and fur seal responses to vertically migrating winter krill swarms in Antarctica. Polar Biology, 10(1), 37-41.

Freeman, R., Dennis, T., Landers, T., Thompson, D., Bell, E., Walker, M., & Guilford, T. (2010). Black Petrels (Procellaria parkinsoni) patrol the ocean shelf-break: GPS tracking of a vulnerable procellariiform seabird. PLoS One, 5(2), e9236.

Fricke, H., Gercken, G., Schreiber, W., & Oehlenschläger, J. (1984). Lipid, sterol and fatty acid composition of Antarctic krill (Euphausia superba Dana). Lipids, 19(11), 821-827.

Friedlaender, A. S., Johnston, D. W., Fraser, W. R., Burns, J., & Costa, D. P. (2011). Ecological niche modeling of sympatric krill predators around Marguerite Bay, Western Antarctic Peninsula. Deep Sea Research Part II: Topical Studies in Oceanography, 58(13-16), 1729-1740.

Folch, J., Lees, M., & Stanley, G. S. (1957). A simple method for the isolation and purification of total lipides from animal tissues. Journal of biological chemistry, 226(1), 497-509.

Folkens, P. A., & Reeves, R. R. (2002). Guide to marine mammals of the world (No. Sirsi) i9780375411410). National Audubon Society.

Fox, J., & Weisberg, S. (2019). An R companion to applied regression (Third). Thousand Oaks CA: Sage.

Gales, N. J., & Mattlin, R. H. (1998). Fast, safe, field-portable gas anesthesia for otariids. Marine Mammal Science, 14(2), 355-361.

Gallon, S., Hindell, M. A., & Muelbert, M. M. C. (2018). Foraging insights from whisker isotopic signatures of southern elephant seals around the Antarctic Peninsula. Deep Sea Research Part II: Topical Studies in Oceanography, 149, 229-239.

Galloway, A. W., Taipale, S. J., Hiltunen, M., Peltomaa, E., Strandberg, U., Brett, M. T., & Kankaala, P. (2014). Diet-specific biomarkers show that high-quality phytoplankton fuels herbivorous zooplankton in large boreal lakes. Freshwater Biology, 59(9), 1902-1915.

Galloway, A. W., Brett, M. T., Holtgrieve, G. W., Ward, E. J., Ballantyne, A. P., Burns, C. W., ... & Strandberg, U. (2015). A fatty acid based Bayesian approach for inferring diet in aquatic consumers. PloS one, 10(6), e0129723.

Gálvez, C., Pardo, M. A., & Elorriaga-Verplancken, F. R. (2020). Impacts of extreme ocean warming on the early development of a marine top predator: The Guadalupe fur seal. Progress in Oceanography, 180, 102220.

Garton, D. W., Hsu, M. J., & Harder, J. D. (1994). Environmental temperature and metabolic rates during gestation and lactation in golden hamsters (Mesocricetus auratus). Physiological zoology, 67(2), 497-514.

Gautestad, A. O., & Mysterud, I. (2010a). The home range fractal: from random walk to memory-dependent space use. Ecological Complexity, 7(4), 458-470.

Gautestad, A. O., & Mysterud, I. (2010b). Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns. Ecological Modelling, 221(23), 2741-2750.

Gautestad, A. O. (2011). Memory matters: influence from a cognitive map on animal space use. Journal of Theoretical Biology, 287, 26-36.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). Bayesian data analysis. CRC press.

Gentry, R. L., & Holt, J. R. (1986). Attendance behavior of northern fur seals. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, NJ, 41-60.

Gentry, R.L. (1998) Behavior and ecology of the northern fur seal (Vol. 382). Princeton University Press.

Georges, J. Y., & Guinet, C. (2000). Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology*, *81*(2), 295-308.

Georges, J. Y., Tremblay, Y., & Guinet, C. (2000). Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island. Polar Biology, 23(1), 59-69

Gerlinsky, C. D., Rosen, D. A., & Trites, A. W. (2013). High diving metabolism results in a short aerobic dive limit for Steller sea lions (Eumetopias jubatus). Journal of Comparative Physiology B, 183(5), 699-708.

Geweke, J. (1991). Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments (Vol. 196). Minneapolis, MN: Federal Reserve Bank of Minneapolis, Research Department.

Gille, S. T. (2008). Decadal-scale temperature trends in the Southern Hemisphere ocean. Journal of Climate, 21(18), 4749-4765.

Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. American zoologist, 28(3), 863-875.

Goebel, M. E., Costa, D. P., Crocker, D. E., Sterling, J. T., & Demer, D. A. (2000). Foraging ranges and dive patterns in relation to bathymetry and time-of-day of Antarctic fur seals, Cape Shirreff, Livingston Island, Antarctica. Antarctic ecosystems: models for wider ecological understanding. New Zealand Natural Sciences, Christchurch, 47-50.

Goebel, M. E., Lipsky, J. D., Reiss, C. S., & Loeb, V. J. (2007). Using carapace measurements to determine the sex of Antarctic krill, Euphausia superba. Polar Biology, 30(3), 307-315.

Goebel M. E., Krause, K., Freeman, S., Burner, R., Bonin, C., Vasquez del Mercado, R., Van Cise, A. M., & Gafney, J., Chapter 7. Pinniped Research at Cape Shirreff, Livingston Island Antarctica, 2008/09 (eds) In: Van Cise A.M., (2009) AMLR 2008/2009 Field Season Report. Objectives, Accomplishments and Tentative Conclusions. United States AMLR Program.

Goetz, K. T., Burns, J. M., Hückstädt, L. A., Shero, M. R., & Costa, D. P. (2017). Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. Deep Sea Research Part II: Topical Studies in Oceanography, 140, 36-44.

Goldsworthy, S. D. (1992). Maternal care in three species of southern fur seal (Arctocephalus spp.) (Doctoral dissertation, Monash University).

Goldsworthy, S. D., Hindell, M. A., & Crowley, H. M. (1997). Diet and diving behavior of sympatric fur seals Arctocephalus gazella and A. tropicalis at Macquarie Island. In Marine mammal research in the Southern Hemisphere (Vol. 1, pp. 151-163).

Goldsworthy, S. D., & Crowley, H. M. (1999). The composition of the milk of Antarctic (Arctocephalus gazella) and subantarctic (A. tropicalis) fur seals at Macquarie Island. Australian Journal of Zoology, 47(6), 593-603.

Goldsworthy, S. D., Page, B., Welling, A., Chambellant, M., & Bradshaw, C. J. (2010). Selection of diving strategy by Antarctic fur seals depends on where and when foraging takes place. Marine Ecology Progress Series, 409, 255-266.

Gon, O., & Heemstra, P. C. (Eds.). (1990). Fishes of the Southern Ocean (Vol. 1). Grahamstown: JLB Smith Institute of Ichthyology.

Grahl-Nielsen, O. (1999). Comment: fatty acid signatures and classification trees: new tools for investigating the foraging ecology of seals. Canadian Journal of Fisheries and Aquatic Sciences, 56(11), 2219-2223.

Grahl-Nielsen, O., & Mjaavatten, O. (1995). Marine mammalian fatty acids: a source of information. Whales, seals, fish and man. Elsevier Science Publishers, Amsterdam, 141-152.

Grahl-Nielsen, O., Haug, T., Lindstrøm, U., & Nilssen, K. T. (2011). Fatty acids in harp seal blubber do not necessarily reflect their diet. Marine Ecology Progress Series, 426, 263-276.

Green, K., & Williams, R. (1986). Observations on food remains in faeces of elephant, leopard and crabeater seals. Polar Biology, 6(1), 43-45.

