

Photogrammetric estimation of mass fluctuation in female southern elephant seals at Marion Island

by

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Submitted in partial fulfilment of the requirements

for the degree of

M.Sc. (Zoology)

In the

Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

South Africa

September 2012

Declaration:

I,.....**Martin Postma**..... declare that the Thesis/dissertation, which I hereby submit for the degree.....**MSc Zoology**.....at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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...their timid herds are to be found in large numbers only on these distant islands, on lonely rocks, and in the midst of the eternal ice where savage beast do not exist, where man, even more formidable, has not made his permanent home.

(Francois Auguste Péron (1775 – 1810) French naturalist an explorer)

SUMMARY

PHOTOGRAMMETRIC ESTIMATION OF MASS FLUCTUATION IN FEMALE SOUTHERN ELEPHANT SEALS AT MARION ISLAND

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The broad objective of the study is to examine mass change as related to other life history parameters of southern elephant seals *Mirounga leonina* at Marion Island. It has been argued that mass plays a fundamental role in their annual life cycle. This study investigates the reproductive investment and strategies of female southern elephant seals over a temporal scale using innovative sampling methods.

Long term population studies are of great interest to life history studies as they provide a unique insight to advance our holistic knowledge of population demography. Marion Islands' intensive 28-year elephant seal mark recapture program provides such a foundation for demographic analysis to further our knowledge of a top predator in a changing environment. Together with advances in the field of photogrammetric measuring methods that allow mass estimation of large marine mammals, the opportunities arise to study southern elephant seal mass fluctuations over a temporal scale. Analysis between populations provided validation of the comparability of the method to physically weighed animals, over a temporal scale. Furthermore, differences between populations could be assessed, which are most likely a result of demographic and/or anthropogenic disturbances.

Previous field advances in identifying mother pup relation, and the ongoing execution thereof presented the prospect of identifying driving factors in age specific fecundity. Together with an accurate mass measuring method that can be applied over a temporal scale, advances were made in understanding specific age related parameters in pup survival. Findings suggest that older females are more successful and their reproductive success is essential for population growth.

Annually interrupted breeding is more common than previously thought in female southern elephant seals at Marion Island. Assessment here, of body mass between females that exhibit different breeding strategies, strengthens this argument. Mass gain for annually breeding females' is shown to be marginally sufficient to sustain them for their obligatory fast. These females are surviving on the edge in terms of body mass requirements. Females with interrupted breeding schedules have greater mass at critical stages in their annual life cycle, which could be beneficial to future reproduction and survival. Perturbations in energy budget may be a factor resulting in different breeding strategies.

Key words: Southern elephant seals, *Mirounga leonina*, Marion Island, Photogrammetry, Methodology advancement, life history theory, mass change, pup survival, age specific reproduction, breeding season, pelagic foraging, and moult.

ACKNOWLEDGEMENTS

We thank the South African Department of Environmental Affairs for providing logistical support within the South African National Antarctic Programme and the Department of Science and Technology (administered through the National Research Foundation) for funding the marine mammal monitoring programme at Marion Island and provide financial bursary within the project. Various Marion Island overwintering team members; Chris Oosthuizen, Mashudu Phalanndwa, Ryan Reisinger, Thomas Mufanadza, Mia Wege, Derek van der Merwe, Jean Purdon de Lange and Tristan Scott. Thanks for Marie Navoux and Trevor McIntyre for their help in statistical guidance. I thank my parents for all their loving support in non academic matters, without their belief in me this would not have been possible. To Karien Van Wyk for the support and assistance throughout this endeavour, many thanks. My friends, more numerous than can be named, for all their encouragement and enthusiasm throughout this venture. Thanks to my supervisors Nico de Bruyn and Marthán Bester for all their guidance and support, and creating opportunities to learn, explore, travel and discover. It is only by the grace of God that we may experience and discover the wonders of the natural world.

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MANUSCRIPTS SUBMITTED FOR PUBLICATION

(Emanating from this dissertation)

Postma, M., Bester, M.N., de Bruyn, P.J.N. (Submitted). Photogrammetry; an accurate non-invasive method to gauge seasonal mass changes in female southern elephant seals (*Mirounga leonina*). *Antarctic Science*

Postma, M., Bester, M.N., de Bruyn, P.J.N. (Submitted). Age-specific maternal mass transfer and pup survival in southern elephant seals at Marion Island. *Journal of Zoology London*

Postma, M., Bester, M.N., de Bruyn, P.J.N. (Submitted). Body mass disparity as a result of different breeding strategies in female southern elephant seals. *Biology letters*

Disclaimer

Each of the research chapters within this thesis was structured with scientific journal publication in mind. Chapters are therefore concise and presented so that they can stand alone. I apologise for the overlap and repetition in Method section.

CHAPTER ONE

GENERAL INTRODUCTION

Introduction

The study of population dynamics and life history has become increasingly important in the field of ecology, and a major objective is to study and analyze individual animals of a population over space and time (Lebreton *et al.* 1992). The most important strategy in the life of mammals is to produce offspring and thereby propagate the species (Weir & Rowland 1973). Females of mammal species bear the cost of reproduction through maternal care of the offspring (Cripps *et al.* 2011). Life history theory predicts a trade off between mass and reproduction when resources are limited; it is also concerned with how resources are allocated to reproduction by an animal to maximize fitness (Roff 1992; Stearns 1992; Roff 2002). Energy storage is an important component in variation of life history (Houston *et al.* 2007). Methods that simplify detection of life history traits over a temporal scale are of great importance to scientists.

Chemical immobilisation of pinnipeds is challenging due to their extreme size, fierce attitude and fast reaction, this makes direct measurements of body mass problematic and potentially dangerous for the researcher and additionally heavy equipment might be required (Boyd *et al.* 1993). A simpler non-invasive method is needed. Photogrammetry is the science of making measurements on photographs (Baker 1960). It is a well-established tool that is widely used in engineering, geography, agriculture, medicine, mapping and more recently in zoology by means of mass estimations in marine mammals (Bell *et al.* 1997; Ireland *et al.* 2006; de Bruyn *et al.* 2009). These techniques can greatly assist longitudinal studies (de Bruyn *et al.* 2008) that would traditionally have required re-weighing of marked animals (Fedak *et al.* 1987).

In the modern day and age where technology is advancing daily, it is the scientist's priority to find accurate, least intrusive methods to assess important biological issues over a temporal scale. Similarly, scientists should investigate and test these methods for accuracy and applicability.

Factors that influence population growth and that address the reasons for variations of growth rates are of major interest in population ecology for both practical and theoretical reasons (Gaillard *et al.* 1998). Mass appears to be the most important state variable in capital breeders (such as southern elephant seals), that influences reproduction (Laws 1956a, b; Boyd *et al.* 1995; Festa-Bianchet *et al.* 1998; Pomeroy *et al.* 1999). The estimation of reproductive effort is easy in capital breeders such as southern elephant seals where feeding is absent during the breeding season (Galimberti *et al.* 2007). Similarly, moulting females are subjected to fast during their annual obligatory moult (Arnbom *et al.* 1997). Given that many marine mammals display seasonal energetic priorities (Rosen & Renouf 2008), it is important to investigate these needs. The knowledge of energy and food requirements of southern elephant seals is of great importance for assessing the potential impact that a change in food abundance could have on population size and species distribution (Carlini *et al.* 2005).

Photogrammetric mass estimations have yet to be tested on a daily basis in an unpredictable environment over time. The Marion Island southern elephant seal mark-recapture programme provides unique, uninterrupted life history data for all individuals, and is the ideal candidate to apply an accurate photogrammetric measuring method (de Bruyn *et al.* 2009) over a temporal scale. Furthermore, southern elephant seals' predictable haulout periods and lack of fear for humans makes them superlative subjects (Le Boeuf & Laws 1994). These factors combined,

provides the opportunity to explore the influence of mass fluctuation over time at critical stages in a southern elephant seal's life cycle.

Southern Elephant Seal Biology

Southern elephant seals (*Mirounga leonina*) are the largest extant seal species and one of the most sexually dimorphic marine mammals (Le Boeuf & Laws 1994) with females weighing anything between 350kg and 800kg and the largest males weighing up to 4000kg. Southern elephant seals haul out on land to breed, moult and overwinter (Condy 1979; Kirkman *et al.* 2003; Kirkman *et al.* 2004), but spend approximately 85% of their lifetimes feeding in the pelagic environment (McIntyre *et al.* 2010). Terrestrial phases are subjected to fasting, where they rely on blubber reserves for survival (Laws 1956a, b; Costa 1991; Oftedal *et al.* 1993). During the breeding season in the austral spring, adult females haul out for approximately 30 days; 21-23 spent suckling their pups (Bell *et al.* 2005). They fast throughout this period, relying exclusively on stored fat reserves for lactation (Arnbom *et al.* 1997). Non-breeders are largely absent from the breeding colonies and the whole population is never ashore at once (Laws 1981). It was previously assumed that female southern elephant seals return every year, uninterruptedly to their natal site to breed (pup and mate) (e.g. Laws 1956; Hindell 1991; Wilkinson 1991; Le Boeuf & Laws 1994; Pistorius *et al.* 2001, 2004, 2008; McMahon *et al.* 2003, McMahon *et al.* 2005, 2009; de Bruyn 2009). Using a 25-year mark-recapture data set at Marion Island, de Bruyn *et al.* (2011) showed that interrupted breeding is more common than previously thought in southern elephant seal females.

After breeding, females make a post-lactation trip to sea, lasting a mean of 72.6 ± 5.0 days to regain their mass before returning to shore for the annual obligatory moult (Boyd *et al.* 1993; Le Boeuf & Laws 1994). The moult of monacine seals (elephant seals (*Mirounga sp.*) and monk seals, (*Monachus schauinslandi*) is a

unique phase amongst pinnipeds as it involves shedding and replacing the hair and top layer of epidermis (Ling 1970). Female southern elephant seals moult for approximately 30 days and males for 50 days, after which they depart for post-moult foraging before returning in the next austral spring (Laws 1960).

Elephant seal females are long-lived mammals that invest large amounts of resources in a single offspring produced in any year. Females need to locate food reliably each year for many years in succession (Le Boeuf & Laws 1994). Variations in environmental conditions and foraging success between individuals result in some animals gaining more weight than others while foraging at sea. Energy stores, as well as body size and age of both males and females, are expected to be important to reproductive success (Le Boeuf & Laws 1994) and future survival (McMahon *et al.* 1999).

Southern Elephant Seal Distribution

Southern elephant seals have a circumpolar distribution in the Southern Ocean (Fig. 1.1), rookeries and haulouts (beaches where seals come ashore) are remote sub-Antarctic islands and at Peninsula Valdés, Argentina, the only continental population (McMahon *et al.* 2005). Preferred haulout sites are gradually sloping beaches that are easily accessible (Le Boeuf & Laws 1994). Their pelagic distribution is essentially to the north of the pack ice zone (Laws 1981) although shelf break areas within the pack ice have recently been shown to be important foraging areas (Jonker & Bester 1998; Bornemann *et al.* 2000; Biuw *et al.* 2007; Tosh *et al.* 2009; de Buyn *et al.* 2011).

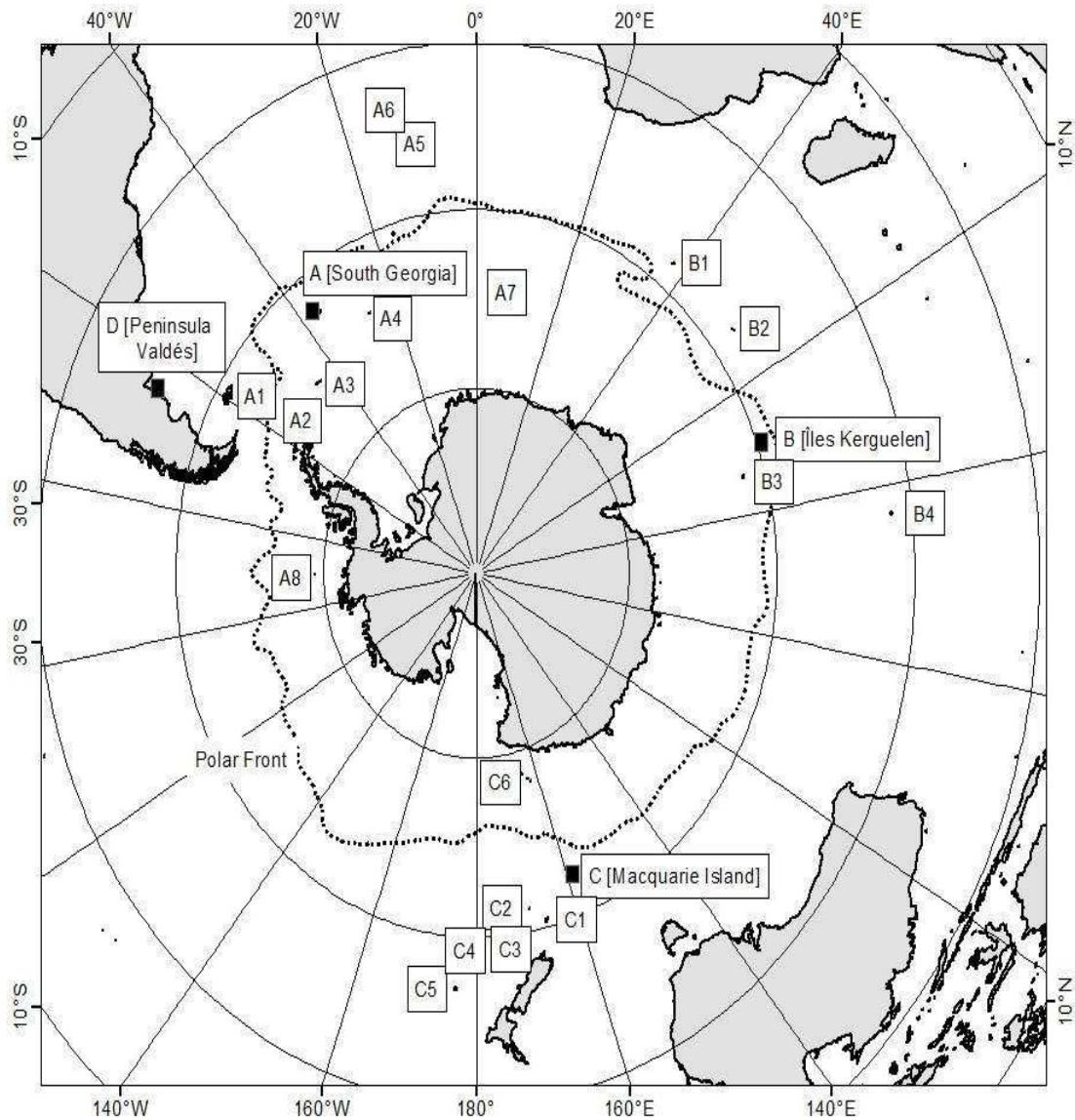


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Present World Population Status

The Southern elephant seal population can be grouped into four genetically distinct stocks (1) Peninsula Valdés stock in Argentina, (2) South Georgia stock in the south Atlantic Ocean, (3) Kerguelen stock in the south Indian Ocean and lastly (4) Macquarie stock in the south Pacific Ocean (Slade *et al.* 1998; Hoelzel *et al.* 2001). Since the 1950s to 1990s, the southern elephant seal population size drastically decreased (some populations as much as 80%) throughout most of their breeding range in the Southern Ocean (McMahon *et al.* 2005). Estimations suggest that some populations have increased (Peninsula Valdés, Argentina) where others have stabilized (South Georgia, Kerguelen Island and Heard Island) (McMahon *et al.* 2005).

Marion Island and Prince Edward Island fall into the Kerguelen population together with Îles Kerguelen, Heard Island and Iles Crozet Islands. After a rapid decline in population size since the 1950s, some of these subpopulations appear to have recently stabilised (Guinet *et al.* 1999; Slip & Burton 1999; Pistorius *et al.* 2001) and show signs of increasing (McMahon *et al.* 2009; Authier *et al.* 2011; Pistorius *et al.* 2011).

Prince Edward Islands and Marine Surrounds

The Prince Edward Islands archipelago of the sub-Antarctic Indian Ocean are among the most isolated shallow terrestrial marine environments around the globe (Branch *et al.* 1993). The Islands are approximately 2,180km southeast of Cape Town and are governed under South African jurisdiction. They are relatively young, their volcanic origin being approximately 2.76×10^5 years before present (McDougall 1971). The volcano on which the two islands rest elevates about 1000km² off the ocean floor to within 200m of the ocean surface (Branch *et al.* 1933). Marion Island (46°54'S, 37°45'E), is the larger of the two islands and lies southwest of the smaller

Prince Edward Island and encompasses an area of 300 km² with a coastline of approximately 100km (Meiklejohn & Smith 2008). The coastline consists mainly of cliffs on the western side of the island with small infrequent pebble beaches on the eastern side of the island where elephant seals predominantly haul out (Condy 1978) (Fig. 1.2).

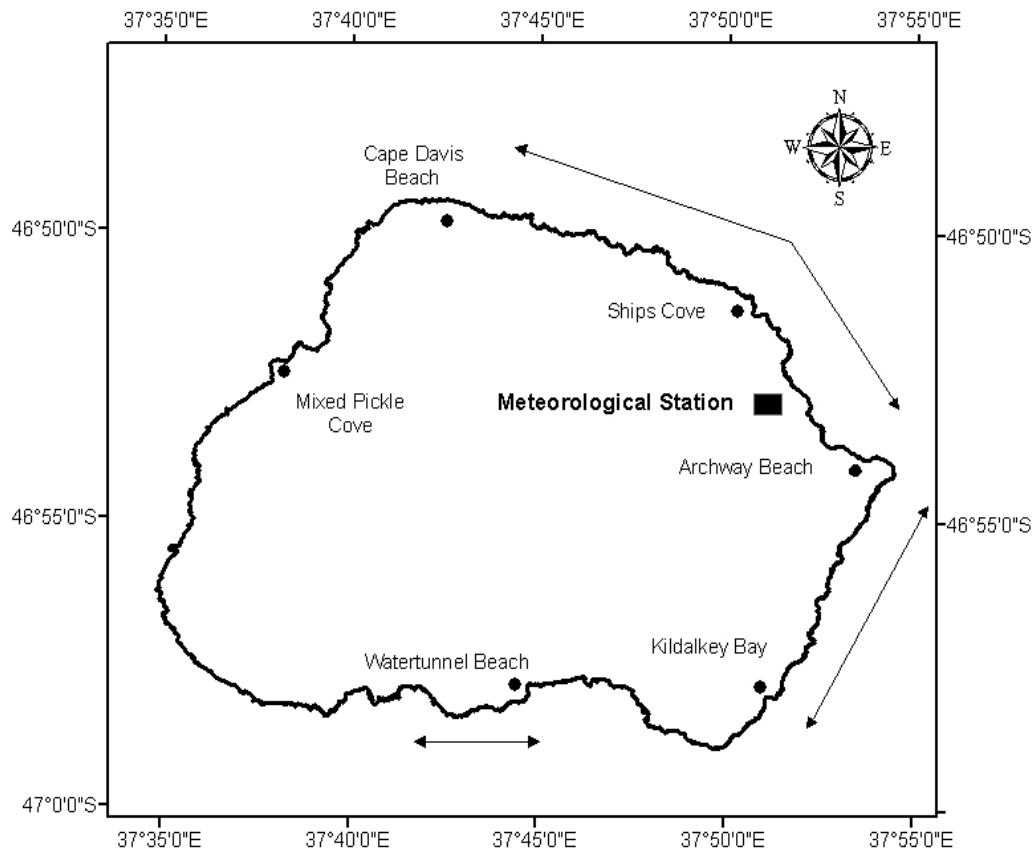


Figure 1.2. Sub-Antarctic Marion Island (46°54'S, 37°45'E). Ar rows indicate areas where southern elephant seals predominantly haul out.

Oceanographically, Marion Island is situated directly in the path of the easterly-flowing Antarctic Circumpolar Current (ACC), between the Sub-Antarctic Front (SAF) and Antarctic Polar Front (APF) (Pakhomov & Froneman 1999) (Fig. 1.3). To the north of the island lies the Sub-Tropical Convergence (STC); it is one of the principal frontal systems in the world oceans and forms a unique biological

habitat (Froneman *et al.* 2007). The circulation in the Southern Ocean is dominated by the ACC. Due to their position; the islands act as obstacles against the current, resulting in extreme mesoscale variability of cold-core eddies in the area (Bryden 1983; Ansorge *et al.* 1999; Pakhomov & Froneman 1999). The oceanographic regime around the island is extremely complex and primary production varies (Pakhomov *et al.* 1999; Froneman *et al.* 2007).

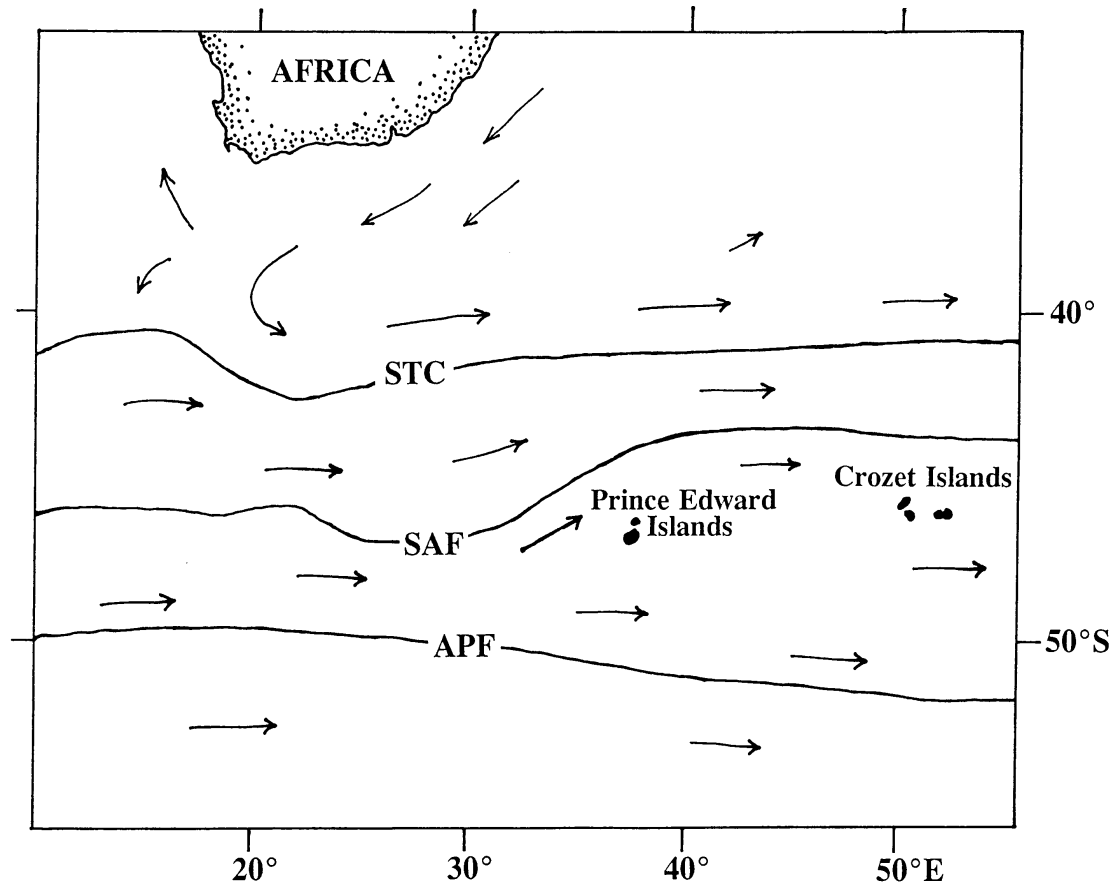


Figure 1.3. The position of Prince Edward Islands in relation to South Africa and the Crozet Islands. Major frontal systems including the Sub-Tropical Convergence (STC), Sub-Antarctic Front (SAF) and Antarctic Polar Front (APF) are shown (taken from Pakhomov & Froneman 1999).

