Maternal foraging behaviour of Subantarctic fur seals from Marion Island

by

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Submitted in partial fulfilment of the requirements

for the degree of

MSc. (Zoology)

In the

Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

South Africa

March 2013

I, **Mia Wege** declare that this 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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"Though comparatively few folk ashore have even heard of them, the Prince Edward Islands are known to and feared by quite a large number of ocean voyagers. Not many have seen them, and few ever want to. They thrust their lava peaks out of that vast sea where the world's wildest weather is born. Their name is synonymous with storm, disaster and death."

John H. Marsh (In: No Pathway Here, 1948)

Summary

Title: Maternal foraging behaviour of Subantarctic fur seals from Marion Island

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Foraging forms the cornerstone of an animal’s life-history. An individual's foraging success shapes the demography and health of a population. Understanding key facets of maternal foraging behaviour are crucial to get a holistic picture of both regional and local environmental factors that drive foraging behaviour. This study aimed to measure the maternal foraging behaviour of a marine top predator, the Subantarctic fur seal (*Arctocephalus tropicalis*), from Marion Island (MI) over a range of spatial and temporal scales.

Arctocephalus tropicalis females from MI have one of the longest duration foraging trips for the species. They are most similar to conspecifics at temperate Amsterdam Island, but differ considerably from those at subantarctic Îles Crozet and Macquarie Island. Hitherto, no diving data existed for MI females. I illustrate how their diving behaviour is more similar to individuals from Îles Crozet despite their differences in foraging trip parameters. Together with Îles Crozet, MI females have one of the deepest mean diving depths (34.5 ± 2.2 m , 45.2 ± 4.8 m summer and winter respectively) and longest dive durations (70.2 ± 3 s , 104.3 ± 7.8 s summer and winter respectively) for the species. In summer, females follow the diel vertical migration of their myctophid prey. Counter intuitively, during the winter, females performed short and shallow crepuscular dives, possibly foraging on different prey. Considering that these individuals dive in deep waters, this is most likely related to myctophids occupying lower depths in the water column during winter. At dusk and dawn they are inaccessible to diving fur seals.

At-sea data from multiple foraging trips per female illustrated that females have both a colony- and individual preferred foraging direction which varied seasonally. Individuals travelled consistently in the same direction regionally, but locally appear to track prey in a heterogeneous environment. The few trips in the winter to the west of MI suggest that this is a short-term response to varying prey availability rather than a long-term foraging tactic.

Six years of observer-based attendance cycle data were used to augment telemetry data. Multi-state mark-recapture models were used to determine the probability of a female being missed when she was present (detection probability). Attendance data were corrected accordingly. Neither El Niño (EN) nor anomalous sea-surface temperature (SSTa) influenced any of the attendance cycle parameters, as foraging trip duration is a poor predictor of weak environmental change. Only season and pup sex had a significant impact on female provisioning rates. Foraging trip duration was longer during winter than during summer. Females spent a higher percentage of time on land when they had female pups rather than male pups. Although observational attendance data remain useful it ideally requires concomitant data on pup growth, production and female body condition to elucidate changes in female provisioning rates.

Temporally, season had the most influence on female foraging behaviour. Spatially, it appears that a lack of prominent local bathymetrical features overshadows MI's favourable position in the productive Polar Frontal Zone. *Arctocephalus tropicalis* females from MI work harder at foraging than at any other island population of conspecifics.

Acknowledgements

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 providing a grantholder-linked bursary for this project.

Thank you to all the various field assistants who wrestled with a female in the hoopnet, glued their fingers to a device, fell on the large slippery boulders at Rockhopper Bay, struggled with fogged up binoculars, lost feeling in their hands from the cold and had a ball doing it all! You are Cheryl Tosh, Nico de Bruyn, Chris Oosthuizen, Mashudu Phalanndwa, Ryan Reisinger, Thomas Mufanadzo, Derek van der Merwe, Martin Postma, Jean Purdon, Tristan Scott and Hugh Purdon.

I had the privilege of spending two glorious years on Marion Island during the 66th (2009-2010) and 69th (2012-2013) expeditions. Martin Postma and Derek van der Merwe, my fellow M66 Sealers, you made me fall over with laughter in the field, pushed me to my limits and had patience with my two left feet. "We will always remember." You made my first year on Marion unforgettable and so extraordinary, I wanted more! Wiam Haddad and Nico Lübcker, my fellow M69 Sealers, you are the guys who made me push myself even harder, raised the bar, and shared elephant seal mother's milk with me - I couldn't have asked for better Sealer men! Dawn Cory-Toussaint, my faithful ‘minion’, thank you for helping me show them that women can really do it all too...and more! Ben Dilley & Delia Davies: two years and you wanted more? Thank you for early morning

coffee, fixing the "aircon" in my blues, two One Day Round Islands (booya!), road trip(s) and countless laughs. Your friendship had a huge positive influence on both my years. My other M66 and M69 team mates - I am grateful you were all part of this unforgettable journey, each and every unique character.

I express my sincere thanks to the people who were always willing to share their hard-earned knowledge on statistics, GIS and general short-cuts, especially Marie Nevoux, Chris Oosthuizen, Cheryl Tosh and Trevor McIntyre.