Green, K., & Burton, H. R. (1987). Seasonal and Geographical Variation in the Food of Weddell Seals, Leptonychotes-Weddelii, in Antarctica. Wildlife Research, 14(4), 475-489.

Green, K., Williams, R., & Burton, H. R. (1991). The diet of Antarctic fur seals during the late autumn and early winter around Heard Island. Antarctic Science, 3(4), 359-361.

Green, K., Williams, R., & Burton, H. R. (1997). Foraging ecology of Antarctic fur seals Arctocephalus gazella Peters around Heard Island. Marine mammal research in the southern hemisphere: status, ecology and medicine, 1, 105-113.

Guerrero, A. I., & Rogers, T. L. (2017). Blubber fatty acid composition and stratification in the crabeater seal, Lobodon carcinophaga. Journal of Experimental Marine Biology and Ecology, 491, 51-57

Guerrero, A. I., & Rogers, T. L., (in prep (a)). Evaluating the performance of the Bayesian mixing tool MixSIAR with fatty acid data for quantitative estimation of diet. Scientific Report.

Guerrero, A. I., & Rogers, T. L., (in prep (b)). Complementary use of stable isotopes and fatty acids for quantitative diet estimation of sympatric predators, the Antarctic pack-ice seals.

Guinet, C., Dubroca, L., Lea, M. A., Goldsworthy, S., Cherel, Y., Duhamel, G., ... & Donnay, J. P. (2001). Spatial distribution of foraging in female Antarctic fur seals Arctocephalus gazella in relation to oceanographic variables: a scale-dependent approach using geographic information systems. Marine Ecology Progress Series, 219, 251-264.

Gutt, J., & Siegel, V. (1994). Benthopelagic aggregations of krill (Euphausia superba) on the deeper shelf of the Weddell Sea (Antarctic). Deep Sea Research Part I: Oceanographic Research Papers, 41(1), 169-178.

Hall-Aspland, S. A., Rogers, T. L., & Canfield, R. B. (2005). Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. Marine Ecology Progress Series, 305, 249-259.

Hanchet, S., Dunn, A., Parker, S., Horn, P., Stevens, D., Mormede, S. (2015). The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross Sea region. Hydrobiologia, 761: 397-414

Happel, A., Stratton, L., Kolb, C., Hays, C., Rinchard, J., & Czesny, S. (2016). Evaluating quantitative fatty acid signature analysis (QFASA) in fish using controlled feeding experiments. Canadian Journal of Fisheries and Aquatic Sciences, 73(8), 1222-1229.

Harcourt, R. G., Bradshaw, C. J., Dickson, K., & Davis, L. S. (2002). Foraging ecology of a generalist predator, the female New Zealand fur seal. Marine Ecology Progress Series, 227, 11-24.

Harcourt, R., Sequeira, A. M. M., Zhang, X., Roquet, F., Komatsu, K., Heupel, M., ... & Brodie, S. (2019). Animal-borne telemetry: an integral component of the ocean observing toolkit. Frontiers in Marine Science, 6, 326.

Harder, J. D., Hsu, M. J., & Garton, D. W. (1996). Metabolic rates and body temperature of the gray short-tailed opossum (Monodelphis domestica) during gestation and lactation. Physiological Zoology, 69(2), 317-339.

Harding, A. M., Piatt, J. F., Schmutz, J. A., Shultz, M. T., Pelt, T. I. V., Kettle, A. B., & Speckman, S. G. (2007). Prey density and the behavioral flexibility of a marine predator: the common murre (Uria aalge). Ecology, 88(8), 2024-2033.

Hassrick, J. L., Crocker, D. E., & Costa, D. P. (2013). Effects of maternal age and mass on foraging behaviour and foraging success in the northern elephant seal. Functional ecology, 27(4), 1055-1063.

Hastie, G. D., Rosen, D. A., & Trites, A. W. (2007). Reductions in oxygen consumption during dives and estimated submergence limitations of Steller sea lions (Eumetopias jubatus). Marine mammal science, 23(2), 272-286.

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., ... & de Bruyn, P. N. (2019). Translating marine animal tracking data into conservation policy and management. Trends in ecology & evolution.

Hecht, T. (1971). A guide to the otoliths of Southern Ocean fishes. *Vol 4*.

Heerah, K., Andrews-Goff, V., Williams, G., Sultan, E., Hindell, M., Patterson, T., & Charrassin, J. B. (2013). Ecology of Weddell seals during winter: Influence of environmental parameters on their foraging behavior. Deep Sea Research Part II: Topical Studies in Oceanography, 88, 23-33.

Heerah, K., Dias, M. P., Delord, K., Oppel, S., Barbraud, C., Weimerskirch, H., & Bost, C. A. (2019). Important areas and conservation sites for a community of globally threatened marine predators of the Southern Indian Ocean. Biological conservation, 234, 192-201.

Hill, S. L., Murphy, E. J., Reid, K., Trathan, P. N., & Constable, A. J. (2006). Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. Biological Reviews, 81(4), 581-608.

Hill, S.L., Atkinson, A., Pakhomov, E.A., Siegel, V., 2019. Evidence for a decline in the population density of Antarctic krill Euphausia superba Dana, 1850 still stands. A comment on Cox *et al*. J. Crustac. Biol. doi: 10.1093/jcbiol/ruz004

Hindell, M. A., McMahon, C. R., Bester, M. N., Boehme, L., Costa, D., Fedak, M. A., ... & Kovacs, K. M. (2016). Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. Ecosphere, 7(5), e01213.

Hindell, M. A., Reisinger, R. R., Ropert-Coudert, Y., Hückstädt, L. A., Trathan, P. N., Bornemann, H., ... & Lea, M. A. (2020). Tracking of marine predators to protect Southern Ocean ecosystems. Nature, 580(7801), 87-92.

Hinke, J. T., Cossio, A. M., Goebel, M. E., Reiss, C. S., Trivelpiece, W. Z., & Watters, G. M. (2017). Identifying risk: concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia Sea. PLoS One, 12(1).

Hocking, D. P., Marx, F. G., Park, T., Fitzgerald, E. M., & Evans, A. R. (2017). A behavioural framework for the evolution of feeding in predatory aquatic mammals. Proceedings of the Royal Society B: Biological Sciences, 284(1850), 20162750.

Hofmann, E. E., & Hüsrevoğlu, Y. S. (2003). A circumpolar modeling study of habitat control of Antarctic krill (Euphausia superba) reproductive success. Deep Sea Research Part II: Topical Studies in Oceanography, 50(22-26), 3121-3142.

Hooker, S. K., Boyd, I. L., Jessopp, M., Cox, O., Blackwell, J., Boveng, P. L., & Bengtson, J. L. (2002). Monitoring the prey-field of marine predators: Combining digital imaging with datalogging tags. Marine Mammal Science, 18(3), 680-697.

Houston, D., & Shine, R. (1993). Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. Journal of Animal Ecology, 737-748.

Hucke-Gaete, R., Osman, L. P., Moreno, C. A., & Torres, D. (2004). Examining natural population growth from near extinction: the case of the Antarctic fur seal at the South Shetlands, Antarctica. Polar Biology, 27(5), 304-311.

Hückstädt, L. A., Burns, J. M., Koch, P. L., McDonald, B. I., Crocker, D. E., & Costa, D. P. (2012a). Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Marine Ecology Progress Series, 455, 287-301.

Hückstädt, L. A., Koch, P. L., McDonald, B. I., Goebel, M. E., Crocker, D. E., & Costa, D. P. (2012b). 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, L. A., Piñones, A., Palacios, D. M., McDonald, B. I., Dinniman, M. S., Hofmann, E. E., ... & Costa, D. P. (2020). Projected shifts in the foraging habitat of crabeater seals along the Antarctic Peninsula. Nature Climate Change, 1-6.