Marion Island is surrounded by kelp beds; they are prominent components of shallow sub-tidal environments at temperate, boreal latitudes (Pakhomov *et al.* 2002). Kelp beds slows surface currents and retain near shore water (e.g. Jackson

1985; Eckman & Duggins 1989; Johnson & Koehl 1994) and are thought to dampen waves to provide a refuge for a variety of marine organisms, that would otherwise be lost from the island ecosystem. Two species of kelp can be found around Marion Island (1) *Durvillaea antarctica* dominates in the infralittoral fringe and (2) *Macrocystis laevis*, the endemic kelp, predominates in deeper water at 5-30m (Attwood *et al.* 1991; Beckley & Branch 1992). These kelp beds provide ample opportunity for killer whales (*Orcinus orca*) to ambush seals. Killer whales are apex predators and have been documented preying on a variety of taxa including cephalopods, bony and cartilaginous fish, reptiles, birds and mammals (Hoyt 1990, Jefferson *et al.* 1991). Elephant seal pups are likely to be the most sensitive to killer whale predation, because of their high energy content and small population size (Reisinger *et al.* 2011). Killer whales could have a significant impact on elephant seal pups, presuming that they feed exclusively on them during the period that they are abundant (Reisinger *et al.* 2011).

Objectives, Key questions and Dissertation Structure

The specific objectives of this research are:

1. To use the photogrammetric method developed by de Bruyn *et al.* (2009) to detect mass fluctuations over a temporal scale in an ever-changing environment?
2. To develop a simple analytical method to obtain accurate mass measurement at specific stages in the life cycle of female southern elephant seal from photogrammetry data.
3. To explore mass loss and gain of different aged female southern elephant seals over the course of an annual life cycle.
4. Investigate the implications of mass loss and gain over an annual cycle for differing life history strategies of female southern elephant seals.

Chapter 2 explains and tests the method that will be used in the subsequent chapters. Results obtained by photogrammetry are compared to results from other population obtained by physically weighing. This will validate the accuracy and effectiveness of the photogrammetry method over a temporal scale. Data were used to illustrate the individual fluctuation of mass over time. Key questions addressed were:

- a) What is the applicability of photogrammetry in detecting individual mass fluctuation over a temporal scale?
- b) To what extent do mass fluctuations of adult females from Marion Island differ from other southern elephant seal populations through the course of an annual cycle?
- c) What implication does disparity in adult female mass between populations?

In **Chapter 3** I investigate the relationship between female age and their offspring survival during their first foraging trip. This is made possible as the exact age and life history of all animals born on Marion Island for the last 28 years are known owing to an intensive mark-recapture programme (Bester 1988; Bester & Wilkinson 1994; de Bruyn *et al.* 2008). This, with the use of photogrammetry, furthermore enables assessment of the age-to-weight ratio as a factor of successful breeding in consecutive years. Key questions addressed were:

- a) How does the age of a mother and maternal expenditure influence weaning mass of her pup?
- b) How does female age and maternal expenditure relate to survival of elephant seal pups during their first foraging trip?

In **Chapter 4** I used data from the 2009/2010 season to investigate the energy requirements of female southern elephant seals in the form of percentage mass loss

and gain during the course of their annual cycle. Recently it was discovered that annually interrupted breeding schedules are more common amongst adult females than previously thought (de Bruyn *et al.* 2011). The 2008, 2009 and 2010 moult photogrammetry database was used to investigate if there was a difference between the weights of females who skipped a breeding season and those who did not. Key questions addressed are:

- a) Do females regain the body mass lost during the terrestrial breeding fast, in the subsequent post-breeding foraging phase?
- b) Is the body mass of a post-partum female at completion of the breeding fast comparable to that at the end of the subsequent terrestrial moult fast?
- c) Do females that breed annually differ in mass at the subsequent terrestrial haulout compared to females that were absent during the breeding season?
- d) Are there consistently different life history breeding strategies in female southern elephant seals?

Finally, **Chapter 5** summarises findings and identifies relevant future avenues of potential research.

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CHAPTER TWO

PHOTOGRAMMETRY; AN ACCURATE NON-INVASIVE METHOD TO GAUGE SEASONAL MASS CHANGES IN FEMALE SOUTHERN ELEPHANT SEALS

Abstract

Photogrammetry has been employed to estimate body mass in large mammals, a recent method (de Bruyn *et al.* 2009 *Aquat Biol* 5:31-39) showing high accuracy in mass estimation of randomly selected individuals of southern elephant seals. As the method has not been applied sequentially for known individuals to estimate mass change, female southern elephant seals ($n=23$) at Marion Island were sampled sequentially with the use of photogrammetry (PG) at various stages of their annual life cycle. For each individual photogrammetry was done (1) pre-partum, (2) post-partum and (3) post-lactation. In the austral summer, photogrammetric projects were done during the moult, following the post-breeding foraging trip: (1) pre-moult (or when animals were first sighted) and (2) post-moult, prior to the seals departing for their post-moult pelagic phase. Three-dimensional models (based on each of the PG projects) were built using the de Bruyn *et al.* (2009) method for estimation of body mass. Data from Marion Island was then compared to data from King George, South Georgia and Macquarie islands to compare mass change amongst the different populations. Females from Marion Island are on average ± 200 kg lighter at the beginning of lactation than their counterparts at King George Island and ± 60 kg lighter than on South Georgia Island, with percentage mass loss constant across populations. Females from Marion Island are smaller; lose less absolute mass during the course of the breeding season, but their percentage lactation mass loss is similar to other populations. MI females forage for longer periods and comparatively gain the same absolute amount of mass, their smaller size necessitating them to regain a

greater relative mass than their counterparts, to sustain them for the extended moult period.

Introduction

The study of population dynamics and life history has long remained important in the field of ecology, with the major objective of studying and analysing individual animals of a population over space and time (Lebreton *et al.* 1992). Methods that simplify detection of life history traits over a temporal scale are of great value to scientists.

Chemical immobilisation of pinnipeds is challenging due to their extreme size, fierce attitude and fast reaction, this makes direct measurements of body mass problematic and potentially dangerous for the researcher and additionally heavy equipment might be required (Boyd *et al.* 1993). A simpler non-invasive method emerged through the use of photogrammetry. Photogrammetry is the science of making measurements from photographs (Baker 1960). It is a well-established tool that is widely used in engineering, geography, agriculture, medicine, mapping and more recently in zoology. One zoological application that enjoyed much attention was the development of methods to estimate mass of marine mammals (e.g. Bell *et al.* 1997; Ireland *et al.* 2006; de Bruyn *et al.* 2009). The de Bruyn *et al.* (2009) technique can greatly assist longitudinal studies (de Bruyn *et al.* 2008) that would traditionally have required reweighing of marked animals (e.g. Fedak *et al.* 1987). Southern elephant seals (*Mirounga leonina*) have predictable haulout periods, high site fidelity and their naivety towards humans makes them excellent subjects for population demography studies.

Southern elephant seals are the largest extant seal species and one of the most sexually dimorphic marine mammals (Le Boeuf & Laws 1994). They have a

circumpolar Southern Ocean distribution, with breeding sites located on sub-Antarctic islands and at continental Peninsula Valdés, Argentina (McMahon *et al.* 2005). Southern elephant seals haul out on land to breed, moult and overwinter (Condy 1979; Kirkman *et al.* 2003, 2004), but spend approximately 85% of their lifetimes feeding in the pelagic environment (McIntyre *et al.* 2010). Breeding and moulting periods are spatially separated from each other and necessitate fasting, when seals rely on blubber reserves for survival (Laws 1956; Costa 1991; Oftedal 1993).

During the breeding season in the austral spring, adult females haul out for approximately 30 days where the last 21-23 days are spent suckling their pups (Bell *et al.* 2005). They fast throughout this period, relying exclusively on stored fat reserves for lactation (Arnbom *et al.* 1997). After breeding, females make a post-lactation trip to sea, lasting a mean of 72.6 ± 5.0 days to regain their mass before returning to shore for the annual obligatory moult (Boyd *et al.* 1993; Le Boeuf 1994). The moult of monacine seals (elephant seals and monk seals) is a unique phase amongst pinnipeds as it involves shedding and replacing the hair and top layer of epidermis (Ling 1970). Female southern elephant seals moult for approximately 30 days and males for 50 days, after which they depart for post moult foraging before returning for the next austral spring (Laws 1960).

Studies of mass loss and gain in female southern elephant seals over the course of an annual cycle have received little attention as a consequence of the logistic limitations associated with weighing these animals. Studies conducted at King George Island (Carlini *et al.* 1997, 1999), South Georgia Island (Boyd *et al.* 1993) and Macquarie Island (Hindell *et al.* 1994), relied on physically weighing and interacting with animals. Sample size was thus limited due to the physical effort required for data capture. Photogrammetry can be an easy non-invasive measuring method to gain larger sample sizes over theoretically unlimited temporal scales. For

populations with concomitant long-term mark-recapture programmes, the value in assessment of individual mass change over time using photogrammetry becomes apparent.

Marion Islands' southern elephant seals have been subject to population demographic studies of known individuals for three decades (Pistorius *et al.* 2011). Despite this intensive research effort, a parameter as simple as individual mass change over an annual cycle was not possible due to circumstance and without an appropriate photogrammetric method. Here I present changes in arrival and departure mass for both breeding and moult haulouts of southern elephant seal females at Marion Island using the photogrammetric method of de Bruyn *et al.* (2009). The applicability of the method in detecting mass fluctuation over time are researched, the results compared with mass fluctuation data of other southern elephant seal populations and the implications for life history strategies of the female component discussed.

Methods

Study site

Marion Island (46°54'S, 37°45'E), one of the two islands in the Prince Edward Islands archipelago is situated in the Southern Indian Ocean. It is approximately 2,180 km southeast of Cape Town, South Africa, and has an area of 300 km² with a coastline of approximately 100 km (Meiklejohn & Smith 2008). The coastline consists mainly of cliffs with pebble beaches on the eastern side of the island where elephant seals predominantly haul out (Condy 1978). For this study, photogrammetry of tagged female southern elephant seals that hauled out for the breeding season was mainly done between Ship's Cove and Archway Bay on the eastern aspect of the island (Fig. 2.1). On returning to the Island for the moult haulout, the same females

were sought out from all the beaches around the Island (Fig. 2.1) and photographed again.

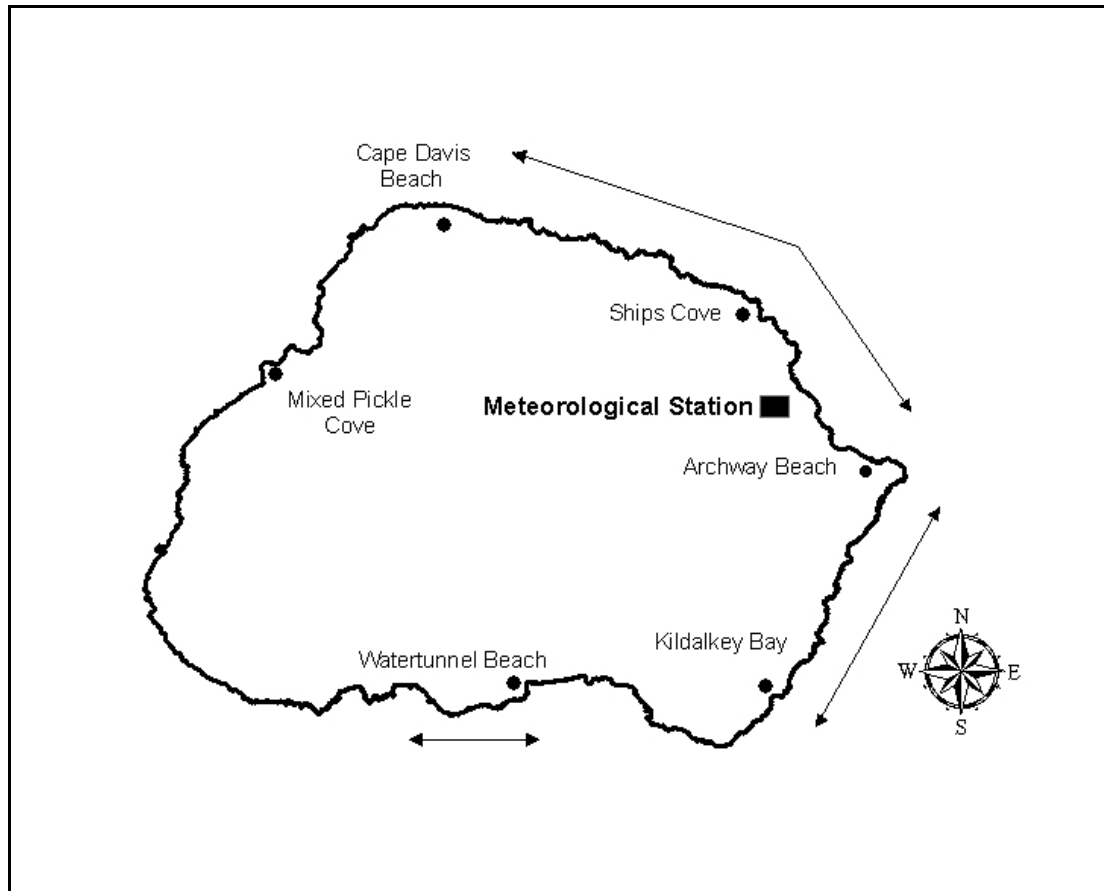


Figure 2.1. MI: Breeding period photogrammetry was performed between Ship's Cove and Archway Beach and all the beaches in the moult. The search for tagged seals along the coastline on all the beaches indicated with arrows, were conducted every 7 days during the breeding season (mid-August to mid-November) and every 10 days from mid-November to the following mid-August since 1983.

Pup tagging

Since 1983 practically all newly-weaned pups born on Marion Island were double tagged in each of their hind flippers with uniquely numbered, colour-coded Dalton jumbo tags (Dalton supplies Ltd, Hendley-on-Thames, U.K; http://www_dalton.co.uk/products/pages_pr/research/r_jumbo.htm) (for further details see de Bruyn *et al.* 2008).

Mark-recapture programme

Since 1983, all hauled out elephant seals were checked for the presence of tags on all popular beaches along the coastline (Fig. 2.1) every 7 days during the breeding season (mid-August to mid-November) and every 10 days for the remainder of the year. Tagged individuals are documented (tag number and cohort specific colour; sex if known; haulout site) to compile life history data for each individual. During the breeding season, daily searches for weaned pups (abandoned by their mothers at weaning) occurred on all the beaches between Archway Beach and Ship's Cove (de Bruyn & Bester 2010, Fig. 2.1) to establish the exact date of weaning of each pup.

Photogrammetry

Photogrammetry was performed with calibrated cameras on unrestrained adult females as described in de Bruyn *et al.* (2009). Eight or more photos were taken from different angles around a seal (subject) to form one project. Twenty three female seals ranging from 3 to 18 years of age were repeatedly photographed between September 2009 and February 2010. For each of the animals, photogrammetric (PG) projects were performed (1) upon their arrival for the breeding season, (2) postpartum and (3) immediately pre-departure for their subsequent post-breeding pelagic foraging phase. Secondly, in the austral summer, photogrammetric projects were done during the moult, following the post-breeding foraging trip: (1) pre-moult (or when animals were first sighted) and (2) post-moult, prior to seals departing for their post-moult pelagic phase. Three-dimensional models (based on each of the PG projects), (Fig. 2.2) were built using the de Bruyn *et al.* (2009) method for estimation of body mass.

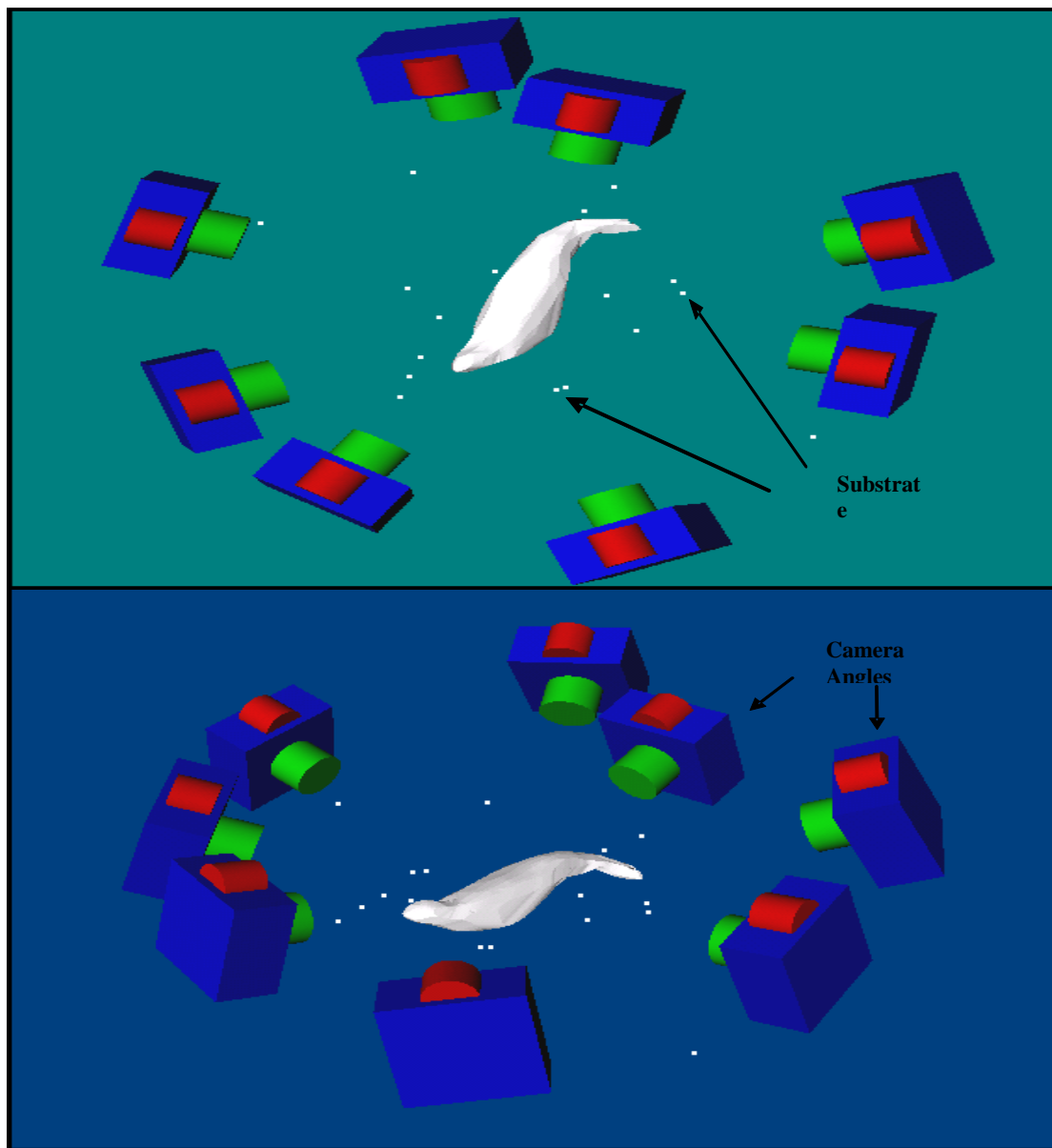


Figure 2.2. Photomodeler example: Three – dimensional model of a female southern seal used to estimate body mass. A (top view) indicate substrate markers; B (side view) indicates camera angles.

Photogrammetric analysis

Volumetric estimation procedures were executed using the commercially available three-dimensional (3-D) modelling package Photomodeler Pro version 6.2 (de Bruyn *et al.* 2009). From the digital photographs, a 3-D spatial model was created using fixed points on the substrate around the animal; these were cross-referenced between photographs to create a 3-D space. The silhouette (outline) of the animal

was traced on all the photographs and cross-referenced between photographs to shape the model of the subject. The volume of the animal's shape was multiplied by a coefficient that is contingent on the mean total body density, the nature of the substrate upon which the animal is resting as well as the number of photographs in a project (Table 2 in de Bruyn *et al.* 2009) to obtain an estimate of body mass (Table 2.1).

Table 2.1. Predictive equations to approximate body mass of southern elephant seals. Full view needs at least 8 photos including all perpendicular and side angles. PBM: Predicted body mass kg, ME: mass estimate from photogrammetric method KGI (de Bruyn *et al.* 2009).

Model Equation	
Even substrates:	
Full view	$PBM = ME - [ME \times (0.085 \pm 0.013)]$
Missing one perpendicular	$PBM = ME - [ME \times (0.108 \pm 0.019)]$
Missing an entire side view	$PBM = ME - [ME \times (0.244 \pm 0.026)]$
Uneven substrates:	
Full view	$PBM = ME - [ME \times (0.006 \pm 0.027)]$
Missing one perpendicular	$PBM = ME - [ME \times (0.004 \pm 0.038)]$
Missing an entire side view	$PBM = ME - [ME \times (0.099 \pm 0.034)]$

Calculation of date of birth, and pre- and post-partum mass

Daily observations along the coastal study area allowed determination of the exact weaning date for all pups, as well as the concomitant departure date for all mothers, in order to calculate the mean duration of suckling. Repeated daily observations allowed a linear time model to be created, from which we could calculate exact time of weaning and mother departure (the two are not always the same but mostly they are). This illustrates the presence of each individual and pup as well as the dates on which PG projects were performed. From this we used mean suckling duration, PG projects and census data to work backwards from weaning date to calculate the date of birth for each individual.

Pre- and post-partum PG projects were performed to assess birthing mass loss for all mothers (Fig. 2.3). Thirteen females were photographed on arrival, the remaining females' arrival mass was estimated by multiplying the calculated mean daily mass loss pre-partum for the 13 females with days elapsed between arrival and birth. Additionally, daily mass loss between post-partum PG and pre-departure PG was calculated from 16 females that all had both a post-partum PG and a pre-departure PG. Where post-partum PG projects could not be done immediately following parturition, daily post-partum mass loss was multiplied with number of days between postpartum PG and date of birth to obtain estimated mass at the start of lactation (mass after birth = MAB). A mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson & van Aarde 2001) and a placenta mass of 3.5 kg (Arnbom *et al.* 1997) were added to estimate mass just before birth (MBB). If pup sex was unknown ($n=4$), a mean value of 46 kg was used. Twelve females were photographed on the day of departure, the remaining females' departure mass was estimated by multiplying the calculated mean mass loss per day (post-partum) with the days elapsed between departure and previous PG.

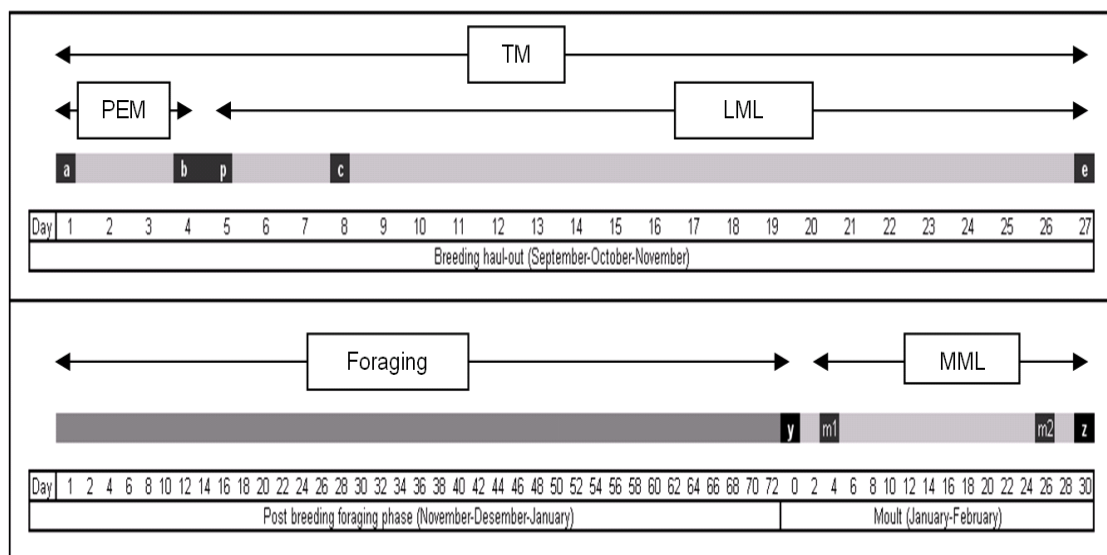


Figure 2.3. Visual representation of annual female life cycle: (TM) total mass loss in breeding haulout, (PEM) pre-partum mass loss, (LML) lactation mass loss, (a) breeding season arrival PG mass, (b) pre-partum PG mass, (c) post-partum PG mass, (d) days elapsed, (e) breeding season departure PG mass, (p) partum. (MML) moult mass loss, (m1) first moult PG, (m2) second moult PG.