 Hulley, P. A., & PA, H. (1981). Results of the research cruises of FRV" Walther Herwig" to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes).

Husson, F., Josse, J., Lê, S., & Mazet, J. (2009). Factominer: Factor Analysis and Data Mining with R. R Package.

Ichii, T., Bengtson, J. L., Boveng, P. L., Takao, Y., Jansen, J. K., Hiruki-Raring, L. M., ... & Naganobu, M. (2007). Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. Marine Ecology Progress Series, 344, 277-297.

Iverson, S. J., Sampugna, J., & Oftedal, O. T. (1992). Positional specificity of gastric hydrolysis of long-chain n− 3 polyunsaturated fatty acids of seal milk triglycerides. Lipids, 27(11), 870-878.

Iverson, S. J. (1993). Milk secretion in marine mammals in relation to foraging: can milk fatty acids predict diet. In Symp Zool Soc Lond (Vol. 66, pp. 263-291).

Iverson, S. J., Arnould, J. P., & Boyd, I. L. (1997a). Milk fatty acid signatures indicate both major and minor shifts in the diet of lactating Antarctic fur seals. Canadian Journal of Zoology, 75(2), 188-197.

Iverson, S. J., Frost, K. J., & Lowry, L. F. (1997b). Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Marine Ecology Progress Series, 151, 255-271.

Iverson, S. J., Lang, S. L., & Cooper, M. H. (2001). Comparison of the Bligh and Dyer and Folch methods for total lipid determination in a broad range of marine tissue. Lipids, 36(11), 1283-1287.

Iverson, S. J., Field, C., Don Bowen, W., & Blanchard, W. (2004). Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs, 74(2), 211-235.

IUCN (International Union for Conservation of Nature, (2020). Spatial data and mapping resources. The IUCN Red List of Threatened Species. Version 2019-3. http://www.iucnredlist.org. Downloaded on 6 March 2020.

Iwami, T., & Naganobu, M. (2011). Annual changes in species composition and abundance of myctophid fish in the north of South Georgia (subarea 48.3), Antarctica, during austral winters from 2002 to 2008. CCAMLR Science, 18, 155-165.

Iwata, T., Sakamoto, K. Q., Takahashi, A., Edwards, E. W., Staniland, I. J., Trathan, P. N., & Naito, Y. (2012). Using a mandible accelerometer to study fine-scale foraging behavior of free-ranging Antarctic fur seals. Marine Mammal Science, 28(2), 345.

Jeanniard-du-Dot, T., Guinet, C., Arnould, J. P., Speakman, J. R., & Trites, A. W. (2017). Accelerometers can measure total and activity-specific energy expenditures in free-ranging marine mammals only if linked to time-activity budgets. Functional Ecology, 31(2), 377-386.

Jennings, S., Reynolds, J.D., Mills, S.C. (1998). Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London. Series B, 265: 333-339

Jones, C. D., Kock, K. H., Ashford, J., DeVries, A., Dietrich, K., Hanchet, S., ... & Wilhelms, S. (2003). Standing stock, biology, diet and spatial distribution of demersal finfish from the 2003 US AMLR bottom trawl survey of the South Shetland Islands (Subarea 48.1). Document WGFSA03/38. CCAMLR, Hobart, Australia.

Kalinowski, J., & Witek, Z. (1980). Diurnal vertical distribution of krill aggregations in the Western Antarctic. Polish Polar Research, 127-146.

Kamerman, J. (2019). QFASA R Package (Doctoral dissertation, UNIVERSITY OF NEW BRUNSWICK).

Kassambara, A., & Mundt, F. (2017). Factoextra: extract and visualize the results of multivariate data analyses. R package version, 1(5), 337-354.

Kawabata, Y., Noda, T., Nakashima, Y., Nanami, A., Sato, T., Takebe, T., ... & Soyano, K. (2014). Use of a gyroscope/accelerometer data logger to identify alternative feeding behaviours in fish. Journal of Experimental Biology, 217(18), 3204-3208.

Kawaguchi, S., Candy, S. G., King, R., Naganobu, M., & Nicol, S. (2006). Modelling growth of Antarctic krill. I. Growth trends with sex, length, season, and region. Marine Ecology Progress Series, 306, 1-15.

Kawaguchi, S., Nicol, S., & Press, A. J. (2009). Direct effects of climate change on the Antarctic krill fishery. Fisheries Management and Ecology, 16(5), 424-427.

Kernaléguen, L., Arnould, J. P., Guinet, C., & Cherel, Y. (2015). Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals. Journal of Animal Ecology, 84(4), 1081-1091.

Kienle, S. E. (2019). Intraspecific variation and behavioral flexibility in the foraging strategies of seals. UC Santa Cruz. ProQuest ID: Kienle_ucsc_0036E_11830. Merritt ID: ark:/13030/m59s6t1r.

Kienle, S. S., Powers, J., Kendall, T., Richter, B., Castle, L., Lentes, G., ... & Mehta, R. S. (2020). Context matters: Hawaiian monk seals switch between feeding strategies depending on ecological context. Integrative and Comparative Biology.

King, J. E. (1970). Some aspects of the anatomy of the Ross seal, Ommatophoca rossi (Pinnipedia: Phocidae) (Vol. 63). British Antarctic Survey.

Kirkman, S. P., Wilson, W., Klages, N. T. W., Bester, M. N., & Isaksen, K. (2000). Diet and estimated food consumption of Antarctic fur seals at Bouvetøya during summer. Polar Biology, 23(11), 745-752.

Kleanthous, N., Hussain, A., Mason, A., & Sneddon, J. (2019). Data Science Approaches for the Analysis of Animal Behaviours. In International Conference on Intelligent Computing (pp. 411-422). Springer, Cham.

Klein, E. S., Hill, S. L., Hinke, J. T., Phillips, T., & Watters, G. M. (2018). Impacts of rising sea temperature on krill increase risks for predators in the Scotia Sea. PLoS One, 13(1).

Klemmedson, A. D., Reiss, C. S., Goebel, M. E., Kaufmann, R. S., Dorval, E., Linkowski, T. B., & Borras-Chavez, R. (2020). Variability in age of a Southern Ocean myctophid (Gymnoscopelus nicholsi) derived from scat-recovered otoliths. Marine Ecology Progress Series, 633, 55-69.

Kock, K. H., & Shimadzu, Y. (1994). Trophic relationships and trends in population size and reproductive parameters in Antarctic high-level predators. Southern Ocean Ecology–the biomass perspective, 287-312.

Kock, K. H., Reid, K., Croxall, J., & Nicol, S. (2007). Fisheries in the Southern Ocean: an ecosystem approach. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1488), 2333-2349.

Kooyman, G. L. (1967). An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. Antarct. Res. Ser, 11, 227-261.

Krause, D. J., Goebel, M. E., Marshall, G. J., & Abernathy, K. (2015). Novel foraging strategies observed in a growing leopard seal (Hydrurga leptonyx) population at Livingston Island, Antarctic Peninsula. Animal Biotelemetry, 3(1), 24.

Krause, D. J., Goebel, M. E., Marshall, G. J., & Abernathy, K. (2016). Summer diving and haul-out behavior of leopard seals (Hydrurga leptonyx) near mesopredator breeding colonies at Livingston Island, Antarctic Peninsula. Marine Mammal Science, 32(3), 839-867.

Krause, D. J., Goebel, M. E., & Kurle, C. M. (2020). Leopard seal diets in a rapidly warming polar region vary by year, season, sex, and body size. BMC Ecology, 20(1), 1-15.

Krüger, L., Paiva, V. H., Petry, M. V., & Ramos, J. A. (2017). Seabird breeding population size on the Antarctic Peninsula related to fisheries activities in non-breeding ranges off South America. Antarctic Science, 29(6), 495-498.

Kuhn, C. E., Crocker, D. E., Tremblay, Y., & Costa, D. P. (2009). Time to eat: measurements of feeding behaviour in a large marine predator, the northern elephant seal Mirounga angustirostris. Journal of Animal Ecology, 78(3), 513-523.

Ladds, M. A., Thompson, A. P., Slip, D. J., Hocking, D. P., & Harcourt, R. G. (2016). Seeing it all: evaluating supervised machine learning methods for the classification of diverse otariid behaviours. PloS one, 11(12), e0166898.

Ladds, M. A., Thompson, A. P., Kadar, J. P., Slip, D. J., Hocking, D. P., & Harcourt, R. G. (2017). Super machine learning: improving accuracy and reducing variance of behaviour classification from accelerometry. Animal Biotelemetry, 5(1), 8.

Laidre, K. L., Heide-Jørgensen, M. P., Logdson, M. L., Hobbs, R. C., Heagerty, P., Dietz, R., ... & Treble, M. A. (2004). Seasonal narwhal habitat associations in the high Arctic. Marine Biology, 145(4), 821-831.

Lake, S., Burton, H., & Wotherspoon, S. (2006). Movements of adult female Weddell seals during the winter months. Polar Biology, 29(4), 270-279.

La Mesa, M., Ashford, J., Larson, E., Vacchi, M. (2004). Age and growth of Scotia Sea icefish, *Chaenocephalus aceratus*, from the South Shetlands Islands. Antarctic Science, 16(3): 253-262

Laws, R. M. (1977). Seals and whales of the Southern Ocean. Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 279(963), 81-96.

Laws, R. M. (1985). The ecology of the Southern Ocean. Amer. Scient., 73, 26-40.

Lea, M. A., Hindell, M., Guinet, C., & Goldsworthy, S. (2002a). Variability in the diving activity of Antarctic fur seals, Arctocephalus gazella, at Iles Kerguelen. Polar Biology, 25(4), 269-279.

Lea, M. A., Cherel, Y., Guinet, C., & Nichols, P. D. (2002b). Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown from fecal and fatty acid analyses. Marine Ecology Progress Series, 245, 281-297.

Lea, M. A., Nichols, P. D., & Wilson, G. (2002c). Fatty acid composition of lipid-rich myctophids and mackerel icefish (Champsocephalus gunnari)–Southern Ocean food-web implications. Polar Biology, 25(11), 843-854.

Lea, M. A., Guinet, C., Cherel, Y., Duhamel, G., Dubroca, L., Pruvost, P., & Hindell, M. (2006). Impacts of climatic anomalies on provisioning strategies of a Southern Ocean predator. Marine Ecology Progress Series, 310, 77-94.

Lea, M. A., Johnson, D., Ream, R., Sterling, J., Melin, S., & Gelatt, T. (2009). Extreme weather events influence dispersal of naive northern fur seals. Biology Letters, 5(2), 252-257.

Le Boeuf, B. J., & Crocker, D. E. (2005). Ocean climate and seal condition. BMC biology, 3(1), 9.

Lee, T., Hobbs, W. R., Willis, J. K., Halkides, D., Fukumori, I., Armstrong, E. M., ... & Wang, O. (2010). Record warming in the South Pacific and western Antarctica associated with the strong central-Pacific El Niño in 2009–10. Geophysical Research Letters, 37(19).

Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T. A., Watanabe, Y. Y., Murgatroyd, M., & Papastamatiou, Y. P. (2017). Analysis of animal accelerometer data using hidden Markov models. Methods in Ecology and Evolution, 8(2), 161-173.

Lipinski, M., & Woyciechowski, M. (1981). Cephalopods in the food of Weddell seals from the Admiralty Bay (King George Island, South Shetland Islands). Polish Polar Research, 2(3-4), 163-167.

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., & Trivelpiece, S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature, 387(6636), 897-900.

Loeb, V. J., Hofmann, E. E., Klinck, J. M., Holm-Hansen, O., & White, W. B. (2009). ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. Antarctic Science, 21(2).

Lowe, C. G., Wetherbee, B. M., Crow, G. L., & Tester, A. L. (1996). Ontogenetic dietary shifts and feeding behavior of the tiger shark, Galeocerdo cuvier, in Hawaiian waters. Environmental Biology of Fishes, 47(2), 203-211.

Lowry, L. F., Testa, J. W., & Calvert, W. (1988). Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. Polar Biology, 8(6), 475-478.

Lunn, N. J., & Boyd, I. L. (1991). Pupping-site fidelity of Antarctic fur seals at Bird Island, South Georgia. Journal of mammalogy, 72(1), 202-206.

Lunn, N. J., Boyd, I. L., Barton, T., & Croxall, J. P. (1993). Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. Journal of Mammalogy, 74(4), 908-919.

Lynch, H. J., Naveen, R., Trathan, P. N., & Fagan, W. F. (2012). Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. Ecology, 93(6), 1367-1377.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. The American Naturalist, 100(916), 603-609.

McCafferty, D. J., Boyd, I. L., Walker, T. R., & Taylor, R. I. (1998). Foraging responses of Antarctic fur seals to changes in the marine environment. Marine Ecology Progress Series, 166, 285-299.

McConnell, B. J., Chambers, C., & Fedak, M. A. (1992). Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarctic science, 4(4), 393-398.

McConnell, B. J., & Fedak, M. A. (1996). Movements of southern elephant seals. Canadian Journal of Zoology, 74(8), 1485-1496.

McDonald, B. I., Goebel, M. E., Crocker, D. E., Tremblay, Y., & Costa, D. P. (2009). Effects of maternal traits and individual behavior on the foraging strategies and provisioning rates of an income breeder, the Antarctic fur seal. Marine Ecology Progress Series, 394, 277-288.

McHuron, E. A., Hazen, E., & Costa, D. P. (2018). Constrained by consistency? Repeatability of foraging behavior at multiple timescales for a generalist marine predator. Marine Biology, 165(8), 122.

McHuron, E. A., Sterling, J. T., Costa, D. P., & Goebel, M. E. (2019). Factors affecting energy expenditure in a declining fur seal population. Conservation Physiology, 7(1), coz103.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., & Hornik, K. (2013). Cluster: cluster analysis basics and extensions. *R package version*, *1*(2), 56.

Martinez Arbizu, P. (2017). pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.0, 1.

Massom, R. A., & Stammerjohn, S. E. (2010). Antarctic sea ice change and variability–physical and ecological implications. Polar Science, 4(2), 149-186.

MathWorks (2016). MATLAB 9.0 and Statistics Toolbox 8.1 (2016). The MathWorks, Inc., Natick, Massachusetts, United States.

MATLAB 9.0 and Statistics Toolbox 8.1 (2016). The MathWorks, Inc., Natick, Massachusetts, United States.

Mattlin, R. H., Gales, N. J., & Costa, D. P. (1998). Seasonal dive behaviour of lactating New Zealand fur seals (Arctocephalus forsteri). *Canadian Journal of Zoology*, *76*(2), 350-360.

Meire, P. M., & Ervynck, A. (1986). Are oystercatchers (Haematopus ostralegus) selecting the most profitable mussels (Mytilus edulis)?. Animal Behaviour, 34(5), 1427-1435.

Merrick, R. L., & Loughlin, T. R. (1997). Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology*, *75*(5), 776-786.