Breeding haulout equations

Pre-partum mass loss (PEM), lactation mass loss (LML) and absolute mass loss (TM) (Fig. 2.3) was calculated for each female using the following equations, where M = mass:

$$PEM = M_{arrival} - M_{pre_partum} \quad (1)$$

$$LML = M_{birth} - M_{departure} \quad (2)$$

$$TM = M_{arrival} - M_{departure} \quad (3)$$

Daily mass loss rates for the pre-partum period were calculated for animals that had arrival PG mass estimates ($n=13$) using the following equation:

$$PEM_{daily} = \frac{M_{arrival} - M_{pre_partum}}{no.days} \quad (4)$$

Daily mass loss rates for the post-partum period were calculated for animals with post-partum and departure PG mass estimates ($n=16$) using the following equation:

$$LML_{daily} = \frac{M_{post_partum} - M_{departure}}{no.days} \quad (5)$$

In order to calculate the amount of mass loss as a result of parturition, the difference between mass directly after and before parturition was measured. Daily mass loss rates were used to calculate the mass of female southern elephant directly after parturition seals using the following equation:

$$Mass_{after_birth} = M_{post_partum} + (no.days \times LML_{daily}) \quad (6)$$

Pup mass (Wilkinson & van Aarde 2001) and placenta mass (Arnbom *et al.* 1997) were added to mass estimates determined from equation 6 to obtain mass estimates directly before birth. Birth mass was set as a constant mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson & van Aarde 2001). If no post-partum PG mass estimates were available, mass directly before birth was estimated from arrival PG mass estimates as:

$$Mass_{before_birth} = M_{arrival} - (no.days \times PEM_{daily}) \quad (7)$$

If mass before birth was obtained as described in equation 7, pup mass (Wilkinson & van Aarde 2001) and placenta mass (Arnbom *et al.* 1997) was subtracted to obtain mass after birth.

Moult Equations

Moult mass loss (MML), was calculated for each female using the following equations, where M = mass:

$$MML = M_{arrival} - M_{departure} \quad (8)$$

Daily mass loss rates for the moult period were calculated for animals that had both post-arrival PG mass estimates and pre departure PG mass estimate ($n=13$) using the following equation:

$$MML_{daily} = \frac{M_{post_arrival} - M_{pre_departure}}{no.days} \quad (9)$$

The duration of the post-breeding foraging phase and the moult durations were obtained through the continuous mark-recapture programme sightings associated with the 10 day resighting cycle for all the beaches on the south-western coastline (Fig. 2.1). Mean moult duration was applied to animals that departed between sightings.

$$Mass_{arrival} = M_{post_arrival} + (no.days \times MML_{daily}) \quad (10)$$

$$Mass_{departure} = M_{pre_departure} - (no.days \times MML_{daily}) \quad (11)$$

Similarly a mean mass loss per day was used for animals that did not have an individual mass loss per day recorded due to a lack of two photogrammetry projects. Rainy weather was the main contributor to missing photogrammetry projects.

Statistical analysis

The program R (R Development Core Team 2011) was used for statistical analysis. The following packages were used: companion to Applied Regression (car) (Fox & Weisberg 2011) and Various R programming tools for plotting data (gplots) (Warnes *et al.* 2010). Breeding and moult data from different Islands were compared statistically using an ANOVA and the post hoc TukeyHSD test. If normality did not hold, data was log transformed. Mass loss per day in the moult was statistically compared using Kruskal-Wallis test. A *t*-test was used for post-breeding foraging duration comparison. Significance was set at $P < 0.05$.

Results

Sample trends

Mass loss and gain of female southern elephant seals from Marion Island, obtained through photogrammetry, and are presented in Table 2.2.

Table 2.2. Dataset: Data from the 2009/2010 austral summer. Data contains information about female mass change throughout the course of their annual life cycle. It includes total mass loss and gain (kg), and percentage mass loss and gain (%) in the breeding, foraging and moulting seasons.

Age	Tag	Breeding Period				Foraging period				Moulting period							
		Arrival mass (kg)	Mass after birth (kg)	Mass loss (kg)	Lactation mass loss	Percentage (%) lactation mass loss	Duration (days)	Departure mass (kg)	Percentage (%) lactation mass regained	Mass gain (kg)	Mass gain per day (kg)	Duration (days)	Arrival mass (kg)	Mass loss (kg)	Duration (days)	Mass loss per day (kg)	Departure mass (kg)
18	OB074	602.6	539.9	235.3	172.6	32.0	30.0	367.3	71.5	123.4	2.1	58.0	490.7	147.6	32.0	4.8	343.1
13	BP081	551.9	486.8	223.7	158.7	32.6	28.0	328.1	95.7	151.9	2.6	58.0	480.1	195.2	42.0	4.8	284.9
12	WR093	623.4	572.6	232.2	181.3	31.7	29.0	391.3	93.0	168.6	2.7	63.0	559.9	161.5	42.0	3.9	398.4
11	PO252	570.6	501.6	235.2	166.2	33.1	29.0	335.4	79.2	131.7	1.6	80.0	467.1	117.7	24.0	4.1	349.4
10	GG094	508.7	444.6	232.9	168.8	38.0	27.0	275.8	115.3	194.7	2.9	68.0	470.5	157.3	31.0	5.2	313.2
9	VW298	603.2	532.1	237.3	166.1	31.2	28.0	366.0	94.9	157.6	2.3	70.0	523.6	138.1	22.0	4.8	385.5
8	OO406	516.1	445.1	227.0	156.0	35.0	28.0	289.1	167.5	261.3	3.7	70.0	550.4	142.8	31.0	4.8	407.6
7	BB349	537.8	477.8	239.6	179.6	37.6	23.0	298.2	89.6	161.0	1.9	85.0	459.2	153.5	20.0	5.3	305.8
6	YY467	475.0	414.3	226.9	166.2	40.1	27.0	248.1	84.7	140.7	1.5	92.0	388.8	138.1	20.0	4.8	250.7
6	YY237	474.3	401.9	235.5	163.1	40.6	28.0	238.8	99.9	162.9	2.5	65.0	401.7	142.8	31.0	4.8	258.9
6	YY218	604.9	544.9	308.5	248.5	45.6	26.0	296.4	50.1	124.4	2.0	61.0	420.8	147.6	32.0	4.8	273.2
6	YY133	499.0	435.8	199.2	135.9	31.2	28.0	299.9	102.9	139.9	2.2	64.0	439.7	145.6	41.0	3.6	294.2
5	RR468	534.6	484.3	226.9	176.6	36.5	26.0	307.7	89.5	158.0	2.5	62.0	465.8	132.8	30.0	4.6	333.0
5	RR435	484.9	431.7	196.7	143.5	33.2	29.0	288.2	147.5	211.7	2.9	74.0	499.9	233.1	21.0	8.0	266.8
5	RR347	533.2	471.2	235.8	173.8	36.9	27.0	297.4	79.6	138.3	1.7	80.0	435.7	160.0	30.0	5.5	275.7
5	RR246	500.2	436.5	238.4	174.7	40.0	26.0	261.8	83.9	146.5	1.9	78.0	408.3	138.1	22.0	4.2	270.2
5	RR101	406.5	352.4	167.7	113.6	32.2	26.0	238.8	116.8	132.7	2.2	60.0	371.5	152.4	33.0	4.8	219.1
5	RR024	493.5	439.5	239.9	185.9	42.3	25.0	253.6	75.1	139.7	1.9	73.0	393.3	127.2	30.0	4.4	266.2
4	PP452	522.1	465.2	245.8	188.9	40.6	36.0	276.3	95.6	180.5	3.0	61.0	456.8	190.4	41.0	4.8	266.4
4	PP203	477.7	405.9	200.2	128.4	31.6	27.0	277.5	126.6	162.6	3.4	48.0	440.1	147.6	32.0	4.8	292.6
4	PP042	514.7	471.7	247.0	204.0	43.2	28.0	267.7	72.7	148.3	2.4	62.0	416.0	138.1	30.0	4.8	277.9
3	GW344	366.9	308.1	147.8	89.0	28.9	26.0	219.1	144.2	128.3	2.0	63.0	347.4	144.0	31.0	4.8	203.4
3	GW037	409.9	360.5	218.1	168.7	46.8	24.0	191.8	70.7	119.3	1.7	69.0	311.1	102.1	31.0	3.4	209.0
	Mean	513.6	453.2	226.0	165.7	36.6	27.4	287.6	97.7	155.8	2.3	68.0	443.4	150.2	30.4	4.8	293.3
	Max	623.4	572.6	308.5	248.5	46.8	36.0	391.3	167.5	261.3	3.7	92.0	559.9	233.1	42.0	8.0	407.6
	Min	366.9	308.1	147.8	89.0	28.9	23.0	191.8	50.1	119.3	1.5	48.0	311.1	102.1	20.0	3.4	203.4
	SD	64.8	63.9	30.6	31.3	5.1	2.5	48.1	27.9	32.4	0.6	10.1	61.1	26.8	6.7	0.8	55.5

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Photogrammetry effectiveness

A total of 195 photogrammetry projects were analysed to obtain mass estimates of southern elephant seals photographed between 2006 and 2011. Sixteen of these 195 projects failed to solve the mass estimate accurately due to insufficient photographs from different angles or the complexity of the substrate around the animal. Some 91.5% of projects could be accurately solved for mass estimation.

Breeding period

Comparisons between female southern elephant seals from Marion Island (MI) $n=23$, King George (KGI) $n=27$ (Carlini *et al.* 1997) and South Georgia Island (SGI) $n=27$ (Fedak *et al.* 1996) focussed on: post-partum mass, duration of lactation, absolute mass loss and percentage mass loss during lactation period (calculated from post-partum mass) (Table 2.3). Mass post-partum (the start of lactation) for MI ranged from 308.1 to 572.6kg (mean = 453.2 ± 63.9 kg) (Fig. 2.4) for females aged 3 to 17 years. Absolute mass loss from the start of lactation to departure for post-breeding foraging from MI ranged from 89.0 to 248.5kg (mean = 165 ± 31.3 kg) (Fig 2.5). Percentage mass loss during the course of lactation for MI ranged from 28.95 to 46.85% (mean = 36.6 ± 5.1 %) (Table 2.3). Mass after parturition from MI differed significantly ($P < 0.001$) from KGI and from SGI ($P = 0.02$). Lactation mass loss significantly differed from KGI ($P < 0.001$) and SGI ($P = 0.01$). Percentage mass loss during the course of lactation from MI did not differ from KGI ($P = 0.9$) or SGI ($P = 0.9$) (Table 2.4).

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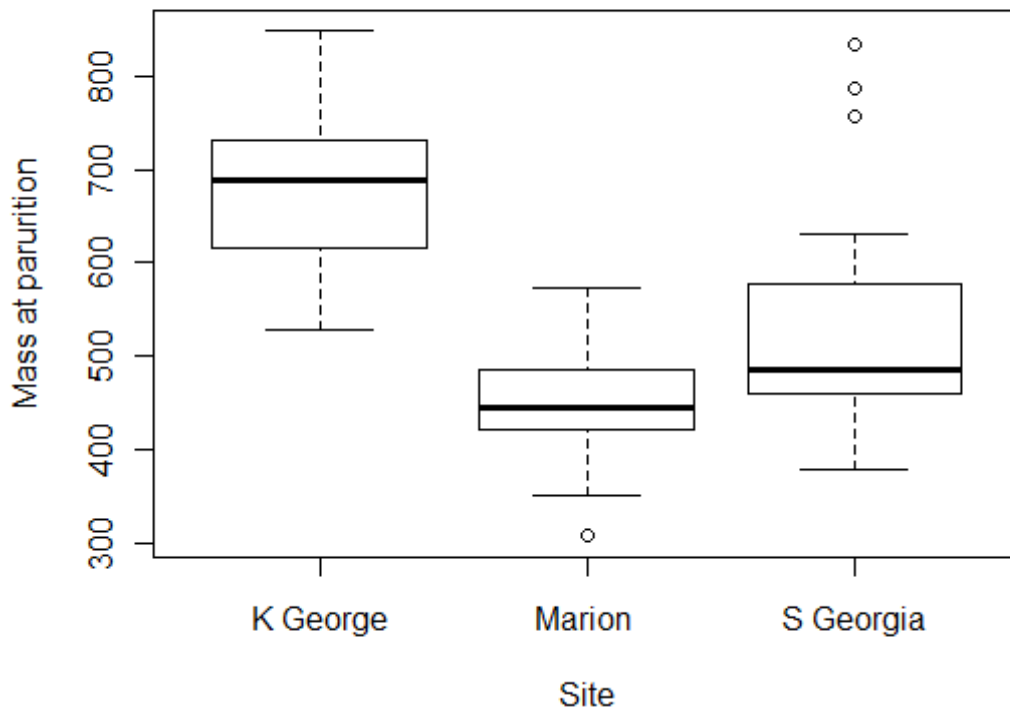


Figure 2.4. Mass comparison Post-Partum (start of lactation) between female southern elephant seals from Marion Island ($n=23$) ranged from 308.1 to 572.6kg, King George Island ($n=27$) ranged from 379.5 to 847.5 kg and South Georgia Island ($n=27$) ranged from 387 to 786 kg.

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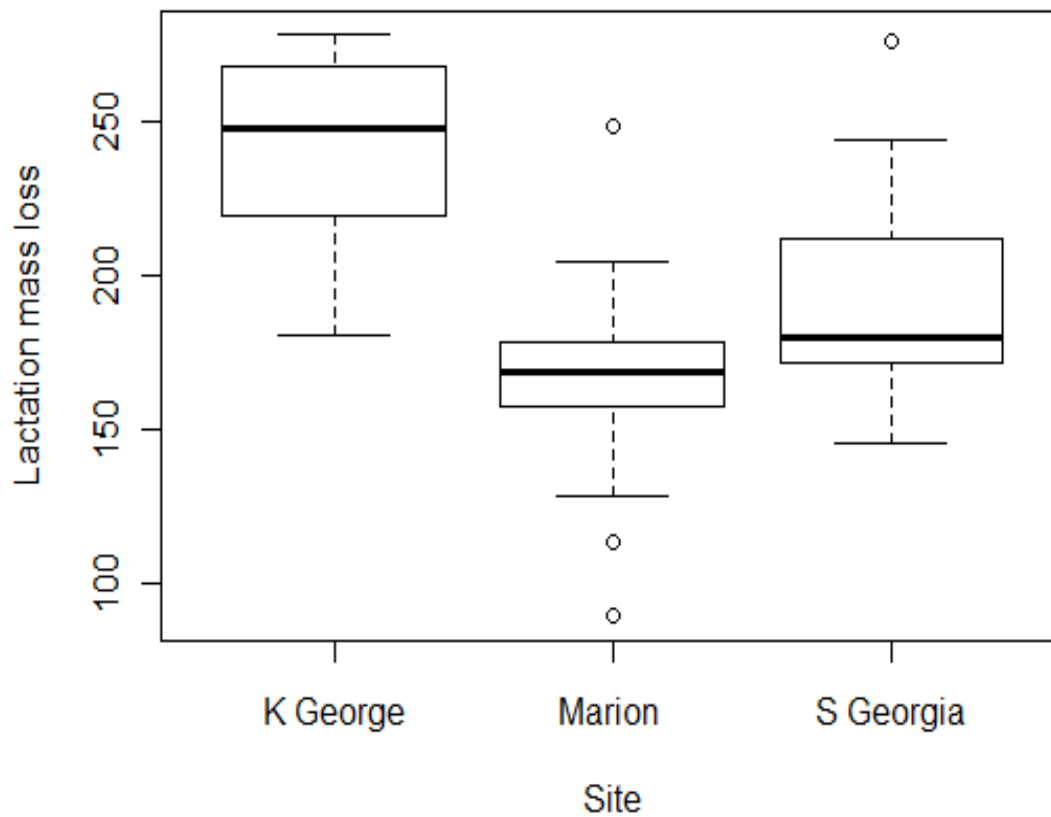


Figure 2.5. Mass loss during the lactation period for female southern elephant seals from Marion Island ($n=23$) ranged from 89.0 to 248.5kg, King George Island 139.5 to 273.5 kg ($n=27$) and South Georgia Island ($n=27$) range from 145 to 276 kg.

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Table 2.3. Breeding seasons from Marion Island 2009/2010, King George Island 1994/1995 and South Georgia Island 1986 & 1988 are compared on bases of post-partum mass (kg), duration of lactation (days), mass loss (kg) and percentage lactation mass loss (kg). Similarly post-breeding foraging phase are compared on bases of foraging duration (days), mass gained (kg), Rate of mass gain (kg per day) and percentage mass gained during post-breeding foraging phase (%). Values for post-breeding foraging for Macquarie Island was not available.

	Breeding haulout		
	Marion Island 2009/2010 ^o	South Georgia ² 1986&1988	King George ¹ 1994/1995
	Mean ± SD	Mean ± SD	Mean ± SD
Post-partum mass (kg)	453.2 ± 63.9	515 ± 100	678.6 ± 96
Duration of lactation (days)	22.6 ± 2.1	23.3 ± 2.2	22.7 ± 1.9
Mass loss (kg)	165.7 ± 31.3	191 ± 36	242.4 ± 31.4
Percentage mass loss during lactation (%)	36.6 ± 5.1	37.1 ± 4.1	35.9 ± 3.9
	Postbreeding Pelagic foraging		
	Marion Island 2009/2010 ^o	P values between MI & KGI	King George ¹ 1994/1995
	Mean ± SD		Mean ± SD
Foraging duration (days)	68 ± 10.7	<i>P</i> = 0.01	60.5 ± 6.2
Mass gained (kg)	155.83 ± 32.42	<i>P</i> = 0.07	132.2 ± 35.6
Rate of mass gain (kg per day)	2.34 ± 0.56	<i>P</i> = 0.6	2.21 ± 0.65
Percentage mass gain during post breeding foraging (%)	35 ± 8.2	<i>P</i> < 0.001	19.9 ± 3.3
n	23		12

^o This study

¹ Carlini *et al.* (1997)

² Fedak *et al.* (1995)

Table 2.4. P values from ANOVA for breeding and Moulting comparison of MI, KGI, SGI and MAQ. Post-partum mass (Mass at the start of lactation); lactation mass loss and percentage mass loss during lactation are compared for the breeding season. Arrival mass, mass loss and duration are compared for the moulting haulout period.

Site	Breeding haulout								
	Marion Island ^o			King George Island ¹			South Georgia Island ²		
	Arrival mass	Mass loss	Days	Arrival mass	Mass loss	Days	Arrival mass	Mass loss	Days
Marion Island				<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> = 0.9	<i>P</i> = 0.02	<i>P</i> = 0.01	<i>P</i> = 0.9
King George Island	<i>P</i> < 0.001	<i>P</i> = 0.1	<i>P</i> = 0.3				<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> = 0.7
South Georgia Island	<i>P</i> = 0.4	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> = 0.03	<i>P</i> = 0.003	<i>P</i> = 0.07			
Maquarie Island ⁴	<i>P</i> = 0.9	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> = 0.003	<i>P</i> < 0.001	<i>P</i> < 0.001	<i>P</i> = 0.7	<i>P</i> = 0.1	<i>P</i> = 0.03

^o This study

¹ Carlini *et al.* (1997)

² Fedak *et al.* (1995)

³ Boyd *et al.* (1993)

⁴Hindell *et al.* (1994)

⁵Carlini *et al.* (1999)

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Post-breeding pelagic foraging period

Pelagic foraging aspects of females that were compared between populations were: time spent foraging, absolute mass gained, rate of mass gain and percentage mass gained. Values for KGI were obtained from Carlini *et al.* (1997). Time spent at sea for MI individuals ranged from 48 to 92 days (mean = 68 ± 10.7 days) and KGI ranged from 51 to 71 days (mean = 60.5 ± 6.2) with ($T_{(-2.7)} = 32$, $P = 0.01$) (Table 2.3) (Fig. 2.6). Mass gain in the post-breeding foraging phase for MI ranged from 119.3 to 261.3 kg (mean = 155.8 ± 32.4 kg) and KGI ranged from 94.0 to 204.0 kg (mean = 132 ± 35.6 kg) with $T_{(-1.9)} = 20.6$, $P = 0.07$ (Table 2.3). Rate of mass gain per day at MI ranged from 1.5 to 3.7 kg.day⁻¹ (mean = 2.34 ± 0.56 kg.day⁻¹) and KGI ranged from 1.5 to 3.4 kg.day⁻¹ (mean = 2.21 ± 0.65 kg.day⁻¹) with $T_{(-0.4)} = 20.7$, $P = 0.6$ (Table 2.3). Percentage mass gain in the post-breeding foraging phase for MI ranged from 22.8 to 58.7% (mean = $35 \pm 8.2\%$) and KGI ranged from 11.3 to 31.5% (mean = $19.9 \pm 6.3\%$) with ($T_{(-6.0)} = 27.9$, $P < 0.001$) (Table 2.3). Percentage mass recovery in the post breeding foraging phase compared to percentage lactation mass loss (calculated from lactation mass loss) for MI ranged from 50.1 to 167.5% (mean = $97.7 \pm 27.9\%$), contrary to females from KGI recovering 55% (Carlini *et al.* 2005).

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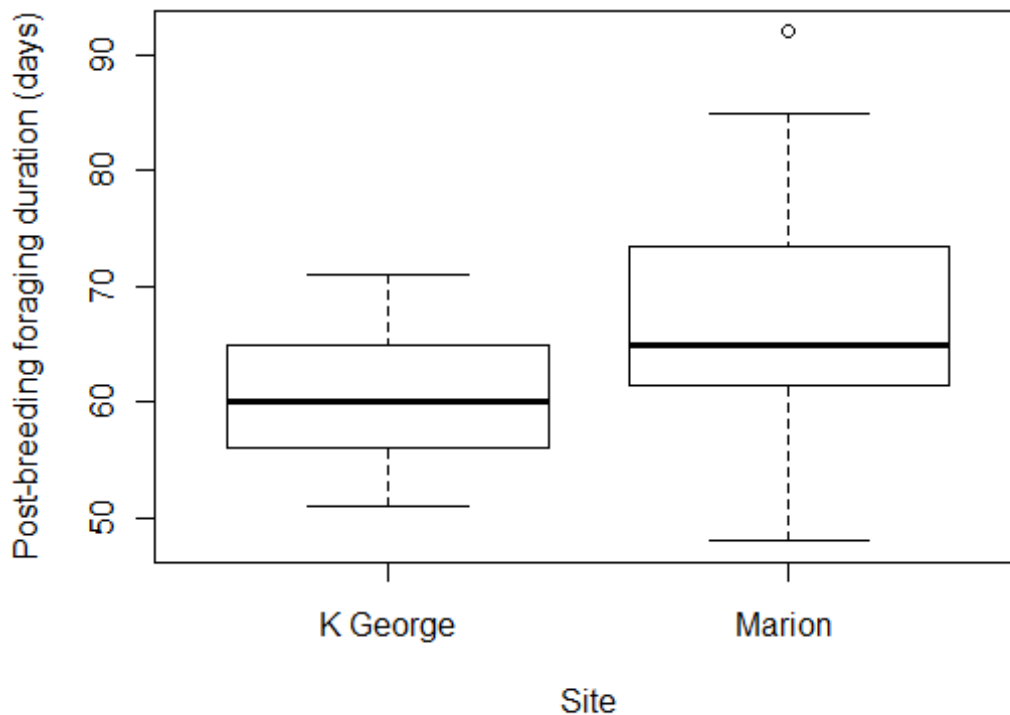


Figure 2.6.Duration of post breeding foraging phase for female southern elephant seals from Marion Island (MI) and King George Island (KGI). Time spent at sea for MI ($n=23$) individuals ranged from 48 to 92 days and KGI ($n=12$) ranged from 51 to 71 days.