Mery, F., & Burns, J. G. (2010). Behavioural plasticity: an interaction between evolution and experience. Evolutionary Ecology, 24(3), 571-583.

Millar, J. S. (1978). Energetics of reproduction in Peromyscus leucopus: the cost of lactation. Ecology, 59(5), 1055-1061.

Mori, Y., Mitani, Y., Watanabe, Y., & Sato, K. (2007). A behavioral indicator of prey patch richness derived from diving behavior: the proportion of residence time to the standard time. Israel Journal of Ecology & Evolution, 53(3-4), 347-354.

Mormede, S., Dunn, A., Parker, S., & Hanchet, S. (2017). Using spatial population models to investigate the potential effects of the Ross Sea region Marine Protected Area on the Antarctic toothfish population. Fisheries Research, 190, 164-174.

Morris, D. W., Kotler, B. P., Brown, J. S., Sundararaj, V., & Ale, S. B. (2009). Behavioral indicators for conserving mammal diversity. Annals of the New York Academy of Sciences, 1162(1), 334-356.

Muelbert, M. M., de Souza, R. B., Lewis, M. N., & Hindell, M. A. (2013). Foraging habitats of southern elephant seals, Mirounga leonina, from the Northern Antarctic Peninsula. Deep Sea Research Part II: Topical Studies in Oceanography, 88, 47-60.

Murphy E.J., Watkins J.L., Reid K., Trathan P.N., Iverson I., Croxall J.P., *et al*. (1998). Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. Fish Oceanogr, 7: 381-390.

Murphy, E. J., Trathan, P. N., Watkins, J. L., Reid, K., Meredith, M. P., Forcada, J., ... & Rothery, P. (2007). Climatically driven fluctuations in Southern Ocean ecosystems. Proceedings of the Royal Society B: Biological Sciences, 274(1629), 3057-3067.

Nachtsheim, D. A., Jerosch, K., Hagen, W., Plötz, J., & Bornemann, H. (2017). Habitat modelling of crabeater seals (Lobodon carcinophaga) in the Weddell Sea using the multivariate approach Maxent. Polar Biology, 40(5), 961-976.

Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Fowler, M., & Takahashi, A. (2013). Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. Functional Ecology, 27(3), 710-717.

Naya, D. E., Ebensperger, L. A., Sabat, P., & Bozinovic, F. (2008). Digestive and metabolic flexibility allows female degus to cope with lactation costs. Physiological and Biochemical Zoology, 81(2), 186-194.

Neises, V., Zeligs, J., Harris, B., & Cornick, L. (2017). Examining the metabolic cost of otariid foraging under varying conditions. Journal of Experimental Marine Biology and Ecology, 486, 352-357.

Neubauer, P., & Jensen, O. P. (2015). Bayesian estimation of predator diet composition from fatty acids and stable isotopes. PeerJ, 3, e920.

Nicol, S., Foster, J., Kawaguchi, S. 2012. The fishery for Antarctic krill - recent developments. Fish and Fisheries 13, 30-40

Nordøy, E. S., Folkow, L., & Blix, A. S. (1995). Distribution and diving behavior of crabeater seals (Lobodon carcinophagus) off Queen Maud Land. Polar Biology, 15(4), 261-268.

Nordstrom, C. A., Wilson, L. J., Iverson, S. J., & Tollit, D. J. (2008). Evaluating quantitative fatty acid signature analysis (QFASA) using harbour seals Phoca vitulina richardsi in captive feeding studies. Marine Ecology Progress Series, 360, 245-263.

Norris, C. E. (2019). Testing the efficacy of unsupervised machine learning techniques to infer shark behaviour from accelerometry data (Doctoral dissertation, Murdoch University).

Nowacek, D. P., Friedlaender, A. S., Halpin, P. N., Hazen, E. L., Johnston, D. W., Read, A. J., ... & Zhu, Y. (2011). Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. PLoS One, 6(4).

Nuijten, R. J., Gerrits, T., Shamoun-Baranes, J., & Nolet, B. A. (2020). Less is more: On-board lossy compression of accelerometer data increases biologging capacity. Journal of Animal Ecology, 89(1), 237-247.

Oftedal, O. T., Boness, D. J., & Tedman, R. A. (1987). The behavior, physiology, and anatomy of lactation in the pinnipedia. In Current mammalogy (pp. 175-245). Springer, Boston, MA.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. A. S. S. (2007). The vegan package. Community ecology package, 10(631-637), 719.

Oliveira-Santos, L. G. R., Forester, J. D., Piovezan, U., Tomas, W. M., & Fernandez, F. A. (2016). Incorporating animal spatial memory in step selection functions. Journal of Animal Ecology, 85(2), 516-524.

Orians, G. H. & Pearson N.E. (1979). On the theory of central place foraging. In: Horn D. J., Stairs, E. T. & Mitchell, R. T. (Eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH. . pp. 155-177.

Øritsland, T. (1977). Food consumption of seals in the Antarctic pack ice.

Orr, A. J., Newsome, S. D., Laake, J. L., VanBlaricom, G. R., & DeLong, R. L. (2012). Ontogenetic dietary information of the California sea lion (Zalophus californianus) assessed using stable isotope analysis. Marine Mammal Science, 28(4), 714-732.

Osman, L. P., Hucke-Gaete, R., Moreno, C. A., & Torres, D. (2004). Feeding ecology of Antarctic fur seals at Cape Shirreff, South Shetlands, Antarctica. Polar Biology, 27(2), 92-98.

Osman, L. P., Moreno, C. A., & Trites, A. W. (2010). Growth rates and differential investment in male and female Juan Fernández fur seal pups. Journal of Mammalogy, 91(5), 1188-1196.

Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1550), 2267-2278.

Owen, K., Dunlop, R. A., Monty, J. P., Chung, D., Noad, M. J., Donnelly, D., ... & Mackenzie, T. (2016). Detecting surface-feeding behavior by rorqual whales in accelerometer data. Marine Mammal Science, 32(1), 327-348.

Pakhomov, E. A., Atkinson, A., Meyer, B., Oettl, B., & Bathmann, U. (2004). Daily rations and growth of larval krill Euphausia superba in the Eastern Bellingshausen Sea during austral autumn. Deep Sea Research Part II: Topical Studies in Oceanography, 51(17-19), 2185-2198.

Parkinson, C. L. (2019). A 40-y record reveals gradual Antarctic sea ice increases followed by decreases at rates far exceeding the rates seen in the Arctic. Proceedings of the National Academy of Sciences, 116(29), 14414-14423.

PSA-LTER (Palmer Station Antarctica LTER) & D. Steinberg. (2020a). Standard body length of Euphausia superba collected with a 2-m, 700-um net towed from surface to 120 m, collected aboard Palmer LTER annual cruises off the coast of the Western Antarctic Peninsula, 2009 - 2019. ver 5. Environmental Data Initiative. https://doi.org/10.6073/pasta/be42bb841e696b7bcad9957aed33db5e.

PSA-LTER (Palmer Station Antarctica LTER) & Steinberg, D. (2020b). Zooplankton collected with a 2-m, 700-um net towed from surface to 120 m, aboard Palmer Station Antarctica LTER annual cruises off the western antarctic peninsula, 2009 - 2019. ver 7. Environmental Data Initiative. https://doi.org/10.6073/pasta/434b2f73803b9d3d8088cd094cf46cca (Accessed 2020-12-07).

Patrick, S. C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W. J., Bodey, T. W., ... & Votier, S. C. (2014). Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. Oikos, 123(1), 33-40.

Perez, M. A., & Mooney, E. E. (1986). Increased food and Energy-consumption of Lactating Northern fur seals, Callorhinus-ursinus. Fishery Bulletin 84(2), 371-381.

Phleger, C. F., Nelson, M. M., Mooney, B. D., & Nichols, P. D. (2002). Interannual and between species comparison of the lipids, fatty acids and sterols of Antarctic krill from the US AMLR Elephant Island survey area. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 131(4), 733-747.

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2017). R Core Team (2017) nlme: linear and nonlinear mixed effects models. R package version 3.1-131.

Piñones, A., Hofmann, E. E., Daly, K. L., Dinniman, M. S., & Klinck, J. M. (2013). Modeling the remote and local connectivity of Antarctic krill populations along the western Antarctic Peninsula. Marine Ecology Progress Series, 481, 69-92.

Plummer, M. (2003, March). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In Proceedings of the 3rd international workshop on distributed statistical computing (Vol. 124, No. 125.10, pp. 1-10).

Polito, M. J., & Goebel, M. E. (2010). Investigating the use of stable isotope analysis of milk to infer seasonal trends in the diets and foraging habitats of female Antarctic fur seals. Journal of experimental marine biology and ecology, 395(1-2), 1-9.

Ponganis, P. J., & Stockard, T. K. (2007). Short Note: The Antarctic toothfish: how common a prey for Weddell seals? Antarctic Science, 19(4), 441-442.

Ponganis, P. (2015). Diving Physiology of Marine Mammals and Seabirds. Cambridge: Cambridge University Press. 333 pp. doi:10.1017/CBO9781139045490

Poppitt, S. D., Speakman, J. R., & Racey, P. A. (1993). The energetics of reproduction in the common shrew (Sorex araneus): a comparison of indirect calorimetry and the doubly labeled water method. Physiological Zoology, 66(6), 964-982.

Polansky, L., Douglas-Hamilton, I., & Wittemyer, G. (2013). Using diel movement behavior to infer foraging strategies related to ecological and social factors in elephants. Movement ecology, 1(1), 13.

Pucci, R., Micheli, A., Chessa, S., & Hunter, J. (2020). Machine learning approaches for identifying prey handling activity in otariid pinnipeds. arXiv preprint arXiv:2002.03866.

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. The quarterly review of biology, 52(2), 137-154.

Rahaman, W., Chatterjee, S., Ejaz, T., & Thamban, M. (2019). Increased influence of ENSO on Antarctic temperature since the Industrial Era. Scientific reports, 9(1), 1-12.

Ramasco, V., Biuw, M., & Nilssen, K. T. (2014). Improving time budget estimates through the behavioural interpretation of dive bouts in harbour seals. Animal Behaviour, 94, 117-134.

Reda, I., & Andreas, A. (2004). Solar position algorithm for solar radiation application. National Renewable Energy Laboratory (NREL) Technical report NREL. TP-560-34302.

Reid, K. & Measures J. (1998). Determining the sex of Antarctic krill Euphausia superba using carapace measurements. *Polar Biology*, *19*(2), 145-147.

Reid, K., & Arnould, J. P. (1996). The diet of Antarctic fur sealsArctocephalus gazella during the breeding season at South Georgia. Polar Biology, 16(2), 105-114.

Reid, K., Croxall, J. P., Briggs, D. R., & Murphy, E. J. (2005). Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. ICES Journal of Marine Science, 62(3), 366-373.

Reiss, C. S., Cossio, A. M., Loeb, V. & Demer, D. A. (2008). Variations in the biomass of Antarctic krill (Euphausia superba) around the South Shetland Islands, 1996-2006. ICES J. Mar. Sci. 65, 497–508.

Richardson, H., & Verbeek, N. A. (1986). Diet selection and optimization by northwestern crows feeding on Japanese littleneck clams. Ecology, 67(5), 1219-1226.

Riginella, E., Mazzoldi, C., Ashford, J., Jones, C., Morgan, C., La Mesa, M. (2016). Life history strategies of the Scotia Sea icefish, *Chaenocephalus aceratus*, along the Southern Scotia Ridge. Polar Biology, 39: 497-509

Rodhouse, P. G., & White, M. G. (1995). Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. The Biological Bulletin, 189(2), 77-80.

Rogowitz, G. L. (1996). Trade-offs in energy allocation during lactation. American Zoologist, 36(2), 197-204.

Rosen, D. A., & Tollit, D. J. (2012). Effects of phylogeny and prey type on fatty acid calibration coefficients in three pinniped species: implications for the QFASA dietary quantification technique. Marine Ecology Progress Series, 467, 263-276.

Rosen, D. A., Hindle, A. G., Gerlinsky, C. D., Goundie, E., Hastie, G. D., Volpov, B. L., & Trites, A. W. (2017). Physiological constraints and energetic costs of diving behaviour in marine mammals: a review of studies using trained Steller sea lions diving in the open ocean. Journal of Comparative Physiology B, 187(1), 29-50.

Rutz, C., & Hays, G. C. (2009). New frontiers in biologging science. doi: 10.1098/rsbl.2009.0089

Sabourenkov, E. N. (1991). Mesopelagic fish of the Southern Ocean—summary results of recent Soviet studies. CCAMLR, Selected Scientific Papers, 1990, 433-457.

Sadleir, R. M. F. S. (1984). Ecological consequences of lactation. Acta Zoologica Fennica[ACTA ZOOL. FENN.]. 1984.

Santa Cruz, F., Ernst, B., Arata, J. A., & Parada, C. (2018). Spatial and temporal dynamics of the Antarctic krill fishery in fishing hotspots in the Bransfield Strait and South Shetland Islands. Fisheries Research, 208, 157-166.

Santora, J. A. (2013). Dynamic intra-seasonal habitat use by Antarctic fur seals suggests migratory hotspots near the Antarctic Peninsula. Marine biology, 160(6), 1383-1393.

Santora, J. A., & Veit, R. R. (2013). Spatio-temporal persistence of top predator hotspots near the Antarctic Peninsula. Marine Ecology Progress Series, 487, 287-304.

Scantlebury, D. M., Mills, M. G., Wilson, R. P., Wilson, J. W., Mills, M. E., Durant, S. M., ... & Speakman, J. R. (2014). Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. Science, 346(6205), 79-81.

SC-CAMLR. 2002. Report of the Working Group on Ecosystem Monitoring and Management. In: Report of the Twenty-first Meeting of the Scientific Committee (SC-CAMLR-XXI), Annex 4. CCAMLR, Hobart, Australia: 121–308.

SC-CAMLR. 2012. Report of the Working Group on Ecosystem Monitoring and Management. In: Report of the Thirty-first Meeting of the Scientific Committee (SC-CAMLR-XXXI), Annex 6. CCAMLR, Hobart, Australia: 169–263.

SG-ASAM. 2019. Report of the Meeting of the Subgroup on Acoustic Survey and Analysis Methods. In: Report of the Thirty-Eight Meeting of the Scientific Committee (SC-CAMLR-XXXVIII), Annex 6. CCAMLR, Hobart, Australia: 253–276

Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., & Fraser, W. R. (2010). How do polar marine ecosystems respond to rapid climate change?. Science, 328(5985), 1520-1523.

Schwartz, M. K., McKelvey, K. S., Cushman, S. A., & Luikart, G. (2010). Landscape genomics: a brief perspective. In Spatial complexity, informatics, and wildlife conservation (pp. 165-174). Springer, Tokyo.

Schwarz, L. K., Goebel, M. E., Costa, D. P., & Kilpatrick, A. M. (2013). Top-down and bottom-up influences on demographic rates of Antarctic fur seals Arctocephalus gazella. Journal of Animal Ecology, 82(4), 903-911.