Moult period

The initial moult haulout mass, duration of the moult, total mass loss and mass loss per day of the obligatory moult phase at Marion Island (MI) are compared to King George Island (KGI) (Carlini *et al.* 1999), South Georgia Island (SGI) (Boyd *et al.* 1993) and Macquarie Island (MAQ) (Hindell *et al.* 1994) (Table 2.5). The mass at the start of the moult for MI animals ranged from 311.1 to 559.9 kg (mean = 443 ± 61 kg) (Table 2.5) for females aged 3 to 17 years. Moult duration ranged from 20 to 40 days (mean = 30.4 ± 6.8 days; Table 2.5). Mass loss per day ranged from 3.3 to 11.1 $\text{kg}\cdot\text{day}^{-1}$ (mean = 4.76 ± 0.81 $\text{kg}\cdot\text{day}^{-1}$). No significance was found amongst

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populations. Total mass loss for the duration of the moult ranged from 102.1 to 233.1 kg (mean = 150 ± 27 kg) in Table 2.5. Population comparison results are represented in Table 2.4 where moult arrival mass from MI is significantly different ($P < 0.001$) from KGI and similar to SGI ($P = 0.4$) and MAQ ($P = 0.9$). Mass loss during the moult from MI significantly differs from SGI and MAQ ($P < 0.001$) but MI and KGI do not differ ($P = 0.1$). Similar results were found for moult duration, where MI significantly differs from SGI and MAQ ($P < 0.001$) but MI and KGI do not differ ($P = 0.3$) (Table 2.4).

Table 2.5. Comparison of four different female southern elephant seal populations during the moult. Comparison was made between initial mass when females arrived, duration of the moult, mass loss per day and total mass loss

	Marion Island ^o Mean \pm SD	King George ¹ Mean \pm SD	South Georgia ² Mean \pm SD	Macquarie ³ Mean \pm SD
Initial mass at moulting (kg)	443 \pm 61	567 \pm 73	483 \pm 86	447 \pm 69
Time (days)	30.4 \pm 6.8	25.7 \pm 4.3	21.0 \pm 4.4	16.8 \pm 3.1
Mass loss (kg per day)	4.76 \pm 0.81	5.04 \pm 0.39	4.46 \pm 0.64	4.46 \pm 0.80
Total mass loss (kg)	150 \pm 27	129 \pm 22	94 \pm 25	73 \pm 18
n	23	9	19	13

*not significant $P > 0.05$

^o This study

¹ Carlini *et al.* (1999)

² Boyd *et al.* (1993)

³ Hindell *et al.* (1994)

Discussion

The mass loss and gain over the course of an annual cycle for female southern elephant seals at MI was previously unknown. This study shows mass change trends within a population according to mass fluctuations in female southern elephant seals in their annual life cycle (Table 2.2) and how they relate to other populations. It also shows the value of the use of photogrammetry over temporal scales.

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Photogrammetry over a temporal scale

Percentage mass loss during the lactation period for KGI is similar to SGI (McCann *et al.* 1989; Fedak *et al.* 1994; Carlini *et al.* 1999) and indicates that females lose approximately 35% of their mass during lactation. Similar percentage lactation mass loss among populations would indicate that there are set physiological limitations devoted to lactation. No significant differences were found between percentage mass loss from the geographically separated populations at MI, KGI and SGI with percentage mass loss apparently a constant in the species (e.g. McCann *et al.* 1989; Le Boeuf 1994, Fedak *et al.* 1996; Arnborn *et al.* 1997 Carlini *et al.* 1997; 1999; this study). Although females from MI are smaller in absolute size (present study) their percentage mass loss is similar to those of KGI and SGI. These results from different populations are analogous to that of MI indicating that photogrammetric mass estimation can be used alongside datasets of physically weighed animals, for comparative studies. Therefore, photogrammetry is an effective method for measuring and comparing mass change of female southern elephant seals over a temporal scale.

Breeding

Phocid seals have a characteristic lactation pattern, where females produce energetically rich milk within a short suckling period with pupping and nursing spatially separated from foraging (Bonner 1984; Oftedal *et al.* 1987). This pattern of pupping and nursing depletes the females' energy reserves (Carlini *et al.* 1997). The mean duration of lactation does not differ significantly between populations ($P = 0.8$). Females spend approximately 23 days suckling their young (Table 2.3). These are similar to the findings of other studies (Laws 1953b, 1956a, 1956b; Le Boeuf *et al.* 1972). However, female mass after parturition differs greatly between MI, KGI and SGI. Females from MI are on average ± 200 kg lighter at the beginning of lactation than their counterparts at KGI and ± 60 kg lighter than females from SGI, supporting

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earlier assertions (Burton *et al.* 1997; Carlini *et al.* 1997). Females from KGI and SGI are larger at arrival; larger size is advantageous in terms of the amount of energy available for lactation (Carlini *et al.* 2004). Female size and reserves at parturition have proven to be the most significant factors determining pup mass gain in large phocid seals (e.g. Costa *et al.* 1986; Tedman & Green 1987; Iverson *et al.* 1993; Fedak *et al.* 1996). Furthermore, smaller marine mammals spend less time submerged and less time foraging at any given depth (Hindell *et al.* 2000). It has been well documented in adult northern (*Mirounga angustirostris*) and southern elephant seals (*Mirounga leonina*) that size of an individual influences the ability to store O₂ and thus limiting the time an individual can spend at depth (Le Boeuf 1994; Hindell *et al.* 1999; 2000; Irvine *et al.* 2000). The smaller size of females from MI could influence their diving abilities (McIntyre *et al.* 2011). Smaller females from MI can not store the same amount of O₂ as KGI and SGI thus limiting their dive depth and duration. In addition smaller individuals will have a higher mass specific metabolic rate than larger individuals (Kleiber's law - Kleiber 1947). The higher mass specific metabolic rate for females at MI compared to larger females from KGI and SGI could in extreme cases lead to smaller individuals adopting different feeding strategies or focus on different prey species (Hindell *et al.* 2000). The ability to forage for longer periods at depth would be advantages for resource acquisition and mass gain. The mass acquired in aquatic foraging is a good indication of the availability of food in feeding grounds and the success of female foraging (Boyd *et al.* 1989).

After 1964 when sealing was stopped the South Georgia and Peninsula Valdes southern elephant seal populations increased or remained stable (Boyd *et al.* 1996). It is presumed that the more stable Atlantic southern elephant seal population is in some way connected to more abundant resources (Vergani *et al.* 2001). The last attempted sealing expedition at the Prince Edward Island was in the 1930's (Rice 1991; Cooper 2008). While SGI and KGI populations increased or stabilized others

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decreased, 84% for Marion Island (Pistorius *et al.* 2011), 57% for Macquarie Island (Laws 1994). The availability of prey has often been hypothesized to be the main factor determining population status in the MI and MAQ populations (Hindell 1991, Hindell *et al.* 1994, Pistorius *et al.* 2011). The drastic decline in MI population size since the 1950s (McMahon *et al.* 2005) may be attributed to the anthropomorphic disturbance caused by sealing in the 1800s and early 1900s (Cooper & Avery 1986; Graham 1989; Headland 1989; Richard 1992; De Villiers & Cooper 2008) and illegal fishery of Patagonian tooth fish (*Dissostichus eleginoides*) which resulted in the near collapse of fishery in the area around the island before the establishment of the Exclusive Economic Zone in 1996 (Pakhomov & Chown 2003), and the implementation of the Marine Living Resources Act in 1998 (Chown *et al.* 2006). Large scale events may cause the reduction in body size of an entire generation and potential long-term consequences to female body size (Huston *et al.* 2011). High food availability per animal is paramount in determining adult body size and can allow high population growth rates (e.g., fecundity and survival) (Huston *et al.* 2011). Thus KGI and SGI populations with their high growth rate and large female body size has a high food availability per animal and MI with its smaller females and previously declining population had a low food availability per capita.

Absolute lactation mass loss for female southern elephant seals from MI is significantly different from those at KGI and SGI. This is not surprising as females from KGI and SGI are significantly larger than MI females at the start of lactation (present study). Females from MI lose approximately 80 kg less mass than their counterparts on KGI and ± 30 kg less than females from SGI. Greater absolute energy loss from larger females is positively related to greater energy gain by their pup (Carlini *et al.* 2004). The smaller size of Marion Island females would imply that their offspring will be smaller, smaller size would imply less reserves for maintenance and avoidance of predators until they can find a good food source.. Weaning mass is

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a function of maternal energy reserves which females acquire in their pelagic foraging bouts (Vergani *et al.* 2001), therefore an increase in weaning mass provides a potentially useful indicator of prey availability and subsequently maternal energy reserves (Vergani *et al.* 2008). Recent population stabilization at Marion Island (Pistorius *et al.* 2011) and increase in weaning mass (McMahon *et al.* 2003) indicates a recovering population. Stabilization after a long decline in the MI population was presumably caused by an increase in per capita prey availability (Pistorius *et al.* 2004).

Post-breeding foraging phase

The post-breeding foraging phase occurs in a period of seasonal abundance and females seem to gain mass at a greater rate than during the post-moult foraging phase (Carlini *et al.* 1999). In the post-breeding foraging phase, females from MI stayed at sea significantly longer than those of KGI (Fig. 2.6). This could be due to differences in prey availability between respective foraging grounds. Another alternative is that the proximity of the feeding grounds relative to the breeding sites differs? The difference between the two post breeding foraging phases is about 8 days (Table 2.3). KGI is less than one days travel from to some highly productive areas west of the Antarctic Peninsula (McConnell *et al.* 1992, McConnell & Fedak 1996, Bornemann *et al.* 2000), where as it could take females at MI three or four days to “commute” to their feeding areas South and South West of the Island (Jonker & Bester 1998; McIntyre *et al.* 2010). The percentage mass gain in the post-breeding foraging phase was also significantly higher for MI females than those at KGI ($P < 0.001$) (Table 2.3). The difference in percentage mass gain between the populations could be necessary to sustain females during the subsequent extended moult duration on MI which is significantly longer than on KGI. The higher percentage of lactation mass regain for MI could be attributed to extended post-breeding foraging duration. As there is no significant difference in rate of mass gain between MI

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females and their counterparts on KGI ($P = 0.6$) and females from MI spend more time foraging, absolute mass gain at the latter island should be greater. On the contrary, absolute mass gain between MI and KGI did not differ significantly ($P = 0.07$).

Moult

Female southern elephant seals return to land after their post-breeding pelagic foraging to moult, losing their hair and top layer of epidermis (Ling 1970). At arrival in the moult females from MI weigh ± 80 kg less than those of KGI and ± 40 kg less than those at SGI. Not surprisingly females from MI did not differ significantly from those at MAQ who also experienced prolonged population decline (Laws 1994). Females from MI arrive for both terrestrial haulouts with a lower mass than their counterparts at KGI and SGI. It appears that the mass loss in the moulting period on MI is similar to that of the mass loss during the lactation period; contrary to findings for other populations. The smaller size and the relative similar absolute mass regain as larger females elsewhere in the post-breeding foraging phase, imply larger percentage mass gain at Marion Island, which could be explained by their smaller physical size.

Due to difference in the observed time spent ashore for MI and KGI compared to MAQ and SGI probably because of sampling artefacts rather than the actual time spent ashore, I dismissed the comparison of moult duration. For females from SGI (Boyd *et al.* 1993) and MAQ (Hindell *et al.* 1994) it is difficult to obtain an exact time spent ashore as females are unmarked and observations are infrequent, while the relatively small size of MI as well as the ongoing extensive mark-recapture programme facilitates calculation of the approximate duration of moult although it requires adjustment (mean moult duration calculated for females that departed between sightings) following Kirkman *et al.* (2003). Rate of mass gain ($2.34 \pm$

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0.56kg.day⁻¹) in the post-breeding season is approximately similar between populations, which poses the question of why female body mass at the end of parturition differs so greatly? Perhaps this could be due to the fact that KGI and SGI population did not show the same population decline as MI (Laws 1994; Boyd *et al.* 1996). Prey availability per individual has likely increased which is evident in the increase in weaning mass and stabilization of the populations. Furthermore, the proximity to highly productive feeding grounds may be the reason for difference in body mass. King George Island animals can forage for longer as the distance to the breeding site is less.

Photogrammetry effectiveness over a temporal scale

Photogrammetry is an effective mass estimation method in various environments, ranging from flat sandy beaches, undulation boulder beaches, grassy *Cotulla* areas and moult wallows (present study). Of all photogrammetry projects done, 91.5% solved accurately (following the 'accuracy checking' procedure outlined in de Bruyn *et al.* 2009). Over 800 projects have been performed since 2006, the field method was improved to make analysis easier and less time consuming, and proves to be fast and efficient and multiple projects can be done on one day whilst collecting a multitude of other data. Less than 10% of photogrammetric projects failed due to environmental and photographic limitations. Photogrammetry should be done on study subjects at every possible opportunity as it is invaluable for assessing mass estimations at critical stages in the annual life cycle of southern elephant seals. Through photogrammetric mass estimation on specific individuals, a longitudinal database can be established which would be invaluable.

Conclusion

Accurately measuring mass of southern elephant seal females throughout both terrestrial phases in the annual cycle enabled us to confirm the effectiveness of

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photogrammetry over a temporal scale. Mass change of individuals within the MI population could be explored and compared to other populations. Females from MI are smaller than their counterparts on KGI and SGI, lose less absolute mass during the course of the breeding season but have the same relative percentage lactation mass loss compared to other populations. The similarity of percentage mass loss during lactation amongst different female populations can be considered the most definitive validation of photogrammetry over a temporal scale. Smaller size may be due to proximity to productive feeding grounds or food availability, reasons for which remain unclear (e.g. anthropomorphic or climate effect on prey availability). The smaller size of MI females could place them under strain on land and at sea. Photogrammetric mass estimation can be used alongside datasets of physically weighed animals and can greatly benefit ecology and life history studies.

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CHAPTER THREE:

AGE-SPECIFIC MATERNAL MASS TRANSFER AND PUP SURVIVAL IN SOUTHERN ELEPHANT SEALS AT MARION ISLAND

Abstract

Although numerous studies have addressed the relationship between pup weaning mass and subsequent survival, none have looked at the survival of successfully weaned pups in relation to the age of their mothers. The unique uninterrupted life history data available for Marion Island's southern elephant seals and the development of an accurate photogrammetric measuring method provided the opportunity to explore the influence of maternal expenditure and age on pup survival. During the 2009 breeding season at Marion Island, known-aged adult females were photographed for photogrammetric mass estimation ($n=29$) and their pups weighed at weaning. Adult female daily pre-partum - (mean = 3.68kg/d) and post-partum mass loss (mean = 7.55kg/d) was calculated. Absolute mass loss ranged from 147.78kg to 308.52kg (mean = 222.06 ± 34.31 kg). Pups weaned at an average of $120\text{kg} \pm 20.46\text{kg}$ (range: 73 to 160kg). Females lose a (mean = 222.06 ± 34.31 kg) absolute mass over the course of the breeding season, however smaller females have higher proportional mass loss than larger females. Females that lose more absolute mass tend to have larger pups at weaning and are usually older. The weaning mass of pups was influenced by maternal age and absolute mass loss. First year pup survival was significantly influenced by weaning mass. Pups of young females aged 3 to 6 years, or females that arrive with a breeding mass below 500kg have a lower 1st year survival probability compared to pups of older and larger females. These findings suggest that older females are more successful and their reproductive success is essential for population growth.

Introduction

Factors that influence population growth are of major interest in population ecology for both practical and theoretical reasons (Gaillard *et al.* 1998). Population abundance and related parameters need to be assessed to implement effective wildlife management but are often difficult to obtain (e.g. Marucco *et al.* 2009). Southern elephant seals range across the Southern Ocean (Biuw *et al.* 2007) foraging for most of the year (McIntyre *et al.* 2010), and spend only short periods in the terrestrial environment (Condy 1979; Kirkman *et al.* 2003; Kirkman *et al.* 2004). Long-term collection of life history data on the species commenced due to observed precipitous declines in the Kerguelen and Macquarie Island stocks from the 1950's to the mid 1990's (Burton 1986; Hindell 1991; Guinet *et al.* 1992; Bester & Wilkinson 1994; Hindell *et al.* 1994; Laws 1994). Continued data collection at some sites indicate recent stabilisation and increase (McMahon *et al.* 2009; Authier *et al.* 2011; Pistorius *et al.* 2011). Haul-out periods are often synchronised and provide researcher access to large numbers of individuals, but data collection of some life history parameters remains difficult. During the breeding season in the austral spring, adult females haul out for approximately 30 days to give birth and suckle their pups for 21-23 days; they are mated during the four days prior to departure (Le Boeuf & Laws 1994). They are extreme capital breeders; females rely completely on their stored energy reserves for maintenance and lactation throughout the terrestrial breeding phase (Arnbom *et al.* 1997). In capital breeders, mass has a fundamental influence on reproduction potential (Festa-Bianchet *et al.* 1998; Boyd *et al.* 1995; Pomeroy *et al.* 1999).

Southern elephant seals, and other seals, differ from terrestrial mammals in the rate and condition of energy transfer. The rapid transfer of energy is a direct result of the high lipid content of the mother's milk. The transfer of energy and thus mass, from the southern elephant seal mother to pup, occurs over the 23 days in

which the pup can treble its birth weight (Bonner 1984; Costa *et al.* 1986; Tedman & Green 1887; Oftedal *et al.* 1993). Pups undergo a protracted phase immediately after weaning during which their thick insulating blubber serves as the main source of energy for maintenance and growth (Carlini *et al.* 2000). The growth of juvenile mammals can have numerous implications on life-history attributes and can manifest either in juvenile or adult life (Bell *et al.* 1997). Juvenile size may determine body size later in life (Gosling & Petrie 1981; Suttie & Hamilton 1983; Festa-Bianchet 1996).

Numerous studies have considered maternal expenditure through the measurement of offspring size (Trillmich 1997) and equally the relationship between maternal expenditure and future survival of progeny (McMahon *et al.* 2000; McMahon & Bradshaw 2004). Similar studies were previously conducted at Marion Island and Macquarie Island (McMahon *et al.* 1999; McMahon *et al.* 2000; Pistorius *et al.* 2000; Pistorius *et al.* 2004; Pistorius *et al.* 2008). Size and therefore the condition at weaning of southern elephant seal pups influenced survival of the pups at both Macquarie Island (McMahon *et al.* 2000) and Marion Island (McMahon *et al.* 2003). The largest females may be three times the mass of the smallest at parturition (Fedak *et al.* 1996). It has been hypothesised that the more the mother weighs, the more energy she has to transfer to her offspring and thus the greater the weaning mass of her pup. Secondly, the greater the weaning mass, the higher the probability of survival (McMahon *et al.* 2000). Yet some questions remain, such as how does female age influence first year pup survival? An aspect of fitness not dealt with previously at Marion Island is the weaning of pups from variously aged females and the pup's subsequent survival (Pistorius *et al.* 2004). The unique uninterrupted life history record of Marion Island southern elephant seals and the development of an accurate photogrammetric measuring method (de Bruyn *et al.* 2009) provide the platform to explore the influence of maternal expenditure and age on pup survival. Mass appears to be the most important state variable, influencing reproduction in

southern elephant seals (Laws 1956a, b). I therefore need to understand how mass at weaning (for both mothers and pups) affects subsequent survival (Arnbom *et al.* 1997; McMahon *et al.* 1999).

Previous data collection complications were related chiefly to the difficulty in weighing these large animals frequently. This spurred the successful experiment of estimating mass by photogrammetric measurement (de Bruyn *et al.* 2009). Using this technique, this study aims to determine: (a) the principal factors that influence weaning mass with regard to age of females and their maternal expenditure at Marion Island, and (b), how female age and maternal expenditure relate to survival of elephant seal pups during their first foraging trip.

Materials and Methods

Southern elephant seals show a high fidelity to their natal (birth) sites (Hofmeyr 2000). This behaviour is expressed early on in their development (McMahon *et al.* 1999). This factor, in conjunction with the long-term southern elephant seal mark-recapture programme on Marion Island (Bester & Wilkinson 1994; de Bruyn *et al.* 2008), allowed us to investigate age specific demographics.

Study site

Marion Island (46°54'S, 37°45'E); one of the two islands in the Prince Edward archipelago is situated in the Southern Indian Ocean. It is approximately 2,180 km southeast of Cape Town, South Africa, and has an area of 300 km² with a coastline of approximately 100km (Meiklejohn & Smith 2008). The coastline consists mainly of cliffs with pebble beaches on the eastern side of the island where elephant seals predominantly haul-out (Condy 1978). For this study, photogrammetry and weaner weighing of elephant seal females and their pups, was mainly conducted on several breeding colony beaches between Ship's Cove and Archway Beach on the eastern

aspect of the island (Fig. 3.1). Females chosen for this study were all tagged (known-age) individuals (see below) that hauled out between these localities (Fig. 3.1).

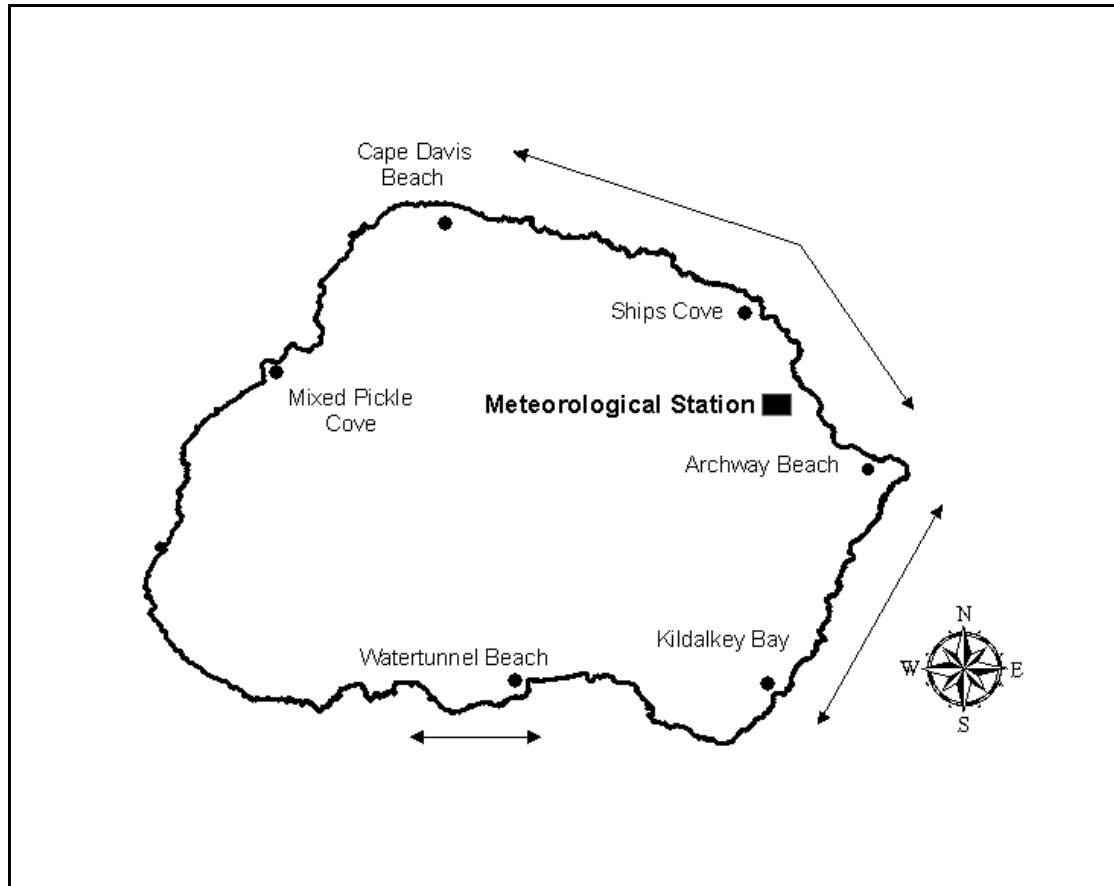


Figure 3.1. Marion Island: Photogrammetry was performed between Ships Cove and Archway Beach. We search for tagged seals along the coastline on all the beaches indicated with arrows every 7 days during the breeding season (mid-August to mid-November) and every 10 days from (mid-November to the following mid-August) since 1983.

Pup tagging:

During the course of every breeding season from 2007, elephant seal researchers identified and tagged mother-pup pairs with temporary super small tags (Dalton supplies Ltd, Hendley-on-Thames, U.K; http://www_dalton.co.uk/products/pages_pr/research/r_jumbo.htm) in the inner inter-digital webbing of the right hind flippers (de Bruyn *et al.* 2008). Once pups are

weaned, the temporary tag is replaced by permanent jumbo Dalton tags (Dalton Ltd) (de Bruyn *et al.* 2008). Almost all weaned pups that were born on Marion Island from 1983 were double tagged in each of their hind flippers with a uniquely numbered, colour-coded Dalton jumbo tag (Pistorius *et al.* 2011).