Sharp, J. A., Cane, K. N., Lefevre, C., Arnould, J. P., & Nicholas, K. R. (2005). Fur seal adaptations to lactation: insights into mammary gland function. Current topics in developmental biology, 72, 275-308.

Shepard, E. L., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., ... & Newman, C. (2008). Identification of animal movement patterns using tri-axial accelerometry. Endangered Species Research, 10, 47-60.

Shero, M. R., Goetz, K. T., Costa, D. P., & Burns, J. M. (2018). Temporal changes in Weddell seal dive behavior over winter: Are females increasing foraging effort to support gestation?. Ecology and Evolution, 8(23), 11857-11874.

Siegel, V., & Piatkowski, U. (1990). Variability in the macrozooplankton community off the Antarctic Peninsula. Polar Biology, 10(5), 373-386.

Siegel, V., & Loeb, V. (1994). Length and age at maturity of Antarctic krill. Antarctic Science, 6(4), 479-482.

Siegel, V., & Loeb, V. (1995). Recruitment of Antarctic krill Euphausia superba and possible causes for its variability. Marine Ecology Progress Series, 123, 45-56.

Siegel, V. (2005). Distribution and population dynamics of Euphausia superba: summary of recent findings. Polar Biology, 29(1), 1-22.

Skinner, J. D., & Klages, N. T. W. (1994). On some aspects of the biology of the Ross seal Ommatophoca rossii from King Haakon VII Sea, Antarctica. Polar biology, 14(7), 467-472.

Siniff, D. B., & Stone, S. (1985). The role of the leopard seal in the tropho-dynamics of the Antarctic marine ecosystem. In Antarctic nutrient cycles and food webs (pp. 555-560). Springer, Berlin, Heidelberg.

Siniff, D. B. (1991). An overview of the ecology of Antarctic seals. American Zoologist, 31(1), 143-149.

Smith, S. J., Iverson, S. J., & Bowen, W. D. (1997). Fatty acid signatures and classification trees: new tools for investigating the foraging ecology of seals. Canadian Journal of Fisheries and Aquatic Sciences, 54(6), 1377-1386.

Stammerjohn, S. E., Martinson, D. G., Smith, R. C., & Iannuzzi, R. A. (2008). Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. Deep Sea Research Part II: Topical Studies in Oceanography, 55(18-19), 2041-2058.

Stammerjohn, S., Massom, R., Rind, D., & Martinson, D. (2012). Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophysical Research Letters, 39(6).

Staniland, I. J. (2002). Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (Arctocephalus gazella) in captive feeding trials. Marine Mammal Science, 18(1), 223-243.

Staniland, I. J., Boyd, I. L., & Reid, K. (2007). An energy–distance trade-off in a central-place forager, the Antarctic fur seal (Arctocephalus gazella). Marine Biology, 152(2), 233-241.

Staniland, I. J., Gales, N., Warren, N. L., Robinson, S. L., Goldsworthy, S. D., & Casper, R. M. (2010). Geographical variation in the behaviour of a central place forager: Antarctic fur seals foraging in contrasting environments. Marine Biology, 157(11), 2383-2396.

Staniland, I. J., Morton, A., Robinson, S. L., Malone, D., & Forcada, J. (2011). Foraging behaviour in two Antarctic fur seal colonies with differing population recoveries. Marine Ecology Progress Series, 434, 183-196.

Southwell, C., Mare, B. D. L., Borchers, D., & Burt, L. (2004). Shipboard line transect surveys of crabeater seal abundance in the pack-ice off East Antarctica: evaluation of assumptions. Marine Mammal Science, 20(3), 602-620.

Southwell, C., Bengtson, J., & Bester, M. (2012). A review of data on abundance, trends in abundance, habitat use and diet of ice-breeding seals in the Southern Ocean. CCAMLR Science, 19, 49-74.

Stephens D.W. & J.R. Krebs (1986) Average-rate maximizing again: changed constraints. En: Foraging theory (eds DW Stephens, JR Krebs). Princeton, NJ: Princeton University Press. Pag. 38-74.

Stock, B. C., Semmens, B. X., & MixSIAR, G. U. I. (2016a). User Manual. Version 3, 1.

Stock, B. C., & Semmens, B. X. (2016b). Unifying error structures in commonly used biotracer mixing models. Ecology, 97(10), 2562-2569.

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ, 6, e5096.

Stowasser, G., McAllen, R., Pierce, G. J., Collins, M. A., Moffat, C. F., Priede, I. G., & Pond, D. W. (2009). Trophic position of deep-sea fish—assessment through fatty acid and stable isotope analyses. Deep Sea Research Part I: Oceanographic Research Papers, 56(5), 812-826.

Stuecker, M. F., Bitz, C. M., & Armour, K. C. (2017). Conditions leading to the unprecedented low Antarctic sea ice extent during the 2016 austral spring season. Geophysical Research Letters, 44(17), 9008-9019.

Sundblad, G., Bergström, U., & Sandström, A. (2011). Ecological coherence of marine protected area networks: a spatial assessment using species distribution models. Journal of Applied Ecology, 48(1), 112-120.

Sur, M., Suffredini, T., Wessells, S. M., Bloom, P. H., Lanzone, M., Blackshire, S., ... & Katzner, T. (2017). Improved supervised classification of accelerometry data to distinguish behaviors of soaring birds. PloS one, 12(4), e0174785.

Suzuki, I., Naito, Y., Folkow, L. P., Miyazaki, N., & Blix, A. S. (2009). Validation of a device for accurate timing of feeding events in marine animals. Polar Biology, 32(4), 667-671.

 Tarroux, A., Lowther, A. D., Lydersen, C., & Kovacs, K. M. (2016). Temporal shift in the isotopic niche of female Antarctic fur seals from Bouvetøya. Polar Research, 35(1), 31335.

Team, R. C. (2013). R: A language and environment for statistical computing.

Team, R. C. (2017). R Core Team (2017). R: A language and environment for statistical computing. R Found. Stat. Comput. Vienna, Austria

Testa, J. W. (1994). Over-winter movements and diving behavior of female Weddell seals (Leptonychotes weddellii) in the southwestern Ross Sea, Antarctica. Canadian Journal of Zoology, 72(10), 1700-1710.

Thomas, J. A., & Rogers, T. (2009). Ross Seal: Ommatophoca rossii. In Encyclopedia of marine mammals (pp. 988-990). Academic Press.Turchin, P. (1998). Quantitative Analysis of Movement. Sunderland, MA: Sinauer Associates.

Thometz, N. M., Staedler, M. M., Tomoleoni, J. A., Bodkin, J. L., Bentall, G. B., & Tinker, M. T. (2016). Trade-offs between energy maximization and parental care in a central place forager, the sea otter. Behavioral Ecology, 27(5), 1552-1566.

Tin, T., Fleming, Z. L., Hughes, K. A., Ainley, D. G., Convey, P., Moreno, C. A., ... & Snape, I. (2009). Impacts of local human activities on the Antarctic environment. Antarctic Science, 21(1), 3-33.

Tollit, D. J., Wong, M., Winship, A. J., Rosen, D. A., & Trites, A. W. (2003). Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller's sea lion (Eumetopias jubatus). Marine Mammal Science, 19(4), 724-744.

Trathan, P. N., Forcada, J., & Murphy, E. J. (2007). Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1488), 2351-2365.

Trathan, P. N., Warwick-Evans, V., Hinke, J. T., Young, E. F., Murphy, E. J., Carneiro, A. P. B., ... & Kokubun, N. (2018). Managing fishery development in sensitive ecosystems: identifying penguin habitat use to direct management in Antarctica. Ecosphere, 9(8), e02392.

Tremblay, Y., Robinson, P. W., & Costa, D. P. (2009). A parsimonious approach to modeling animal movement data. *PLoS One*, *4*(3), e4711

Trillmich, F., Ono, K. A., Costa, D. P., DeLong, R. L., Feldkamp, S. D., Francis, J. M., ... & York, A. E. (1991). The effects of El Nino on pinniped populations in the eastern Pacific. In *Pinnipeds and El Niño* (pp. 247-270). Springer, Berlin, Heidelberg, p 247-270.

Trillmich, F. (1996). Parental investment in pinnipeds. In ''Parental Care: Evolution, Mechanisms, and Adaptive Significance. Advances in the Study of Behaviour'' (J. S. Rosenblatt and C. T. Snowdon, Eds.), Academic Press, San Diego, CA. Vol. 25, pp. 533–577.

Trillmich, F., & Weissing, F. J. (2006). Lactation patterns of pinnipeds are not explained by optimization of maternal energy delivery rates. Behavioral Ecology and Sociobiology, 60(2), 137-149.

Trites, A. W., & Joy, R. (2005). Dietary analysis from fecal samples: how many scats are enough?. Journal of Mammalogy, 86(4), 704-712.

Tsalyuk, M., Kilian, W., Reineking, B., & Getz, W. M. (2019). Temporal variation in resource selection of African elephants follows long-term variability in resource availability. Ecological Monographs, 89(2), e01348.

Tucker, S., Bowen, W. D., Iverson, S. J., Blanchard, W., & Stenson, G. B. (2009). Sources of variation in diets of harp and hooded seals estimated from quantitative fatty acid signature analysis (QFASA). Marine Ecology Progress Series, 384, 287-302.

Turchin, P. (1998). Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants (Vol. 1). Sunderland: Sinauer associates.

Turner, J. (2004). The el nino–southern oscillation and antarctica. International Journal of Climatology: A Journal of the Royal Meteorological Society, 24(1), 1-31.

Turner, J., Phillips, T., Marshall, G. J., Hosking, J. S., Pope, J. O., Bracegirdle, T. J., & Deb, P. (2017). Unprecedented springtime retreat of sea ice in 2016. Geophysical Research Letters, 44(13), 6868-6875.

Vales, D. G., Cardona, L., García, N. A., Zenteno, L., & Crespo, E. A. (2015). Ontogenetic dietary changes in male South American fur seals Arctocephalus australis in Patagonia. Marine Ecology Progress Series, 525, 245-260.

Vargas, R., Osman, L. P., & Torres, D. (2009). Inter-sexual differences in Antarctic fur seal pup growth rates: evidence of environmental regulation?. Polar Biology, 32(8), 1177-1186.

Veloso, C., & Bozinovic, F. (2000). Effect of food quality on the energetics of reproduction in a precocial rodent, Octodon degus. Journal of Mammalogy, 81(4), 971-978.

Vianna, J. A., Fernandes, F. A., Frugone, M. J., Figueiró, H. V., Pertierra, L. R., Noll, D., ... & Le Bohec, C. (2020). Genome-wide analyses reveal drivers of penguin diversification. Proceedings of the National Academy of Sciences, 117(36), 22303-22310.

Villegas-Amtmann, S., Simmons, S. E., Kuhn, C. E., Huckstadt, L. A., & Costa, D. P. (2011). Latitudinal range influences the seasonal variation in the foraging behavior of marine top predators. PLoS One, 6(8), e23166.

Viviant, M., Trites, A. W., Rosen, D. A., Monestiez, P., & Guinet, C. (2010). Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. Polar biology, 33(5), 713-719.

Viviant, M., Monestiez, P., & Guinet, C. (2014). Can we predict foraging success in a marine predator from dive patterns only? Validation with prey capture attempt data. PLoS One, 9(3), e88503.

Viviant, M., Jeanniard-du-Dot, T., Monestiez, P., Authier, M., & Guinet, C. (2016). Bottom time does not always predict prey encounter rate in Antarctic fur seals. Functional Ecology, 30(11), 1834-1844.

Volpov, B. L., Hoskins, A. J., Battaile, B. C., Viviant, M., Wheatley, K. E., Marshall, G., ... & Arnould, J. P. (2015). Identification of prey captures in Australian fur seals (Arctocephalus pusillus doriferus) using head-mounted accelerometers: field validation with animal-borne video cameras. PLoS One, 10(6), e0128789.

Volpov, B. L., Rosen, D. A., Hoskins, A. J., Lourie, H. J., Dorville, N., Baylis, A. M., ... & Hindell, M. A. (2016). Dive characteristics can predict foraging success in Australian fur seals (Arctocephalus pusillus doriferus) as validated by animal-borne video. Biology open, 5(3), 262-271.

Watanabe, Y., Mitani, Y., Sato, K., Cameron, M. F., & Naito, Y. (2003). Dive depths of Weddell seals in relation to vertical prey distribution as estimated by image data. Marine Ecology Progress Series, 252, 283-288.

Watt, W. B., & Dean, A. M. (2000). Molecular-functional studies of adaptive genetic variation in prokaryotes and eukaryotes. Annual review of genetics, 34(1), 593-622.

Waters, K. J., & Smith, R. C. (1992). Palmer LTER: A sampling grid for the Palmer LTER program. Antarctic Journal of the United States, 27(5), 236-239.

Watters, G. M., Hill, S. L., Hinke, J. T., Matthews, J., & Reid, K. (2013). Decision-making for ecosystem-based management: evaluating options for a krill fishery with an ecosystem dynamics model. Ecological Applications, 23(4), 710-725.

Watters, G. M., Hinke, J. T., & Reiss, C. S. (2020). Long-term observations from Antarctica demonstrate that mismatched scales of fisheries management and predator-prey interaction lead to erroneous conclusions about precaution. Scientific reports, 10(1), 1-9.

Watts, D. P. (1988). Environmental influences on mountain gorilla time budgets. American Journal of Primatology, 15(3), 195-211.

Werner, E. E., & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology, 69(5), 1352-1366.

Werth, A. J. (2000). Feeding in marine mammals. Feeding: form, function and evolution in tetrapod vertebrates, 475-514.

White, E. R. (2019). Minimum time required to detect population trends: the need for long-term monitoring programs. BioScience, 69(1), 40-46.

Whitehouse, M. J., Meredith, M. P., Rothery, P., Atkinson, A., Ward, P., & Korb, R. E. (2008). Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century:

forcings, characteristics and implications for lower trophic levels. Deep Sea Research Part I: Oceanographic Research Papers, 55(10), 1218-1228.

Williams, T. M., Estes, J. A., Doak, D. F., & Springer, A. M. (2004). Killer appetites: assessing the role of predators in ecological communities. Ecology, 85(12), 3373-3384.

Williams, T. M., Rutishauser, M., Long, B., Fink, T., Gafney, J., Mostman-Liwanag, H., & Casper, D. (2007). Seasonal variability in otariid energetics: implications for the effects of predators on localized prey resources. Physiological and Biochemical Zoology, 80(4), 433-443.

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology, 96(7), 1741-1753.

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. Journal of Animal Ecology, 77(6), 1082-1091.

Zhu, W., Mu, Y., Liu, J., & Wang, Z. (2015). Energy requirements during lactation in female Apodemus chevrieri (Mammalia: Rodentia: Muridae) in the Hengduan Mountain region. Italian Journal of Zoology, 82(2), 165-171.

Zuur A, Ieno EN, Smith GM (2007). Analyzing ecological data. Springer Science & Business Media

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R. Springer Science & Business Media