Mark-recapture program

Since 1983, all hauled out elephant seals were checked for the presence of tags on all popular beaches along the coastline (Fig. 3.1) every 7 days during the breeding season (mid-August to mid-November) and every 10 days for the remainder of the year. Tagged individuals are documented (tag number and cohort specific colour; sex if known; haulout site) to compile life history data for each individual. During the breeding season, daily searches for weaned pups (abandoned by their mothers at weaning) were performed on all the beaches between Archway Beach and Ship's Cove (de Bruyn & Bester 2011, Fig. 3.1) to establish the exact date of weaning of each pup. All pups were physically weighed either immediately upon weaning or at earliest opportunity to the nearest 0.5 kg with a calibrated Salter 200 kg scale, using a weighing net and lifting pole.

Photogrammetry

Photogrammetry was performed with calibrated cameras on unrestrained adult females as described in de Bruyn *et al.* (2009). Eight or more photos were taken from different angles around a seal (subject) to form one project. Twenty-nine female seals ranging from 3 to 19 years of age were repeatedly photographed between September 2009 and November 2009. For each of the animals, photogrammetric (PG) projects were performed (1) upon their arrival for the breeding season, (2) post-partum and (3) immediately pre-departure for their subsequent post breeding pelagic foraging phase. Three-dimensional models (based on each of the

PG projects, (Fig. 3.2), were built using the de Bruyn *et al.* (2009) method for estimation of body mass.

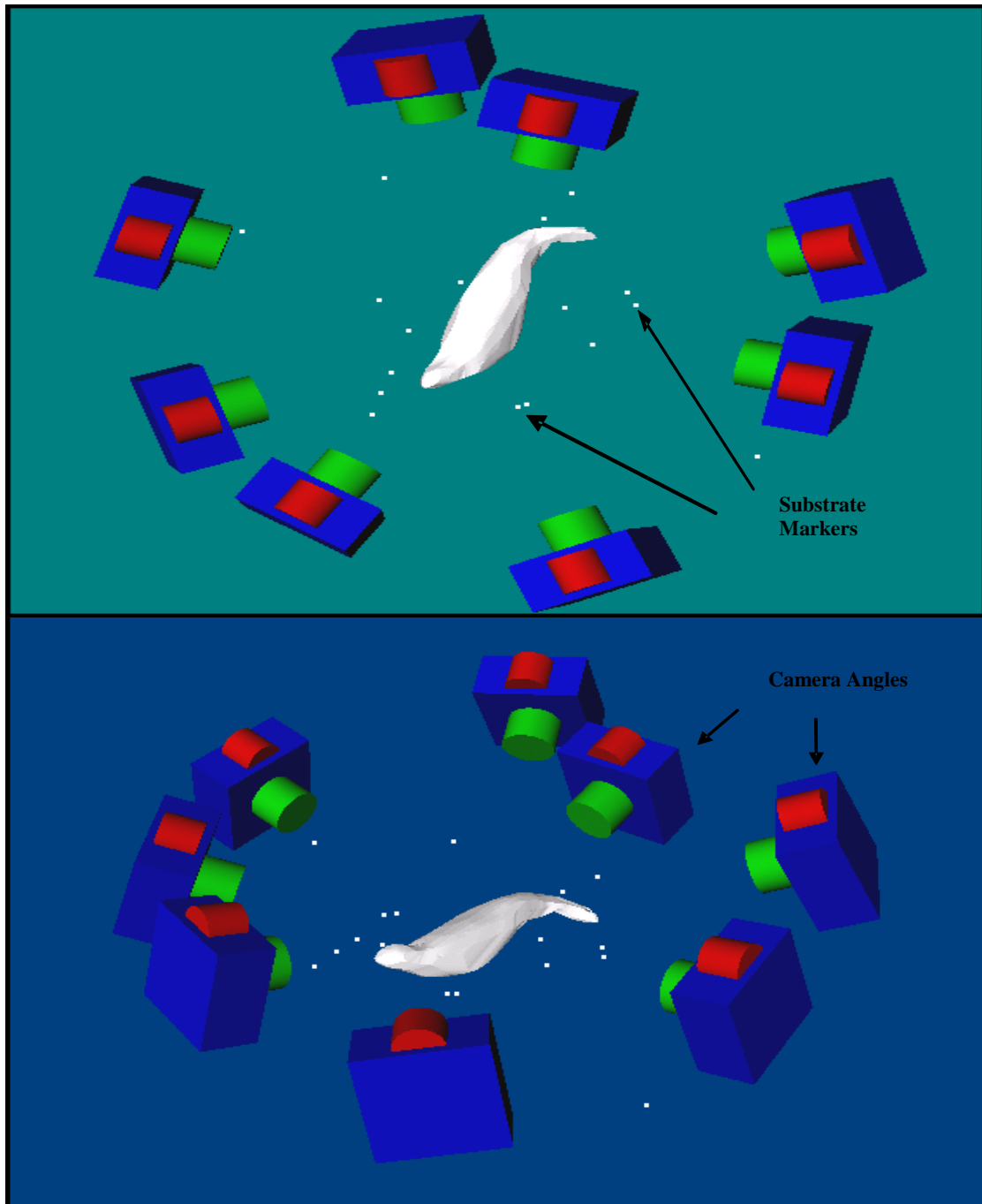


Figure 3.2. Photomodeler example: Three – dimensional model of a female southern seal used to estimate body mass. A (top view) indicate substrate markers; B (side view) indicates camera angles.

Photogrammetric analysis

Volumetric estimation procedures were executed using the commercially available 3-dimensional (3-D) modelling package Photomodeler Pro version 6.2 (de Bruyn *et al.* 2009). From the digital photographs, a 3-D spatial model was created using fixed points on the substrate around the animal; these were cross-referenced between photographs to create a 3-D space. The silhouette (outline) of the animal was traced on all the photographs and cross-referenced between photographs to shape the model of the subject. The volume of the animal's shape was multiplied by a coefficient that is contingent on the mean total body density, the nature of the substrate upon which the animal is resting, and the number of useable photographs in a project (Table 2. in de Bruyn *et al.* 2009) to obtain an estimate of body mass.

Calculation of date of birth, and pre- and postpartum mass

Daily observations along the coastal study area allowed determination of the exact weaning date for all pups, as well as the concomitant departure date for all mothers, in order to calculate the mean duration of suckling. Repeated daily observations allowed a linear time model to be created, from which we could calculate exact time of weaning and mother departure (the two are not always the same but mostly they are). This illustrates the presence of each individual and pup as well as the dates on which PG projects were performed. From this we used mean suckling duration, PG projects and census data to work backwards from weaning date to calculate the date of birth for each individual.

Pre- and post-partum PG projects were performed to assess birthing mass loss for all mothers (Fig. 3.3). Thirteen females were photographed on arrival, the remaining females' arrival mass was estimated by multiplying the calculated mean daily mass loss pre-partum for the 13 females with days elapsed between arrival and birth. Additionally, daily mass loss between post-partum PG and pre-departure PG

was calculated from 16 females that all had both a post-partum PG and a pre-departure PG. Where post-partum PG projects could not be done immediately following parturition, daily post-partum mass loss was multiplied with number of days between postpartum PG and date of birth to obtain estimated mass at the start of lactation (MAB). A mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson & van Aarde 2001) and a placenta mass of 3.5 kg (Arnbom *et al.* 1997) were added to estimate mass just before birth (MBB). If pup sex was unknown (n = 4), a mean value of 46kg was used. Twelve females were photographed on the day of departure, the remaining females' departure mass was estimated by multiplying the calculated mean mass loss per day (post-partum) with the days elapsed between departure and previous PG.

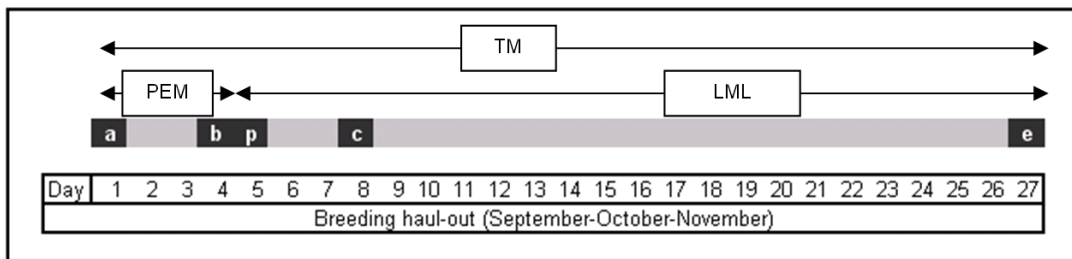


Figure 3.3. Visual representation of annual female life cycle: (TM) total mass loss in breeding haul-out, (PEM) Pre-partum mass loss, (LML) lactation mass loss, (a) breeding season arrival PG mass, (b) pre-partum PG mass, (c) post-partum PG mass, (d) days elapsed, (e) breeding season departure PG mass, (p) partum.

Breeding haulout equations

Pre-partum mass loss (PEM), lactation mass loss (LML) and absolute mass loss (TM) (Fig. 3.3) was calculated for each female using the following equations, where M = mass:

$$PEM = M_{arrival} - M_{pre_partum} \quad (1)$$

$$LML = M_{birth} - M_{departure} \quad (2)$$

$$TM = M_{arrival} - M_{departure} \quad (3)$$

Daily mass loss rates for the pre-partum period were calculated for animals that had arrival PG mass estimates ($n=13$) using the following equation:

$$PEM_{daily} = \frac{M_{arrival} - M_{pre_partum}}{no.days} \quad (4)$$

Daily mass loss rates for the post-partum period were calculated for animals with post partum and departure PG mass estimates ($n=16$) using the following equation:

$$LML_{daily} = \frac{M_{post_partum} - M_{departure}}{no.days} \quad (5)$$

In order to calculate the amount of mass loss as a result of parturition, the difference between mass directly after and before parturition was found. Daily mass loss rates were used to calculate the mass of female southern elephant directly after parturition seals using the following equation:

$$Mass_{after_birth} = M_{post_partum} + (no.days \times LML_{daily}) \quad (6)$$

Pup mass (Wilkinson *et al.* 2001) and placenta (Arnbom *et al.* 1997) was added to mass estimates obtained from equation 6 to obtain mass estimates directly before birth. Birth mass was set as a constant mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson *et al.* 2001). If no post-partum PG mass estimates were available, mass directly before birth was estimated from arrival PG mass estimates as:

$$Mass_{before_birth} = M_{arrival} - (no.days \times PEM_{daily}) \quad (7)$$

If mass before birth was obtained as described in equation 7, pup mass (Wilkinson *et al.* 2001) and placenta (Arnbom *et al.* 1997) was subtracted to obtain mass after birth.

Statistical analysis

The program R (R Development Core Team 2011) was used for statistical analysis. Packages used; Linear mixed-effects models using Eigen and syntax (lme4) (Bates, Maechler & Bolker, 2011), Multi-model inference (MuMIn) (Bartoń 2011), An implementation of the Grammar of Graphics (ggplot2) (Wickham 2009), Companion to Applied Regression (car) (Fox & Weisberg 2011). Shapiro-Wilks test was used to test for normality. Normally distributed datasets were compared using single and multiple linear regression models and a general linear model with mixed effects was used to assess pup survival. Significance was set at $P = 0.05$

Pup survival

Pup survival was determined by investigating census data for the pups' first year of life. Pups that survived their first foraging trip and successfully returned to Marion Island were considered. As females have a single pup each year and the study includes data from 2006, 2007 and 2009, independence did not hold and a simple linear regression model could not be used. A generalized linear model with a mixed effects approach was implemented.

Female arrival and departure mass

I tested for the influence of age on arrival and departure mass, in southern elephant seal mothers using the 2009 data only, as intensive breeding photogrammetry only commenced in 2009. Linear regression was used to compare female breeding season arrival mass to female age, and departure mass was similarly compared to age. Shapiro-Wilks and Durbin-Watson tests were performed, normality and independence was found to be present. Constant error variance was checked with a Breusch-Pagan test, and was found to be present.

Results

Sample trends

Female southern elephant seals ($n=29$), (range: 3 to 19 years of age) present during the 2009 breeding season haul-out were photographed and their pups weighed at weaning. Daily mass loss was calculated for the pre-partum (mean = 3.68 kg/d) and post-partum (mean = 7.55 kg/d) phases for mothers. Female's arrival mass ranged from 366.89 kg to 685.95 kg (mean = 525.05kg \pm 70.85 kg) and female departure mass ranged from 191.79 kg to 460.10 kg (mean = 296.65 \pm 52.62 kg). Mass of mothers immediately pre-partum ranged from 357.08 kg to 660.17 kg (mean = 509.39 \pm 71.92 kg). Maternal mass immediately post-partum, ranged from 308.08 kg to 611.17 kg (mean = 463.89 \pm 72.41 kg). Absolute mass loss ranged from 147.78 kg to 308.52 kg (mean = 222.06 \pm 34.31 kg). Percentage mass loss ranged from 32.92% to 53.21% (mean = 42.29 \pm 4.58%). Minimum and maximum pup weaning mass were 73 kg and 160 kg respectively with a mean of 120 \pm 20.46 kg.

Pup weaning mass for 2009 breeding haul-out

To establish which variables were significant in pup weaning mass, a multiple linear regression model was performed. Shapiro-Wilks and Durbin-Watson tests were performed, assuming normality and independence. Constant error variance was checked with a Breusch-Pagan test, and was shown to be present. Co-linearity between variables was present between two variables (age and total number of pups produced per female). Model fit was assessed by plotting the residuals against the fitted values and Akaike Information Criteria (AIC; Table 3.1) was used for model selection (Burnham & Anderson 2002). Female mass loss and age were used as variables and the number of pups a female had produced in her lifetime was eliminated from the final model as it was found to be non-significant and co-linear with female age. From the multiple linear regression model, female mass loss was found to be significant with ($P < 0.01$) as well as female age ($P < 0.01$) with an

adjusted R -squared value of 0.448. Female age and mass loss variables seem to be biologically linked. Furthermore, female age and mass loss combined, accounted for 45% of variation in relative mass gain in southern elephant seal pups.

Table 3.1. Model selection table for multi linear regression produced in the statistical analysis program R. Variables include female age (age), female mass loss (f..) and number of pups produced (pp.). Variables were removed and AIC values compared. The first model including age and female mass loss was most parsimonious.

Model selection table												
	(Int)	age	f..	pp.	k	R.sq	Adj.R.sq	RSS	AIC	AICc	delta	weight
5	42.51	2.2590	0.2511		4	0.4875	0.4481	6074	245.3	247.0	0.0000	0.469
7	52.28		0.2220	3.692	4	0.4744	0.4340	6230	246.0	247.7	0.7326	0.325
8	45.24	1.6720	0.2411	1.069	5	0.4897	0.4285	6048	247.2	249.8	2.8180	0.115
4	99.71			4.707	3	0.3380	0.3135	7846	250.7	251.7	4.7160	0.044
2	96.90		2.7150		3	0.3014	0.2755	8280	252.3	253.2	6.2780	0.020
3	45.63	0.3055			3	0.2880	0.2616	8439	252.8	253.8	6.8290	0.015
6	99.06	0.3686		4.148	4	0.3388	0.2880	7837	252.7	254.3	7.3880	0.012
1	115.60				2	0.0000	0.0000	11850	260.7	261.1	14.1800	0.000

Absolute female mass loss

Absolute mass loss of a mother during the breeding season haul-out phase equates to maintenance mass loss plus mass transferred to her offspring. The single linear regression model which was performed to establish the influence of female age on absolute mass loss during the course of the breeding season returned values $P = 0.276$ and $R^2 = 0.008$ (Fig. 3.4). Shapiro-Wilks and Durbin-Watson tests showed that normality and independence were present, as well as constant error variance (Breusch-Pagan test). No significant difference over female age gradient was apparent in absolute mass loss over the course of the breeding haul-out. Females lose a mean of 222.06 ± 34.31 kg.

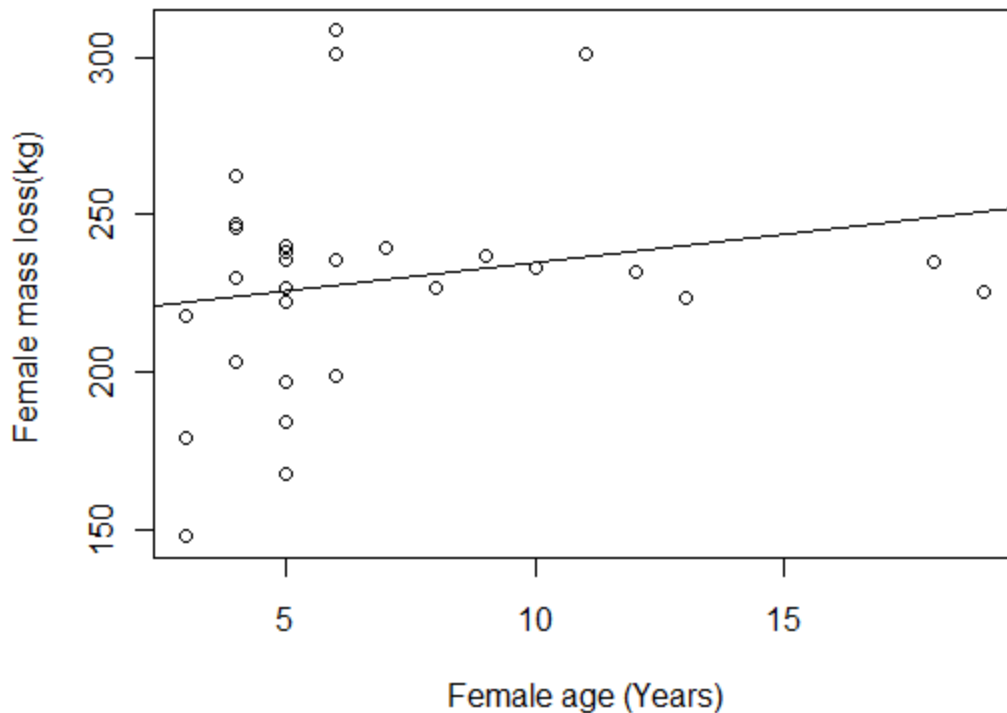


Figure 3.4. Southern elephant seal 2009 breeding season mass loss compared to female age. ($P = 0.276$) with and adjusted (Is more accurate goodness of fit than R square) ($R^2 = 0.008$).

Percentage female mass loss

Percentage mass loss over the duration of the breeding haul-out ranged from 32.92% to 53.21% with a mean of $42.29 \pm 4.58\%$. A single linear regression model established the relationship between age and percentage mass loss for females during the course of the breeding season with ($P = 0.00347$) and adjusted $R^2 = 0.25$ (Fig. 3.5). Shapiro-Wilks and Durbin-Watson tests indicated normality and independence for the 2009 dataset. Constant error variance was also present (Breusch-Pagan test). Female age accounted for 25 % of observed variation in relation to percentage mass loss in southern elephant seals.

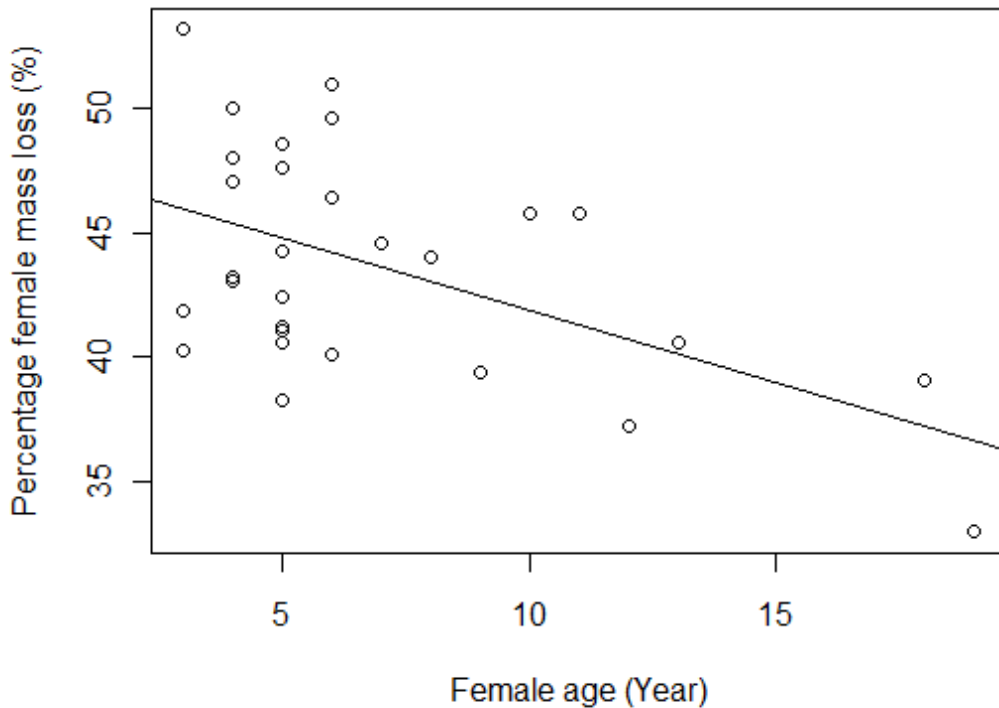


Figure 3.5. Female southern elephant seal percentage mass loss compared to female age ($P = 0.00347$) and adjusted R square (Is more accurate goodness of fit than R square) ($R^2 = 0.25$).

Female arrival and departure mass

Female arrival mass greatly influenced the female's post-breeding departure mass. Furthermore, age accounted for 45% of variation in female breeding haul-out variation and 63% of post breeding departure mass. Arrival mass was significantly influenced by female age, ($P < 0, 0001$ and $R^2 = 0.4487$) (Fig. 3.6) and departure mass was similarly influenced ($P < 0.0001$ and $R^2 = 0.6284$) (Fig. 3.7).

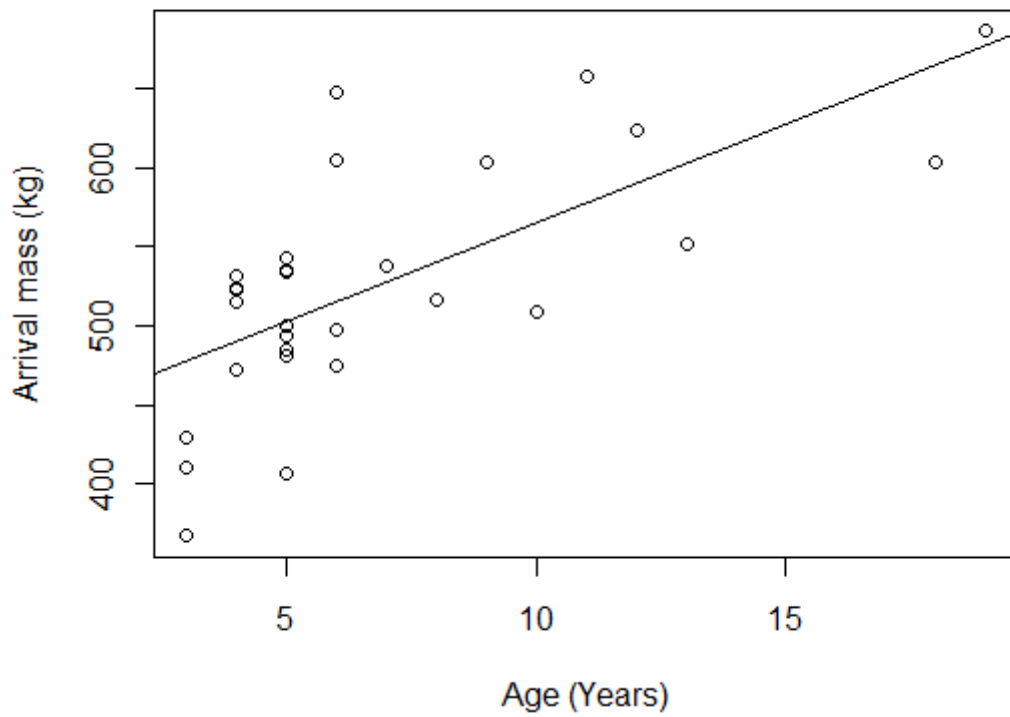


Figure 3.6. Female southern elephant seal breeding season arrival mass compared age, ($P < 0, 0001$) with and adjusted R square (Is more accurate goodness of fit than R square) ($R^2 = 0.4487$).

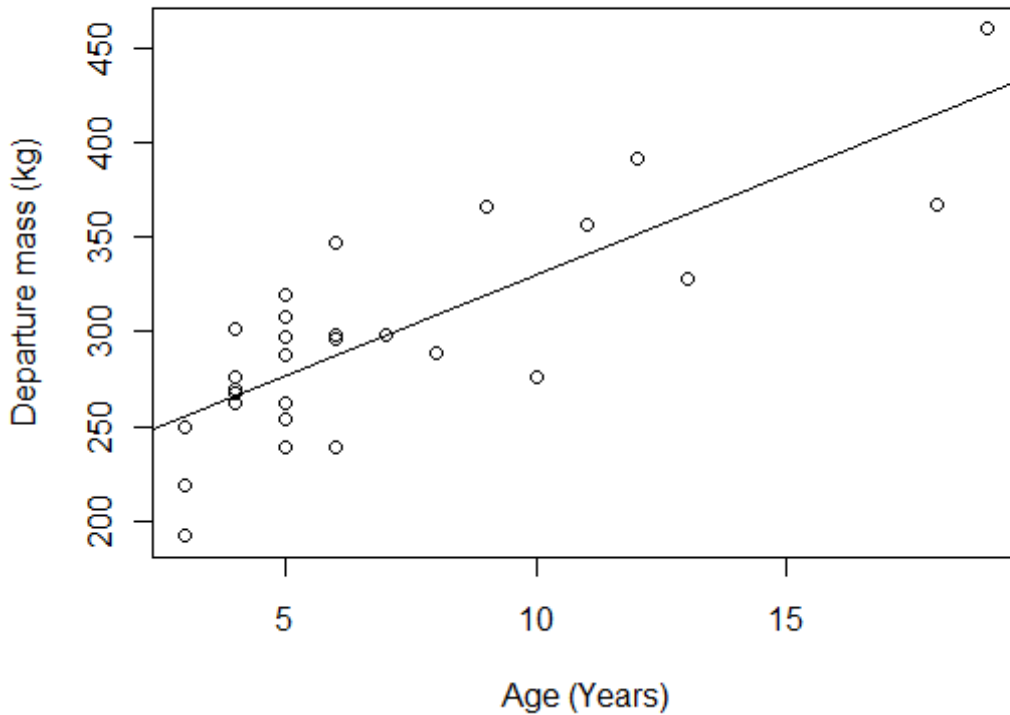


Figure 3.7. Female southern elephant seal breeding season departure mass compared to age, $P < 0.0001$ with an adjusted $R^2 = 0.6284$ (Is more accurate goodness of fit than R square).

Pup survival

Intensive photogrammetry to estimate female absolute mass loss, percentage mass loss, arrival mass and departure mass (de Bruyn *et al.* 2009) only commenced in 2009 and thus only one year of pup weaning mass could be incorporated in the analyses. As the 2009 sample size was too small to estimate survival and a larger dataset was required, the 2006 and 2007 data were included, without considering female mass in all its different aspects for that year, however mother pup relation was known for all females. 2008 data was not available as weaner weighing was absent during that year.

Females ($n=79$) from the 2006, 2007, 2009 data ranged from 3 to 19 years of age, while the number of pups born to each of these females during their lifetime ranged from 1 to 9. Mother pup relation was known for all weighed pups. Pups were not split in to sexes as previous studies e.g. (McMahon *et al.* 1999) indicate no difference in survival between sexes. Pup weaning masses ranged from 68.42 kg to 160.60 kg with a mean of 115.24 ± 20.62 kg. Thirty-six of the pups born in the sample were female and 40 were male, while 3 were of unknown sex. Female age and number of pups born to each female were eliminated from the model as non-significant variables, based on model fit, assessed by plotting the residuals against the fitted values and Akaike Information Criteria (AIC; Table 3.2.) was used for model selection (Burnham & Anderson 2002). Leaving only pup weaning mass as a sufficient explanatory variable. Weaned pup mass has a significant influence on pup survival ($P < 0.01$). Pup weaning mass accounted for 4% of variation observed in survival to the end of the first foraging trip.

Table 3.2. Model selection table for generalized linear model with a mixed effects approach produced in the statistical analysis program R. Variables include female age (Age), Pup mass (Pp.) and number of pups produced (Pp..1.). Variables were removed and AIC values compared. The first model included Pup mass and was most parsimonious.

Model selection table										
	(Int)	Age	Pp.	Pp..1	k	Dev.	AIC	AICc	delta	weight
3	-3.8080		0.03858		3	96.75	102.8	103.1	0.000	0.329
7	-3.1000		0.02812	0.1606	4	95.77	103.8	104.3	1.231	0.178
4	-0.3232			0.3022	3	98.37	104.4	104.7	1.615	0.147
5	-3.5020	0.05994	0.03244		4	96.38	104.4	104.9	1.846	0.131
2	-0.4657	0.16020			3	99.78	105.8	106.1	3.024	0.072
8	-3.0230	-0.09098	0.02929	0.2907	5	95.53	105.5	106.4	3.278	0.064
6	-0.2362	-0.04058		0.3625	4	98.32	106.3	106.9	3.785	0.050
1	0.5880				2	103.60	107.6	107.8	4.711	0.031

Discussion

A decline in the numbers of a population that is not subjected to emigration or immigration can be attributed to their reproductive and/or survival success (York 1994). The general model for self regulation in long lived species suggest that regulation is driven by variation in juvenile mortality, the age of first reproduction and the rate of adult female reproduction (Eberhardt 1977). Population growth rates in large mammals appear to be influenced more by their ability to survive than their fecundity (Choquenot 1991; Lima & Páez 1997; Saether 1997).

Many mammals with seasonal life cycles, including southern elephant seals, have predictable changes in their metabolic rate, mass and body condition (Ashwell-Erickson *et al.* 1986; Rosen & Renouf 1998; Fitzgerald & McManus 2000). Their predictable seasonal haul-outs are dependent on mass gain during their pelagic foraging phases while sufficient stored mass is necessary to survive terrestrial haul-outs. The arrival mass of females for the breeding season is vital for successful pup production as maternal expenditure is limited to this initial amount (Laws 1953; Fedak & Anderson 1982; Costa *et al.* 1986; Kovacs & Lavigne 1986; Fedak *et al.* 1994; Arnboom 1994; Fedak *et al.* 1996; Trillmich 1996; Arnboom *et al.* 1997; Hindell & Slip 1997). Their reserves should be adequate to successfully wean their pups and serve to sustain themselves for the duration of the haul-out. Additionally, sufficient reserves should remain to aid post-breeding individuals back to their pelagic feeding grounds.

Absolute mass loss during a breeding season in adult females at Marion Island does not differ significantly between age classes. Marion females lose 222.06 ± 34.31 kg over the course of a breeding season. Age and size differ significantly among individuals, but absolute mass loss does not follow the same trend which suggests that percentage mass loss must differ significantly. Females lost 40% of their body mass from the beginning to the end of the breeding season at South

Georgia (Arnbom *et al.* 1997) with females from Marion Island losing a mean of 43% over the course of the breeding season (present study). Females that lose a large percentage of mass are younger and smaller animals ranging from 3 to 6 years of age (Fig. 3.4) or have an arrival mass between 375 kg and 525 kg (Fig. 3.5). Thus, females that are older are bigger, have more reserves remaining and are in better condition at the conclusion of the breeding season than younger females. Not all females between 3 and 6 years of age have a percentage mass loss higher than the mean. Variance in body size between individuals of the same age class could be responsible. Heavier departure mass could leave females in better condition the following year.

Pup weaning mass

Female breeding season mass loss was obtained by an accurate photogrammetric technique (de Bruyn *et al.* 2009). Female mass loss, age and previous breeding success (enumerated as number of pups successfully weaned in their lifetime) were used as determining variables for pup weaning mass. Previous breeding success was identified as a co-linear factor as well as a non-significant variable (Table 3.1). Pup weaning mass does increase with the mother's age ($R^2 = 0.4481$). Younger females are smaller at arrival (Fig. 3.5) and at departure (Fig. 3.6) than older females. Smaller size implies fewer reserves for breeding haul-out. Reduced reserves in younger females can lead to two outcomes, (1) pups gain less mass which reduces survival probability in first pelagic foraging trips, (2) female reserves reach a critical threshold, where her own survival and reproduction could be compromised. Here I focus on the former (pup survival in relation to limiting factors), female mass loss and female age. The latter (female survival and reproduction) could not be adequately assessed through lack of photographed females in consecutive years at this initial stage of the study.

Percentage mass loss is significantly influenced by female age. Younger females lose a larger percentage of mass than older females. Figure 3.4 emphasizes the fact that percentage of energy expended between females differs according to age. Older females which utilize less mass relative to their size would have more reserves for their own metabolism. The difference between small and large females is even greater if I take into account that some body fat and proteins are structural, and to use these for lactation could be detrimental to the viability of the female (Fedak *et al.* 1996). It seems doubtful that small females can spend the calculated average amount of energy without any consequences to them or their offspring. The small numbers of 3 year old females in the sample could be due to the majority of this female age class gaining insufficient mass to breed and are therefore absent (Pistorius *et al.* 2011). This supports the fact that phocid seals must acquire a critical body size to achieve sexual maturity and mass plays an important role in their reproductive potential (Laws *et al.* 1956; Arnboom *et al.* 1994).

Pup birth mass was obtained from Fedak *et al.* 1996 as it was not possible to physically weigh pups at birth. Although these values were obtained from a different population of southern elephant seals, the effect is not significant as it was used as a constant and pup mass gain was not assessed in this study. Lower weaning mass of pups from 3 year old females (mean = 81.67 ± 7.76 kg) compared to 4 year old pup weaning mass (mean = 117.40 ± 24.14 kg) supports this hypothesis, as the main contributors to pup mass are the females' age and mass loss. This supports Pistorius *et al.* (2004) in that with the delay of onset of reproduction results in females being in better condition and able to reproduce pups that are larger. Delaying the onset of reproduction by a year in order to invest in growth rather than reproduction (Reiter & Le Boeuf 1991) may therefore increase the probability of survival of the offspring (Pistorius *et al.* 2004). Conversely, the smaller size of younger females with less absolute weight may negatively influence their pup survival and weaning mass.

Pup survival

The limited availability of terrestrial breeding sites in the oceans force seals to aggregate at limited sites (Cassini 1999). Females show fidelity to these sites in the Southern Ocean although this may vary according to their breeding performance (Switzer 1997; McMahon & Bradshaw 2004). Marked animals rarely permanently emigrate from Marion Island and are therefore not lost for potential future recapture (Oosthuizen *et al.* 2010; Pistorius *et al.* 2011). This assumption is important for survival estimates of weaned pups. I can thus confidently assume that if an animal does not return in two years after birth, it is unlikely to have survived.

A key aspect that has not previously been linked to pup survival is female age. According to Pistorius *et al.* (2001), pre-weaning pup mortality at Marion Island is higher at smaller harems, which contain many smaller inexperienced females giving birth for the first time. Similarly first year mortality rate is higher for pups that are born from younger females (present study). Southern elephant seal pups that survive their first year at sea are on average 4% heavier at weaning than the non survivors (McMahon *et al.* 2000). At Marion Island first year survival also increased 4% with increased weaning mass (present study). The significant difference between the studies is that the exact female age at Marion Island can be positively correlated to pup weaning mass.

Pup weaning mass was influenced by female mass loss and age ($R^2 = 0.448$) in the 2009 dataset. A larger weaning mass would imply that pups have a larger reserve for development in the post-weaning phase. Phocid pups are advanced in development; their large birth size and fast growth are advantages to thermoregulation (Kovacs & Lavigne 1986; Worthy 1987) and supposed survival benefits at sea. As with other mammals, the first year of their life is a critical growth period for phocid seals as pups must grow rapidly during the short suckling period to

obtain adequate blubber for thermoregulation (Bryden 1969) and for the following protracted post weaning phase (Worthy & Lavigne 1983). During their post weaning phase pups mature and simultaneously lose mass, up to 30% of their weaning mass in southern elephant seal pups at Marion Island (Wilkinson & Bester 1990). It has been shown in northern elephant seals that this phase is crucial for the development of their ability to store oxygen and lower their metabolic rates to improve diving abilities (Thorson & Le Boeuf 1994). Southern elephant seal pups have a differential growth order of fat, bone and then muscle (Bell *et al.* 1997). Muscle growth for pups attains its maximum rate once pups are at sea (Bryden 1969). Sufficient amount of fat is necessary for development of bone and muscle. Thus, heavier pups could undergo a protracted period before departing their birth sites for the first time and develop their diving capabilities better, but ultimately deplete their reserves more (Arnbom *et al.* 1993). Therefore, pups that have a heavier weaning mass should be more developed both in their diving ability and muscle development and can survive longer do develop to improve foraging ability this conceivably significantly influence pup survival. Adequate blubber must be available as an energy source to rapidly develop swimming and foraging skills in their aquatic environment (Worthy & Lavigne 1983; Thorson & Le Boeuf 1994). Smaller pups at weaning have fewer reserves to rely on and depart from breeding sites at an earlier date than pups with a larger weaning mass, the underlying ability to fast be determined by available energy stores (Wilkinson & Bester 1990).

In conclusion, photogrammetry proves to be a useful and accurate tool to obtain size/mass data with minimal disturbance over a temporal scale. As the specific age of all females used in the study are known from tag resights, the female mass loss, size and pup survival could be linked to age (this study) and not simply estimates of age according to size (Fedak *et al.* 1996). The first-year survival of pups is positively linked to their weaning mass. Weaning mass is in turn positively related

to female age and mass loss. Older and larger females have larger pups that have a greater probability of surviving their first foraging trip. Pups that are born from young females or females that do not gain sufficient mass prior to breeding season do have a lower probability of survival than pups that are born from older and larger females.

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CHAPTER FOUR

BODY MASS DISPARITY AS A RESULT OF DIFFERENT BREEDING

STRATEGIES IN FEMALE SOUTHERN ELEPHANT SEALS

Abstract

Energy storage is an important component causing variation in life-history; females can alter their behaviour in response to the energy demands for reproduction. The response can be seen in the mass loss/gain of individual females. An extreme example is capital breeding marine mammals such as the southern elephant seal. Southern elephant seals adhere to specific annual terrestrial phases (breeding and moulting) interspersed by long periods of pelagic foraging. Sufficient mass gain at sea is necessary for successful return to and completion of terrestrial phases. Mass loss/gain is a good indicator of the cost of reproduction. Calculation of mass loss by photogrammetry during terrestrial phases allows for assessment of individual haulout and foraging success. Annually interrupted breeding is more common than previously thought in female southern elephant seals at Marion Island. Lower resources could lead to differing long-term breeding strategies in female southern elephant seals. Significant mass differences are shown between females that breed annually and females with interrupted breeding cycles. Mass gain during post-breeding foraging trips for females with an annual breeding strategy is only marginally sufficient to sustain them metabolically for the duration of the subsequent moult haulout. Resource limitation may dictate energy budget, resulting in different breeding strategies. Females that exhibit interrupted breeding have greater mass at critical stages in their annual life cycle, which could be beneficial to future survival of females and successful weaning and survival of their offspring.

Introduction

The most important strategy in the life of mammals is to produce offspring and thereby propagate the species (Weir *et al.* 1973). Females of a species bear the cost of reproduction through gestation and maternal care of offspring (Cripps *et al.* 2011). Life history theory predicts a trade off between mass and reproduction when resources are limited and how resources are allocated to reproduction by an animal to maximize fitness (Roff 1992; Stearns 1992; Roff 2002). Energy storage is an important component in variation of life-history (Houston *et al.* 2006). Previous models (Boyd 1998; Trillmich & Weissing 2006) and correlative approaches (Boyd 2000) support the hypothesis that body mass has a probable strong influence on female breeding strategies. In general organisms may use two different breeding strategies (income or capital breeders) each with its advantages and disadvantages in resource and energy costs (Ingemar *et al.* 1997). Mass loss and gain have been used to indicate cost of reproduction from birds (Hussell 1972; Askenmo 1977; Bryant 1979; De Steven 1980; Nur 1984) to mammals (Arnbom 1994; Fedak *et al.* 1996; Carlini *et al.* 1997; Pistorius *et al.* 2004; 2008). Females can alter their behaviour in response to the energy demands for reproduction (Cripps *et al.* 2011). I propose that variation within a species that exhibits distinct breeding strategies can be influenced by an insufficient amount of resources and will be evident in individual mass differences. I test this hypothesis by monitoring the body mass of southern elephant seal females that breed annually as opposed to those that skip breeding seasons.

Southern elephant seals (*Mirounga leonina*) are circumpolar Southern Ocean predators (Laws 1977) and are dependent on terrestrial sites (mostly sub-Antarctic Islands) for the breeding and moult phases of their annual cycle (Kirkman *et al.* 2003, 2004). The moult is obligatory and both moulting and breeding elephant seals fast completely (Arnbom *et al.* 1997).

Marion Island (46°54'S, 37°45'E), one of the two islands in the Prince Edward Islands archipelago, is situated in the Southern Indian Ocean approximately 2,180 km southeast of Cape Town and is under South African jurisdiction. The island encompasses an area of 300 km² with a coastline of approximately 100 km (Meiklejohn & Smith 2011). The coastline consists mainly of cliffs with pebble beaches on the eastern side of the island where elephant seals predominantly haul out (Condy 1978).

During the breeding season in the austral spring, adult females haul out for approximately 30 days where 21-23 days are spent suckling their pups (Bell *et al.* 2005). They fast throughout this period, relying exclusively on stored fat reserves for lactation (Arnbom *et al.* 1997). After breeding, females make a post-lactation trip to sea, lasting a mean of 72.6 ± 5.0 days (Le Boeuf 1994), to regain their mass before returning to shore for the annual obligatory moult (Boyd *et al.* 1993; Le Boeuf 1994). The moult of *Monacine* seals (elephant seals and monk seals) is a unique phase amongst pinnipeds as it involves shedding and replacing the hair and top layer of epidermis (Ling 1970). Female southern elephant seals remain ashore for 30 days and males for 50 days during the moult phase, after which they depart for post-moult foraging before returning for the next austral spring (Kirkman *et al.* 2003; 2004).

The characteristic lactation pattern of phocid seals implies that females have to produce energetically rich milk within a short suckling period, which poses the problem of pupping and nursing that are spatially separated from foraging (Bonner 1984; Oftedal *et al.* 1987). This lactation pattern depletes an important proportion of females' reserves (Carlini *et al.* 1997). Regaining a proportion of this lost mass in the post breeding foraging phase is crucial to facilitate the subsequent terrestrial moult haulout phase.

Given that many marine mammals display seasonal energetic priorities (Rosen *et al.* 2008), it is important to investigate these needs. The knowledge of energy and food requirements of southern elephant seals is of great importance for assessing the potential impact that a change in food abundance could proximally have on individual survival and fecundity, and thus ultimately on population size and species distribution (Carlini *et al.* 2005). Consequently, females not acquiring sufficient energy and food may have trouble in sustaining themselves during the following haulouts, be it breeding or moulting. Furthermore, contrary to the previously held assumption that female southern elephant seals breed (pup and mate) annually (e.g. Laws 1956; Hindell 1991; Wilkinson 1991; Le Boeuf & Laws 1994; Pistorius *et al.* 2001, 2004, 2008; McMahon *et al.* 2003, 2005, 2009; de Bruyn 2009), de Bruyn *et al.* (2011) showed that interrupted breeding is more common in southern elephant seal females at Marion Island. A sound understanding of the underlying mechanisms is needed to appreciate the evolution of such breeding strategies. To this end I formulate the following questions to assess metrics of body mass at critical stages in the annual life cycle of females with continuous breeding schedule and those with interrupted breeding schedule:

- 1) Do females regain the body mass lost during the terrestrial breeding fast, in the subsequent post-breeding foraging phase?
- 2) Is the body mass of a post-partum female at completion of the breeding fast comparable to that at the end of the subsequent terrestrial moult fast?
- 3) Do females that breed annually differ in mass at the subsequent terrestrial haulout compared to females that were absent during the breeding season?
- 4) Are there consistently different life history breeding strategies in female southern elephant seals?

Methods

Photogrammetry of elephant seal females in the breeding haulout was mainly done on beaches between Ship's Cove and Archway Bay on the eastern aspect of the island (Fig. 4.1). Females chosen for this study were all known-aged (tagged) animals. Upon returning to the Island, the same females were sought out from all the beaches around the Island (Fig. 4.1) and repeatedly photographed on each occasion.

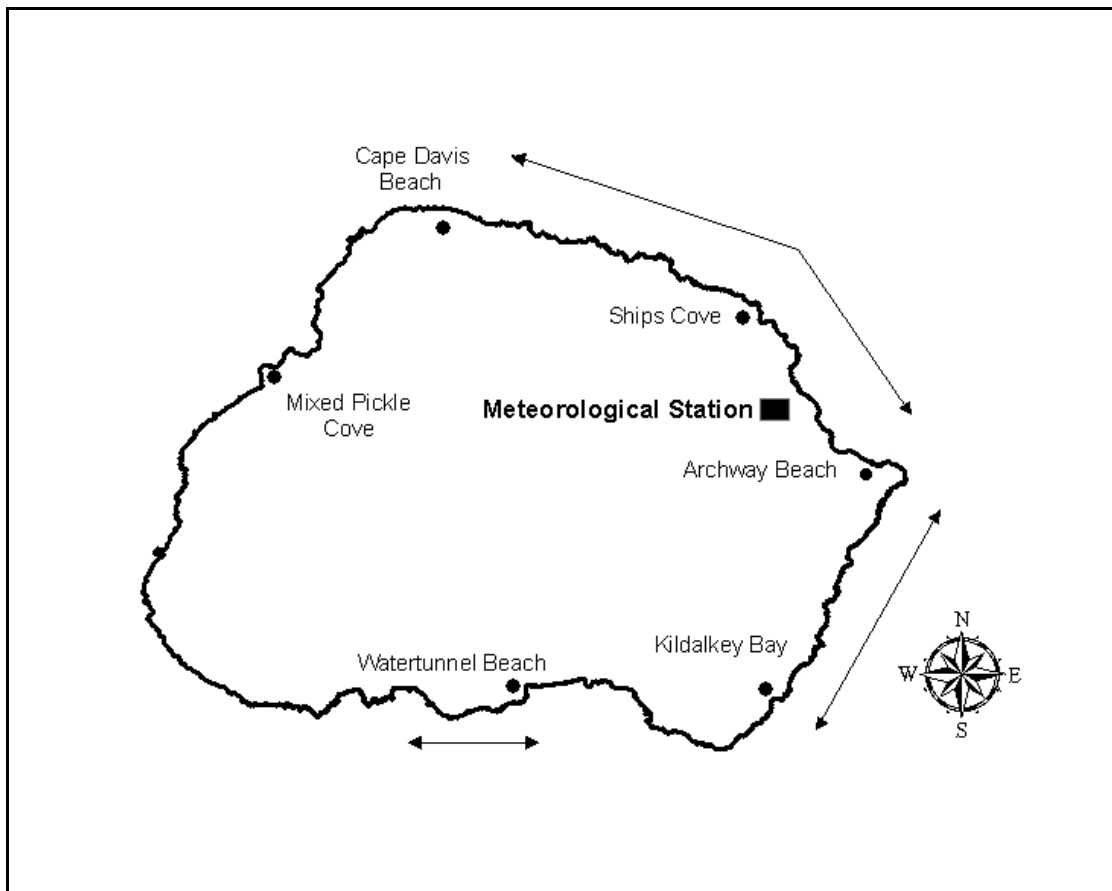


Figure 4.1. Marion Island: Breeding period photogrammetry was performed between Ships Cove and Archway Bay, but at all beaches during the moult. The search for tagged seals along the coastline on all the beaches, indicated with arrows, were conducted every 7 days during the breeding season (mid-August to mid-November) and every 10 days from mid-November to the following mid-August since 1983.

Pup tagging

Almost all weaned pups born on Marion Island were double tagged in each of their hind flippers with a uniquely numbered, colour-coded Dalton jumbo tag (Dalton supplies Ltd, Hendley-on-Thames, U.K; http://www_dalton.co.uk/products/pages_pr/research/r_jumbo.htm) (for further details see de Bruyn *et al.* 2008).

Mark-recapture program

Since 1983, all hauled out elephant seals were checked for the presence of tags on all popular beaches along the coastline (Fig. 4.1) every 7 days during the breeding season (mid-August to mid-November) and every 10 days for the remainder of the year. Tagged individuals are documented (tag number and cohort specific colour; sex if known; haulout site) to compile life history data for each individual. During the breeding season, daily searches for weaned pups (abandoned by their mothers at weaning) were performed on all the beaches between Archway Beach and Ship's Cove (de Bruyn & Bester 2010, Fig. 4.1) to establish the exact date of weaning of each pup.

Photogrammetry

Photogrammetry was executed with calibrated cameras on unrestrained adult females as described in de Bruyn *et al.* (2009). Eight or more photos were taken from different angles around a seal (subject) to form one project. Twenty-three female seals ranging from 3 to 18 years of age were repeatedly photographed between September 2009 and February 2010. For each of the animals, photogrammetric (PG) projects were performed (1) upon their arrival for the breeding season, (2) postpartum and (3) immediately pre-departure for their subsequent post breeding pelagic foraging phase. Secondly, in the austral summer, photogrammetric projects were done during the moult, following the post-breeding season foraging trip:

(1) pre-moult (or when animals were first sighted) and (2) post-moult, prior to seals departing for their post-moult pelagic phase. Additional photogrammetry projects were done upon deployment of satellite-linked data loggers on adult (known-aged) animals and whenever these females hauled out in the period 2008 to 2010. Three-dimensional models (based on each of the PG projects) (Fig. 4.2) were built using the de Bruyn *et al.* (2009) method for estimation of body mass.

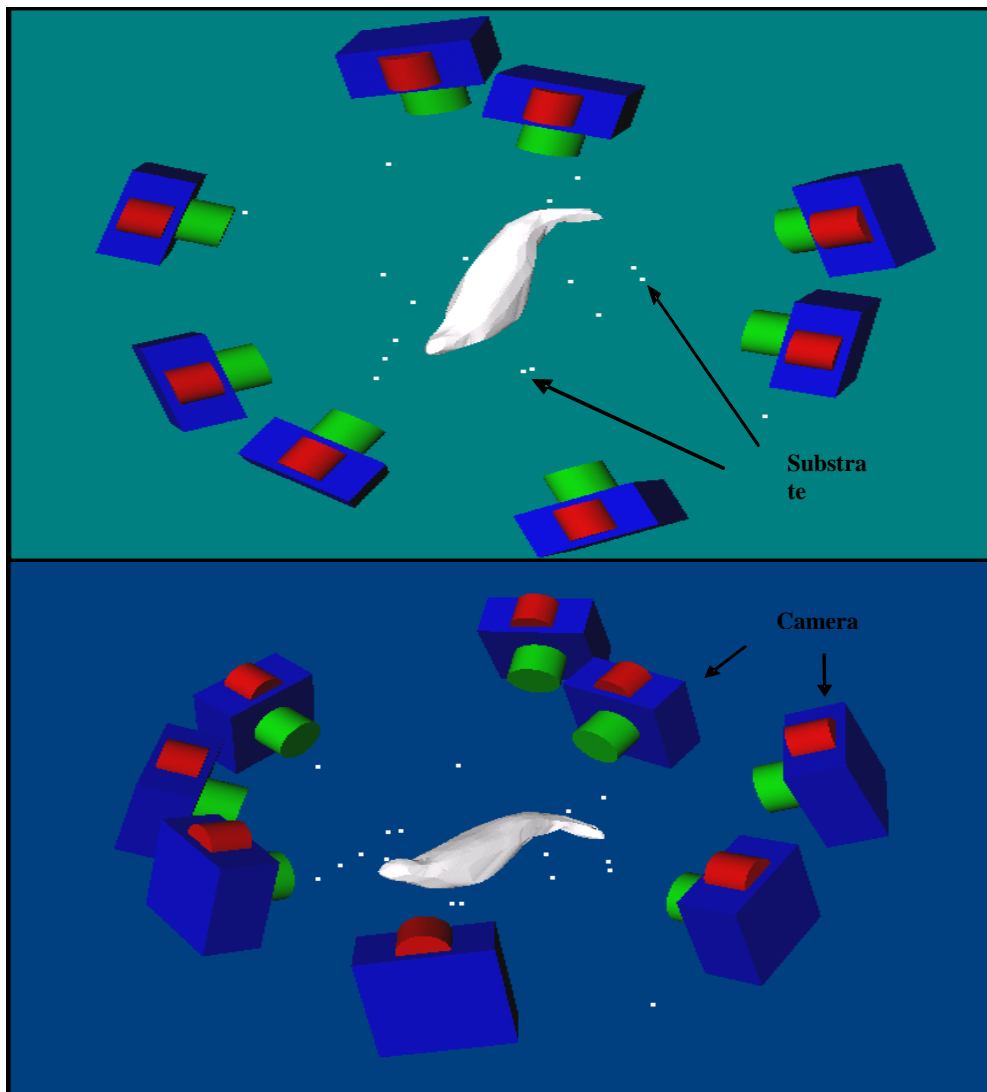


Figure 4.2. Photomodeler example: Three – dimensional model of a female southern seal used to estimate body mass. A (top view) indicate substrate markers; B (side view) indicates camera angles.

Photogrammetric analysis

Volumetric estimation procedures were executed using the commercially available 3-dimensional (3-D) modelling package Photomodeler Pro version 6.2 (de Bruyn *et al.* 2009). From the digital photographs, a 3-D spatial model was created using fixed points on the substrate around the animal; these were cross-referenced between photographs to create a 3-D space. The silhouette (outline) of the animal was traced on all the photographs and cross-referenced between photographs to shape the model of the subject. The volume of the animal's shape was multiplied by a coefficient that is contingent on the mean total body density, the nature of the substrate upon which the animal is resting as well as the number of photographs in a project (Table 2 in de Bruyn *et al.* 2009) to obtain an estimate of body mass.

Calculation of date of birth, and pre- and postpartum mass

Daily observations along the coastal study area allowed determination of the exact weaning date for all pups, as well as the concomitant departure date for all mothers, in order to calculate the mean duration of suckling. Repeated daily observations allowed a linear time model to be created, from which we could calculate exact time of weaning and mother departure (the two are not always the same but mostly they are). This illustrates the presence of each individual and pup as well as the dates on which PG projects were performed. From this we used mean suckling duration, PG projects and census data to work backwards from weaning date to calculate the date of birth for each individual.

Pre- and post-partum PG projects were performed to assess birthing mass loss for all mothers (Fig. 4.3). Thirteen females were photographed on arrival, the remaining females' arrival mass was estimated by multiplying the calculated mean daily mass loss pre-partum for the 13 females with days elapsed between arrival and birth. Additionally, daily mass loss between post-partum PG and pre-departure PG

was calculated from 16 females that all had both a post-partum PG and a pre-departure PG. Where post-partum PG projects could not be done immediately following parturition, daily post-partum mass loss was multiplied with number of days between postpartum PG and date of birth to obtain estimated mass at the start of lactation (MAB). A mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson & van Aarde 2001) and a placenta mass of 3.5 kg (Arnbom *et al.* 1997) were added to estimate mass just before birth (MBB). If pup sex was unknown ($n = 4$), a mean value of 46kg was used. Twelve females were photographed on the day of departure, the remaining females' departure mass was estimated by multiplying the calculated mean mass loss per day (post-partum) with the days elapsed between departure and previous PG.

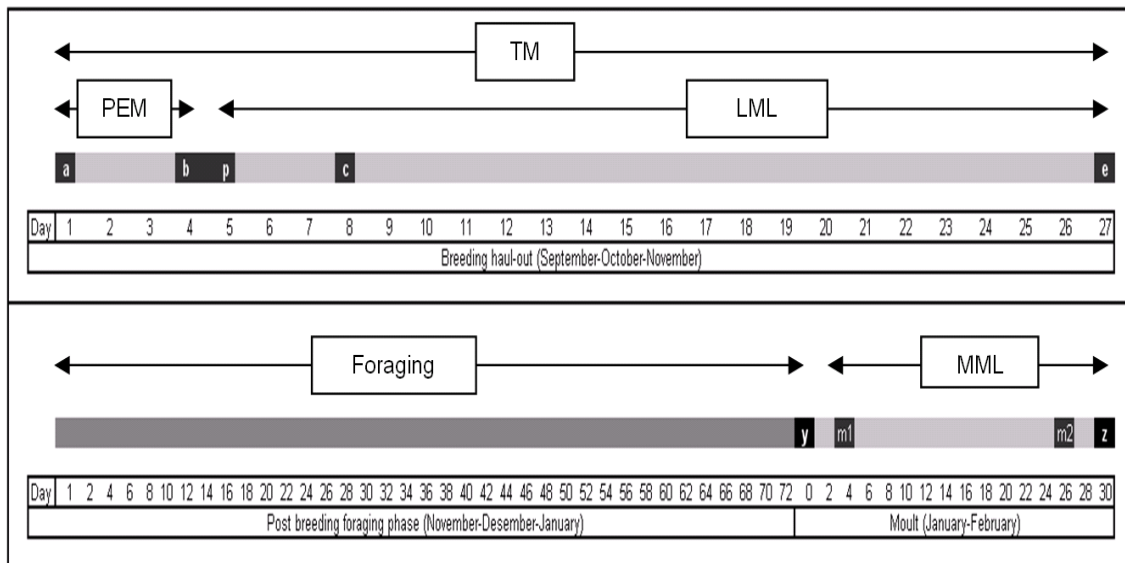


Figure 4.3. Visual representation of annual female life cycle: (TM) total mass loss in breeding haulout, (PEM) Pre-partum mass loss, (LML) lactation mass loss, (a) breeding season arrival PG mass, (b) pre-partum PG mass, (c) post-partum PG mass, (d) days elapsed, (e) breeding season departure PG mass, (p) partum. (MML) moult mass loss, (m1) first moult PG, (m2) second moult PG.

Breeding haulout equations

Pre-partum mass loss (PEM), lactation mass loss (LML) and absolute mass loss (TM) (Fig. 4.3) was calculated for each female using the following equations, where M = mass:

$$PEM = M_{arrival} - M_{pre_partum} \quad (1)$$

$$LML = M_{birth} - M_{departure} \quad (2)$$

$$TM = M_{arrival} - M_{departure} \quad (3)$$

Daily mass loss rates for the pre-partum period were calculated for animals that had arrival PG mass estimates ($n=13$) using the following equation:

$$PEM_{daily} = \frac{M_{arrival} - M_{pre_partum}}{no.days} \quad (4)$$

Daily mass loss rates for the post-partum period were calculated for animals with post-partum and departure PG mass estimates ($n=16$) using the following equation:

In order to calculate the amount of mass loss as a result of parturition, the difference between mass directly after and before parturition was measured. Daily mass loss rates were used to calculate the mass of female southern elephant directly after parturition seals using the following equation:

$$Mass_{after_birth} = M_{post-partum} + (no.days \times LML_{daily}) \quad (6)$$

Pup mass (Wilkinson & van Aarde 2001) and placenta mass (Arnbom *et al.* 1997) were added to mass estimates determined from equation 6 to obtain mass estimates directly before birth. Birth mass was set as a constant mean of 34.1kg for female pups and 40.3kg for male pups (Wilkinson & van Aarde 2001). If no post-partum PG mass estimates were available, mass directly before birth was estimated from arrival PG mass estimates as:

$$Mass_{before_birth} = M_{arrival} - (no.days \times PEM_{daily}) \quad (7)$$

If mass before birth was obtained as described in equation 7, pup mass (Wilkinson & van Aarde 2001) and placenta mass (Arnbom *et al.* 1997) was subtracted to obtain mass after birth.

Moult Equations

Moult mass loss (MML), was calculated for each female using the following equations, where M = mass:

$$MML = M_{arrival} - M_{departure} \quad (8)$$

Daily mass loss rates for the moult period were calculated for animals that had both post arrival PG mass estimates and pre departure PG mass estimate ($n=13$) using the following equation:

$$MML_{daily} = \frac{M_{post_arrival} - M_{pre_departure}}{no.days} \quad (9)$$

The duration of the post-breeding foraging phase and the moult durations were obtained through the continuous mark-resighting programme associated with the 10 day resighting cycle for all the beaches on the south-western coastline (Fig. 4.1). Due to the nature of the moult haulout and the 10 day resight cycle a mean moult duration was applied to animals that arrived and departed between sightings to obtain moult arrival and departure mass, using the following equations:

$$Mass_{arrival} = M_{post_arrival} + (no.days \times MML_{daily}) \quad (10)$$

$$Mass_{departure} = M_{pre_departure} - (no.days \times MML_{daily}) \quad (11)$$

Similarly a mean mass loss per day was used for animals that did not have an individual mass loss per day recorded due to a lack of two photogrammetry projects.

Statistical analysis

The program R was used for statistical analysis. Data from the 2009/2010 season was used for mass gain and loss results. A linear model was fitted to investigate the relationship between percentage mass loss during all stages of the breeding season and the duration of the post breeding foraging phase. A non-parametric dependant 2 group Wilcoxon test was performed. Significance was set at $P < 0.05$. Data from the 2008, 2009 and 2010 moult was used for consecutive breeding success mass. A Cochran test was performed to test for outlying variance, and when found to be present; a nested ANOVA was performed to test for significance between moult arrival mass from females that skipped a breeding season and those that did not.

Results

Mass gain and loss

By calculating daily mass loss for (1) pre-partum (mean = 3.68kg/d), (2) postpartum (mean = 7.55kg/d) and (3) moult (mean = 4.76kg/d), exact arrival and departure masses could be obtained. Females lost a mean $44.1 \pm 4.3\%$ body mass from arrival to departure for the entire breeding haulout, while lactation mass loss (immediately postpartum to departure) had a mean of $32.2 \pm 4.7\%$. Percentage mass gained in the post-breeding foraging phase (from departure after weaning a pup, to arrival for moult) ranged from 20.5 to 50.6 % had a mean mass gain of $30.7 \pm 6.9\%$. Females lost a mean of $29.6 \pm 6.2\%$ body mass during an entire moult haulout (Fig. 4.4). A linear model was performed to investigate the relationship between percentage mass loss during all stages of the 2009 breeding season and the duration of the post breeding foraging phase. No correlation was found. Shapiro-Wilks test showed that normality was not present. A non-parametric dependant 2-group Wilcoxon test was performed between foraging mass gain and moult mass loss. No

significance $P = 0.69$ (Fig. 4.5) was found between percentage mass gain in the post breeding foraging phase and the percentage mass loss in the moult.

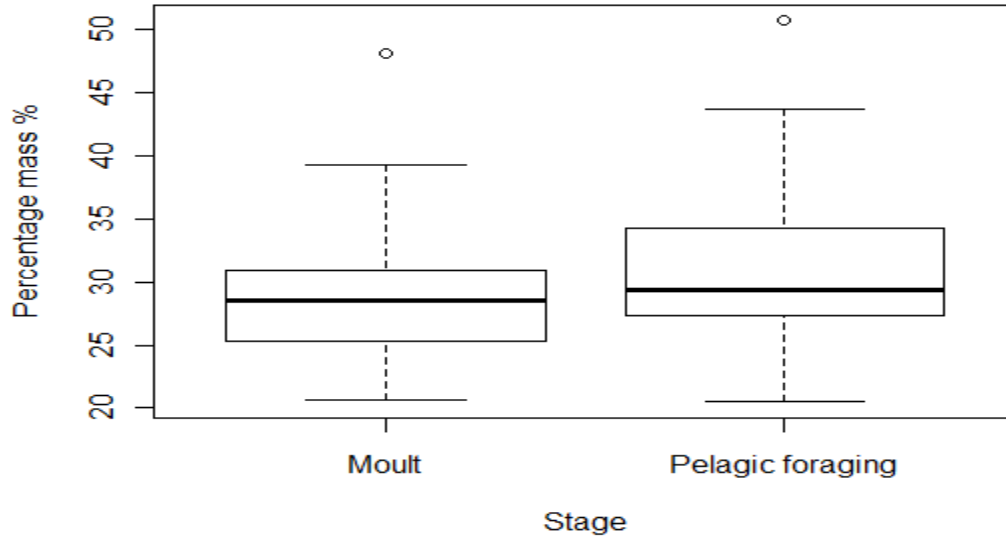


Figure 4.4. Percentage mass gain of the female southern elephant seals in the post-breeding pelagic foraging period 2009 compared to their percentage mass loss in the moult 2009/2010 in southern elephant seals ($n=23$). Pelagic foraging percentage mass ranged from 20.5 to 50.6 % and percentage moult mass lost ranged from 20.63 to 48.07 %

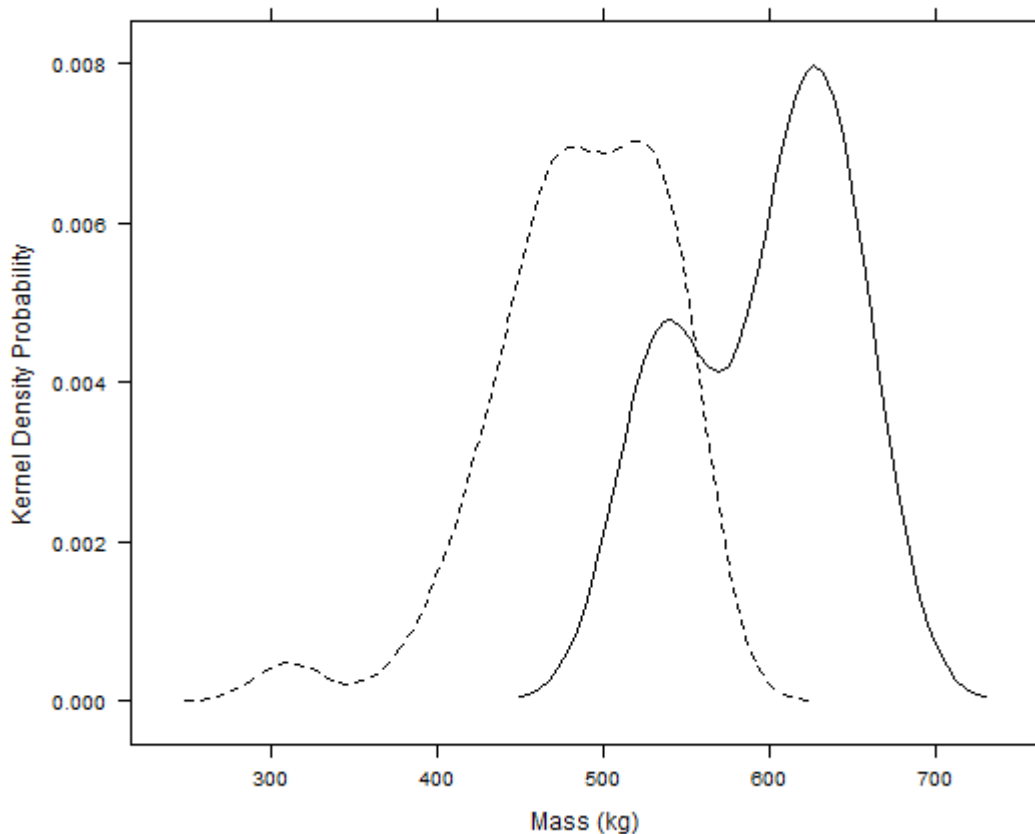


Figure 4.5. Kernel density plot of female southern elephant seal moult arrival mass, dashed line represents female mass change for those with uninterrupted breeding schedule and the solid line represents female mass change for those with interrupted breeding schedules.

Female mass: Annual vs. interrupted breeding

Many female southern elephant seals at Marion Island have interrupted breeding cycles; meaning they skip breeding seasons throughout the course of their breeding lives (de Bruyn *et al.* 2011). I investigated the implication of this interrupted breeding cycle on the females' mass at arrival in the subsequent moult. Three out of 18 females monitored and photographed showed interrupted breeding. Females that skipped a breeding season had a mean moult arrival mass of $596.9 \pm 54.95\text{kg}$ and females that had an uninterrupted breeding cycle had a lower mean moult arrival mass of $486.04 \pm 52.05\text{kg}$. A Kernel density plot was performed to iterate the

difference between the two systems (Fig. 4.5). Similarly, the moult departure mass for females with an interrupted breeding cycle had a mean of $408.60 \pm 52.39\text{kg}$ compared to females with an uninterrupted breeding system mean of $333.15 \pm 49.86\text{kg}$. A Kernel density plot illustrated the difference (Fig. 4.6). A significant difference ($P < 0.0001$) was found in female moult arrival mass, between females that did not breed the previous season and those that did (Fig. 4.7). Similarly a significant difference was found between the interrupted and uninterrupted breeding cycle departure mass ($P = 0.001$) after the moult (Fig. 4.8).

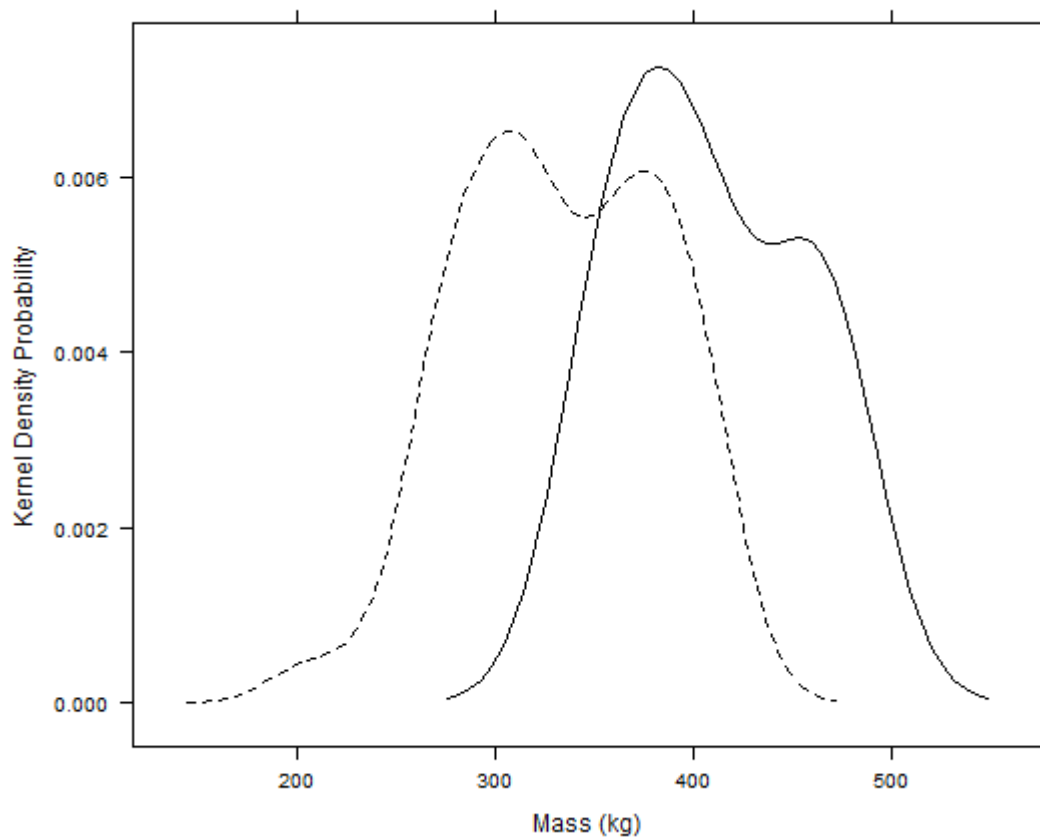


Figure 4.6. Kernel density plot of female southern elephant seal moult departure mass, dashed line represents female mass change for those with uninterrupted breeding schedule and the solid line represents female mass change for those with interrupted breeding schedules.

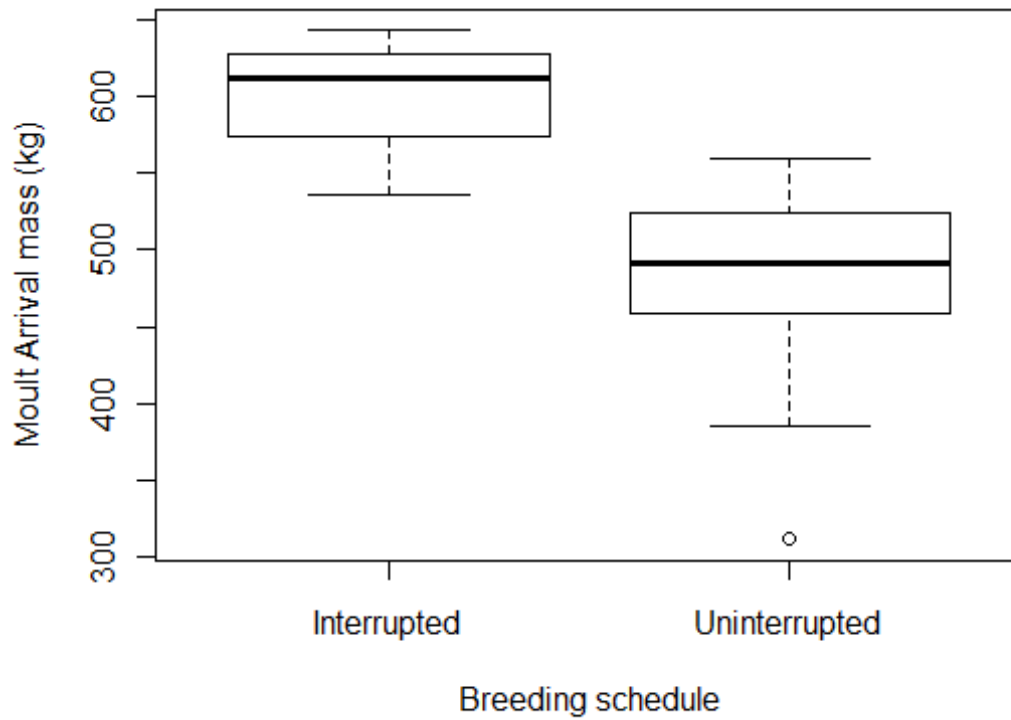


Figure 4.7. Comparison between female southern elephant moulting arrival mass that have an interrupted breeding schedule ($n=3$) ranged from 536.1 to 643 kg and those who have an uninterrupted breeding schedule ($n=18$) ranged from 311.1 to 559.9 kg.

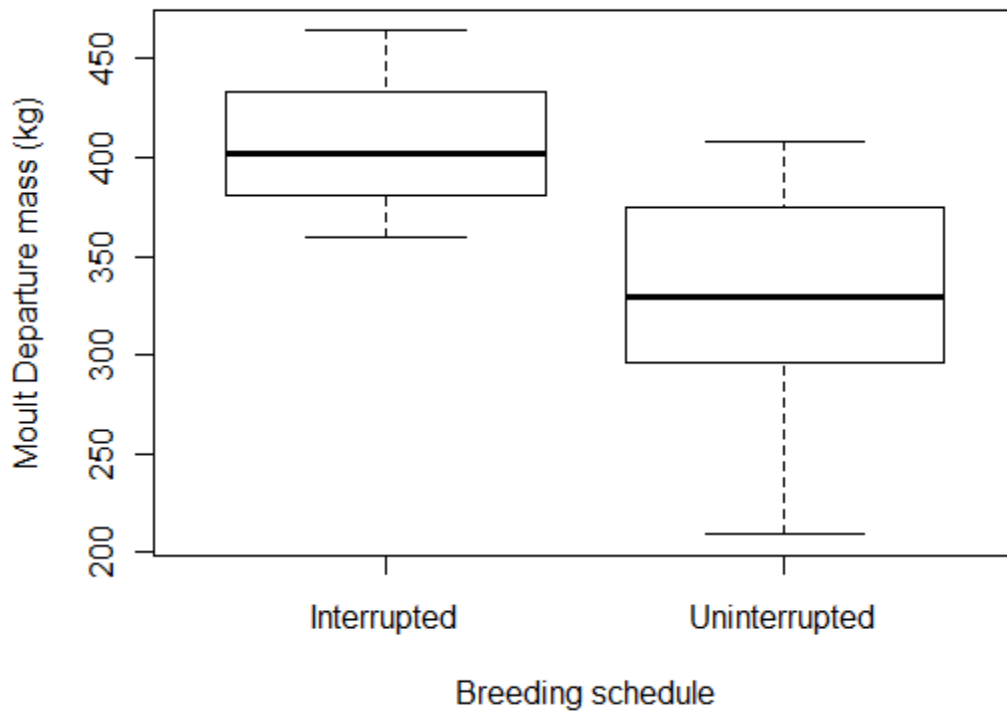


Figure 4.8. Comparison between female southern elephant seal moulting departure mass that have an interrupted breeding schedule ($n=3$) ranged from 360 to 464 kg and those who have an uninterrupted breeding schedule ($n=18$) ranged from 209 to 407.6 kg.

Discussion

Mass gain and loss

Many mammals with seasonal life cycles have predictable changes in their metabolic rate, mass and body condition (Ashwell-Erickson *et al.* 1986; Rosen & Renouf 1998; Fitzgerald & McManus 2000). For southern elephant seals, predictable seasonal haulouts are dependent on mass gain during their pelagic foraging phases, while sufficient stored mass is necessary to survive terrestrial haulouts. The haulout mass of Phocid females for the breeding season is vital for successful pup production as maternal expenditure is limited to this amount (Laws 1953; Fedak & Anderson 1982; Costa *et al.* 1986; Kovacs & Lavigne 1986; Fedak *et al.* 1994; Arnborn 1994;

Fedak *et al.* 1996; Trillmich 1996; Arnbom *et al.* 1997; Hindell & Slip 1997). Thus breeding season arrival mass was set as the baseline from which percentage mass gained in post-breeding foraging as well as percentage mass lost in moult were derived. Females at Marion Island lose a mean of $44.1 \pm 4.3\%$ mass in the breeding season with $32.2 \pm 4.7\%$ of the total mass lost during the lactation period. The mass loss depicts the amount of mass a female has to recover during her subsequent pelagic foraging phases and this annual pattern depletes an important proportion of females' reserves (Carlini *et al.* 1997). The mass loss during the breeding season has to be regained in the post-breeding foraging phase to ensure that sufficient resources are available for the obligatory moult, without neglecting physiological maintenance and growth. The same can be said of the post-moult foraging phase, often with the added physiological strain of advanced gestation (Laws 1956). The post-breeding foraging phase occurs in a period of seasonal prey abundance and females seem to gain mass at a greater rate than during the post-moult foraging phase (Carlini *et al.* 1999). Females from Marion Island regained $30.7 \pm 6.9\%$ body mass in the post partum foraging phase, thus 95.3% of the mass they lost during the lactation period was regained. As a result, females start the moult with a ~ 5% mass deficit compared to the mass post-partum at the start of the lactation period. Regaining such a large percentage mass is necessary as females require sufficient amounts of body protein to grow the new integument as well as fat for metabolic demands in the moult (Carlini *et al.* 2005).

After post breeding pelagic foraging, females return to moult their hair and top layer of epidermis (Ling 1970). During this process at Marion Island, females lose $29.6 \pm 6.2\%$ of the arrival body mass, and therefore 96.4% of mass gained in the post breeding foraging phase is lost in the moult. Consequently departing with virtually similar mass at both terrestrial phases. This highlights the foraging effectiveness needed by females during the post-moult phase to ensure and maintain

foetal growth as well as their own preservation and growth for the next breeding season. No significant difference was found between mass gain in post-breeding foraging phase and mass loss during the subsequent moult. The absence of difference between these physiological parameters may indicate that predetermined barriers of percentage mass loss and gain are set to alter female behaviour and bring about change between different seasonal life stages. Moreover, hormones act as a mechanism for mediating seasonal changes in physiology; this includes altering and protecting seasonal 'check-points' in body mass, body composition, and metabolism (Adam & Mercer 2001; Armitage & Shulenberger 1972; Ward & Armitage 1981). I propose that a certain percentage mass gain and loss act as thresholds to behavioural change from one annual phase to the next in female southern elephant seals.

Percentage mass loss in the breeding season and the duration of the following foraging phase was not significantly correlated. Similarly, time spent at sea was also not linked to percentage mass gain during the foraging phase (this study) as found elsewhere by Carlini *et al.* (2005). As there is a difference between time spent at sea between individuals (Bradshaw *et al.* 2004), there must be another driving factor that determines foraging duration. Consequently, time spent foraging is influenced by foraging ability and previous experience, seasonal environmental unpredictability and prey distribution (Bradshaw *et al.* 2004). The close correlation between percentage mass loss and gain (Fig. 4.9) strengthens the argument that these metrics act as a mechanism for altering animal behaviour between life stages.

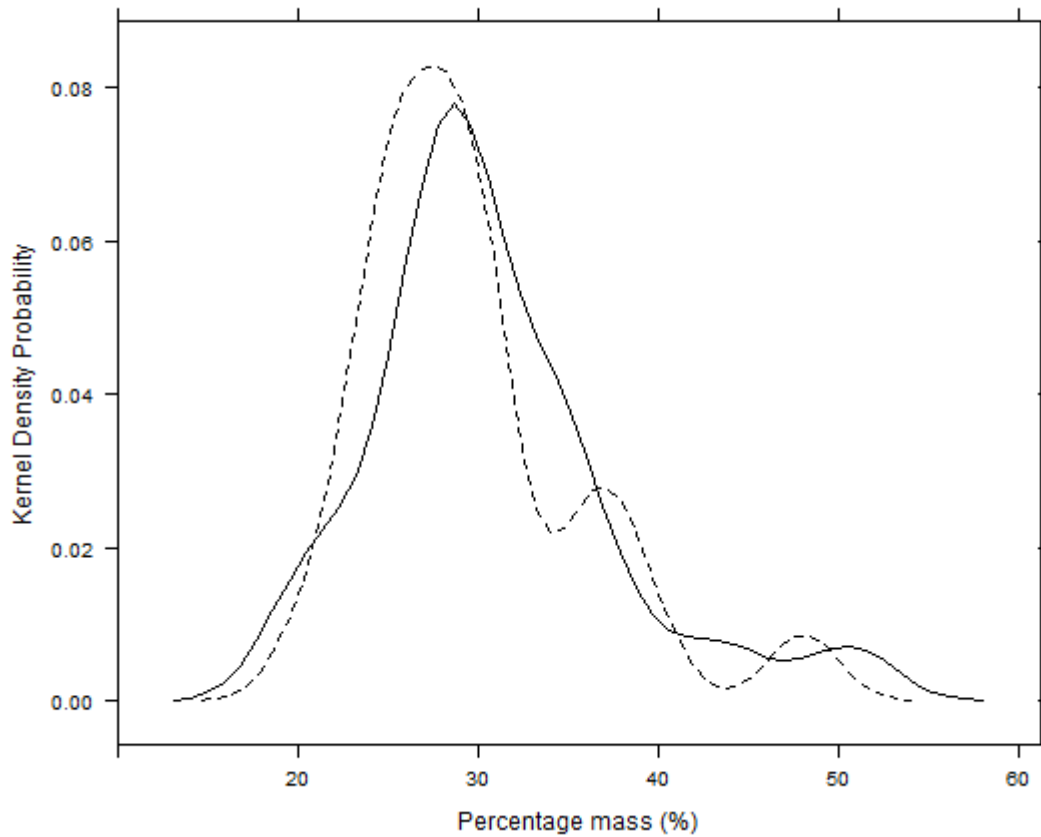


Figure 4.9. Percentage mass gain in pelagic foraging period compared to percentage mass loss in the moult in southern elephant seals during the 2009/2010 breeding season. Dashed line represents percentage mass gain in pelagic foraging phase; solid line represents percentage mass loss in the moult.

Given that southern elephant seals have such seasonal divergences in energetic priorities, the effect of unexpected disturbances on an animal's energy budget may have altering consequences depending on the timing (Nunes *et al.* 2002; Owen-Smith 1994; Rea *et al.* 2007). Breeding southern elephant seal females appear to be living on the edge in terms of percentage mass gain to sustain them through their obligatory moult.

Different breeding schedules

If southern elephant seals' accurately timed and synchronized breeding–moulting cycles are under the control of environmental factors (Carrick *et al.* 1962b), the terrestrial portion of their annual life cycle may be linked to seasonal at sea food supplies (Ling 1969). If the terrestrial proportion of southern elephant seals' life cycle is linked to seasonal food supplies, females could miss breeding seasons due to poor foraging conditions prior to the breeding season haulout. Many female southern elephant seals at Marion Island have interrupted breeding cycles (de Bruyn *et al.* 2011) contrary to prevailing assumption that female southern elephant seals breed (pup and mate) annually (e.g. Hindell 1991; Wilkinson 1991; Le Boeuf & Laws 1994; Pistorius *et al.* 2008; McMahon *et al.* 2009; de Bruyn 2009). Conceivably, the skipping of breeding season(s) could therefore be related to food availability.

The mark recapture search effort at Marion Island is extensive and females that are not recorded during the breeding season are most likely at sea, produce no pup and thus avoid a terrestrial breeding haulout (de Bruyn *et al.* 2011). Consequences and advantages of such different breeding strategies should be evident in females' mass at critical stages. Indeed a significant difference was apparent in mass between three females with interrupted breeding (pupping) schedules which copulated at sea, compared to 15 females with annual uninterrupted breeding (pupping)(this study). Females that skipped a breeding season returned with an increased arrival mass in the following moult ($\pm 100\text{kg}$ greater) over that of similar-aged females that had an uninterrupted seasonal breeding schedule. Similarly, their departure mass was $\pm 80\text{kg}$ heavier than their continuously breeding counterparts. The lack of terrestrial fasting and the absence of accompanying lactation costs for females with interrupted breeding (pupping) contribute to a greater arrival mass in the following moult. Greater arrival mass in females with an interrupted breeding schedule, conceivably is the result of an alternative mating

system based on non-polygynous opportunistic sexual encounters at sea (de Bruyn *et al.* 2011) which foregoes terrestrial fasting during the breeding season. Increasing pressures on marine stock from human exploitation which is now commonly accepted to be the main source of disturbance in marine ecology (Gislason *et al.* 2000; Goñi 1998; Jackson *et al.* 2001; Heithaus *et al.* 2008; Gasche *et al.* 2011), as well as the added stress of breeding and suckling pups presumably strain female southern elephant seals. This strain is evident in the non-significant difference between percentage mass gain in the post breeding foraging phase and the percentage mass loss in the moult. Females barely regain enough mass after the rigours of the terrestrial breeding season, and this strain in mass gain and loss may have forced some females to adopt an interrupted breeding strategy.

Consequently, females with an uninterrupted breeding schedule have less mass at the beginning of the subsequent breeding haulout than their counterparts that were absent in the previous season. Although our sample size is small, it is evident that females that have an interrupted breeding system have greater body mass than those who breed annually. Mass appears to be the most important state variable, influencing reproduction in southern elephant seals (Laws. 1956a, b). Thus if females haulout with a greater body mass at the beginning of the breeding haulout resulting from a skipped previous breeding season(s), they would have more resources for breeding. This may lead to greater survival of offspring as heavier weaned southern elephant seal pups are more likely to survive their first year (McMahon *et al.* 1999; McMahon *et al.* 2000; Pistorius *et al.* 2000; Pistorius *et al.* 2004; Pistorius *et al.* 2008).

In conclusion, percentage mass gained during the post-breeding foraging and mass lost during the moult phases may be the trigger mechanism for change in behaviour. Females regain equal percentage body mass in the post-breeding

foraging phase as what they lose over the course of the lactation period. Mass gain in post-breeding foraging is marginally sufficient to sustain females for the moult haulout. The close correlation of mass gain and loss is an indication that southern elephant seals are surviving on the edge. An unexpected disturbance or a decline in food resources could have substantial implications for their energy budgets with concomitant survival and fecundity consequences. Perturbations in energy budget may be a factor resulting in different breeding strategies. Females that exhibit an interrupted breeding schedule have greater mass at critical stages in their annual life cycle, which could be beneficial to future survival of females and successful weaning and survival of their offspring. We propose to explore successful weaning of pups in relation to different breeding strategies and how these could be beneficial to offspring and enhance female fecundity. Disparity in body mass gain/loss at critical stages in female southern elephant seals' life cycle (annual versus interrupted breeding system) supports the hypothesis (de Bruyn *et al.* 2011) that there are two different life history breeding strategies in southern elephant seals at Marion Island.

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CHAPTER FIVE:

GENERAL CONCLUSION

The unique uninterrupted life history records of southern elephant seals at Sub-Antarctic Marion Island over the last twenty eight years provided the foundation for understanding the driving factors that influence the southern elephant seal population. Complete life histories of individual animals are invaluable in studying life history traits of large mammals. Such data allow assessment of reproductive parameters associated with a population. The most important strategy in the life of mammals is to produce offspring and thereby propagate the species (Weir & Rowlands 1973). The relationship between reproduction, population density and body mass are of great interest for life history studies, as theories predict a trade-off between reproduction and mass when resources are limited (Stearns 1992). Lactation is the most energetically expensive attribute of mammal reproduction. Females of a species bear the cost of reproduction through maternal care of the offspring (Cripps *et al.* 2011), consequently it dictates their energy budget, and an extreme example is capital breeders such as southern elephant seals.

Together with the long-term mark-recapture programme, advances in scientific methods allow the researcher to investigate key aspects in long lived top marine predators over a temporal scale. One such method is photogrammetry, as used by de Bruyn *et al.* (2009) to accurately estimate southern elephant seal mass. Mass in capital breeders, such as southern elephant seals is critical and may affect their reproduction potential (Festa-Bianchet *et al.* 1998). Experimental tests of such theories are exceptional as uninterrupted long-term data of individual reproductive success and body mass under varying levels of resource availability are required, and how different levels of reproductive expenditure may affect subsequent survival (Festa-Bianchet *et al.* 1998).

The southern elephant seal population at Marion Island has been studied extensively (e.g. Bester 1989; Bester & Pansegrouw 1992; Bester & Hofmeyr 2005; de Bruyn *et al.* 2008, 2009, 2011, Kirkman *et al.* 2004; Pistorius *et al.* 1999, 2000, 2001, 2008, 2011; McIntyre *et al.* 2010, 2011). Other populations, specifically at King George Island (Carlini *et al.* 1997, 1999, 2000, 2005), at Macquarie Island (Hindell *et al.* 1987, 1994; Bell *et al.* 1997, 2005; McMahon *et al.* 1999, 2000, 2003), and at South Georgia Island (Boyd *et al.* 1993) have similarly been studied. Mass fluctuation over time was accurately obtained in these previous studies. However, these previous studies relied on physically weighing or interacting with animals. Yet some questions still need to be answered. I addressed these questions by systematically investigating the different annual life stages (breeding haulout, post-breeding foraging phase and moult haulout) of adult female southern elephant seals at Marion Island.

For the breeding haulout I investigated female size from different populations. Marion Island females are smaller than their counterparts on King George, lose less absolute mass during the course of the breeding season but have the same relative percentage lactation mass loss than do similar aged individuals at other populations. Comparing different populations' lactation mass loss, I discovered that mean percentage mass loss in the lactation period is apparently a constant in the species. Further breeding haulout investigation was done on the relation between female age and their offspring survival during the first foraging trip, which was possible as the exact age and life history of all animals born on Marion Island for the last 28 years is known due to an intensive mark-recapture programme (see de Bruyn *et al.* 2008). This enabled us to assess the age-to-weight ratio as a factor of successful breeding in consecutive years. According to life history theory, individual's reproductive performance should change with increased age, because of the trade-off between present offspring, future reproduction as well as the optimal reproductive effort

(Proffitt *et al.* 2007). The female mass loss, size and pup survival could be linked to age and not simply estimates of age according to size. The first year survival of pups is positively linked to their weaning mass. Weaning mass is in turn positively related to female age and mass loss. Older and larger females should have larger pups that have a greater probability of surviving their first foraging trip. Pups that are born from young females or females that do not gain sufficient mass prior to the breeding season show poorer survival probability than pups that are born to older and larger females. This annual pattern of mass loss during the breeding season depletes an important proportion of females' reserves (Carlini *et al.* 1997). Their mass loss depicts the amount of mass a female has to recover during her subsequent pelagic foraging phases.

The mass loss during the breeding season has to be regained in the post-breeding foraging phase to ensure that sufficient resources are available for the obligatory moult, without neglecting physiological maintenance and growth. Consequently, females not acquiring sufficient energy and food during this foraging trip may have trouble in sustaining themselves during the following haulout. Marion Island females forage for longer periods and gain relatively the same absolute amount of mass, their smaller size necessitating them to regain a greater relative mass than their counterparts at other islands, to sustaining them for the extended moult period. Mass gain of female southern elephant seals in post breeding pelagic foraging phase could also be accurately obtained. Percentage mass gained during the post-breeding foraging and mass lost during the moult phases look to be the trigger mechanism for change from one phase to the next. Females regain equal percentage mass in the post-breeding foraging phase compared to what they lost over the total course of the lactation period. Mass gain in post-breeding foraging is marginally sufficient to sustain females for the subsequent moult haul-out. The investigation of energy requirements of female southern elephant seals during the

course of their annual life cycle enlightened us to the close correlation of mass gain and loss as an indication that southern elephant seals are surviving on the edge. An unexpected disturbance or a decline in food resources could affect their energy budgets which are already marginal.

I found that the duration of the moult on Marion Island is longer than for other island populations, but this could be attributed to different sampling methods. A significant recent discovery showed that annually interrupted breeding schedules are more common in female elephant seals than previously thought (de Bruyn *et al.* 2011). Which lead my investigation to assess differences in female mass during the moult for individuals that skipped the previous breeding season and those who bred continuously? Females that exhibit an interrupted breeding system have greater mass at critical stages in their annual life cycle, which could be beneficial to future survival of females and successful weaning and survival of their offspring. Disparity in body mass gain/loss at critical stages in female southern elephant seals' life cycle (annual versus interrupted breeding system) supports the hypothesis (de Bruyn *et al.* 2011) that there are two different breeding strategies in southern elephant seals at Marion Island.

The mass of female southern elephant seals vary considerably over the course of their annual life cycle and differs greatly between different age classes, however it is an aspect not previously studied at Marion Island. The main reason for this was the inaccessibility of the breeding haul-outs and the sheer size of the animals. The method devised by de Bruyn *et al.* (2009) enabled elimination of this obstacle and I could study these animals with minimal disturbance over a temporal scale. The similarity of percentage mass loss in lactation period can be seen as a definitive validation of photogrammetry over a temporal scale. Photogrammetry was found to be a convenient and accurate field method in various environments, ranging

from flat sandy beaches, undulation boulder beaches, grassy *Cotulla* areas and moult wallows (present study). Female mass could be accurately measured by a single field researcher over a temporal scale in both the breeding and moult periods. 91.5% of photogrammetry projects solved accurately. Over 800 projects have been performed since 2006, the field method was improved to make analysis easier and less time consuming. The field method for taking the photographs is fast and efficient and multiple projects can be done on one day whilst collecting a multitude of other data. Less than 10% of photogrammetric projects failed due to environmental and photographic limitations. I have substantiated that photogrammetric mass estimation can be used alongside datasets of physically weighed animals and can greatly benefit ecology and life history studies of this species. Photogrammetry should be done on study subjects at every possible opportunity as they are invaluable for assessing mass estimations at critical stages in the annual life cycle of southern elephant seals.

Studying the mass fluctuation of an individual has clarified age specific reproductive success of female southern elephant seals within different breeding strategies that are operational within the species. It also highlighted the marginally sufficient mass gain of breeders during their post-breeding foraging. Furthermore the smaller size of females at Marion Island (as compared to other studied populations) could be problematic if an unexpected disturbance or a decline in food resources occurred, which in turn could have substantial implications for their energy budgets with concomitant survival and fecundity consequences. Excess mass loss in a terrestrial phase and an insufficient mass gain in pelagic phase could lead to a cascade of subsequently lower resources for breeding. Lower resources could in turn lead to different breeding strategies.

These findings indicate a currently stable Marion Island population that is marginally meeting mass requirements by employing different breeding strategies to survive an ever changing environment.

Future studies and recommendations

Photogrammetry should be continued at Marion Island as the benefit of photogrammetric mass estimation on specific individuals in a longitudinal study would be invaluable to providing an accurate insight into the life of southern elephant seals. Photogrammetry should be done on study subjects at every possible opportunity as it is invaluable for assessing mass estimations at critical stages in the annual life cycle of southern elephant seals. I propose that future studies should investigate the relation between successful weaning of pups from mothers employing different breeding strategies and how they could be beneficial to offspring survival and female fecundity. Furthermore, it should be investigated if other southern elephant seal populations exercise different breeding strategies and also if other phocid seals exhibit similar variation in reproductive strategies.

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(Marion Sealers M66)

"Men wanted for hazardous journey. Low wages, bitter cold, long hours of complete darkness. Safe return doubtful. Honour and recognition in event of success."

(Advert for Nimrod Expedition, Ernest Shackleton, 1874 - 1922)



(Marion Team)