I am indebted to my supervisors, Prof. Marthán Bester and Dr. Nico de Bruyn. Thank you for putting your faith in me, your willingness to offer advice and support and steering me down the right track. And it was always done with such good humour. Marthán, thank you for captivating my imagination back at that University Open Day in 2003. If it weren't for you, I would have probably been stuck in some boring office job. I couldn't have asked for better.

I am fortunate to have supportive and loving parents. Thank you for your support through all of my concocted endeavours. It would not have been possible without your love and encouragement. Of course, none of this would be possible without Him.

Disclaimer

Chapters 2, 3 and 4 of this dissertation were prepared for publication as separate manuscripts. The reader will therefore have to bear a fair amount of repetition, particularly in the "Methods" sections. I apologise for this.

Subantarctic fur seal pup suckling

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Chapter 1:

General Introduction

Introduction

Foraging forms the cornerstone of an animal’s life-history. Successful synchronisation of foraging behaviour with reproductive costs, environmental fluctuations and seasonal cycles forms the boundary between success and failure of an individual or of whole populations. An animal’s foraging behaviour can therefore be interpreted as a combination of factors acting on the individual and its food resources at a hierarchy of spatial scales (e.g. Senft *et al.* 1987; Ward & Saltz 1994; Brown & Morgan 1995). The individual first has to choose a home range, then a habitat within the home range before finally arriving at the foraging patch. Within the patch the individual further has to make choices about which prey to utilise or even which part of the prey (Mysterud *et al.* 1999). In return, the distribution of prey is influenced by environmental factors acting upon it, also at a hierarchy of both spatial and temporal scales. In the marine environment the same holds true. Unlike on land, where most predators only have to make choices in a two-dimensional space, a third dimension is added as most prey move not only on the surface from area to area but also up and down the water column.

The Southern Ocean is probably the largest marine ecosystem on the planet (Knox 2007) constituting *c.* 10% of the marine environments of the world (Constable *et al.* 2003) and plays a crucial role in global climate (Weimerskirch *et al.* 2003). It is the dominant force of the southern higher latitudes, with islands sparsely distributed throughout its range. Although it is considered to be highly productive, the distribution of resources is dependent on certain physical and chemical variables and is often unpredictable and subject to high seasonality and vertical fluctuations (Lutjeharms *et al.* 1985; Knox 2007). Physical processes are therefore critical to Southern Ocean productivity. One of these main physical controls, acting at a large geographical scale, is the prevailing westerly wind caused by the pressure difference between bands of low pressure systems surrounding the Antarctic continental plateau and the tropical anti-cyclones to its north (Knox 2007). The latitudinal band between 40°S and 50°S is known as the "roaring forties" and drives the Antarctic Circumpolar Current (ACC). It is an east-flowing current, uniquely encircling the globe and flows almost entirely unobstructed (Tynan 1998; Knox 2007). It is bounded to the south by the Antarctic Polar Front (APF; Antarctic Convergence) and to the north by the Subantarctic Front (SAF); collectively this area is known as the Polar Frontal Zone (PFZ). To the north of the SAF is the Subtropical Convergence (a.k.a. the Subtropical Front - STF), which is where Subantarctic and Subtropical surface water meet (Lutjeharms *et al.* 1985). The STF also receives warmer water and the biota (and nutrients that come with it) from the Agulhas Return Current. All three of these fronts show considerable temporal changes in their latitudes (Lutjeharms 1990) and operate more at a regional scale in terms of resource distribution. With the APF bringing colder water and biota from the south and the SAF and the STF bringing warmer water and biota from the north, the PFZ is an area characterised by biological enhancement (Lutjeharms *et al.* 1985) and might be considered a marine ecotone.

At a local scale, bathymetry is key to the distribution of productivity. When the ACC hits an underwater ridge, an island's plateau or peri-insular shelf, water flow is slowed and eddies are formed. In the southern hemisphere, eddies could either be warmer, anti-cyclonic (counter-clockwise rotating) or colder cyclonic (clockwise rotating) bodies of water. Clockwise rotating eddies spin up, which leads to upwelling in the centre and downwelling on the edges. When it slows, forces are reversed and downwelling occurs in the centre and upwelling on the edges (Bakun 2006). This brings the nutrient rich Deep Antarctic Water to the surface, which provides the much needed nutrients to the phytoplankton and subsequently blooms occur (Hart 1934; Lutjeharms *et al.* 1985). Furthermore, the eddy-core transports resources within it and the outer part leads to stirring with the surrounding waters (Olson 1991). This means that biological particles present in the core are subsequently trapped there. Eddies are key foraging areas for several predators (e.g. Nel *et al.* 2001; Weimerskirch *et al.* 2004; Campagna *et al.* 2006; Poloyina *et al.* 2006; Bailleul *et al.* 2010; Dragon *et al.* 2010).

Over the past ~50 years the occurrence and importance of changes in global climate, especially the warming of our oceans, have become increasingly prominent (e.g. Reid & Croxall 2001). For example, Southern Ocean westerlies have shifted poleward and increased in intensity (Weimerskirch *et al.* 2012). As a result, the ACC has migrated south approximately 50 to 70 km (Gille 2002). These changes influence the distribution and abundance of prey (Loeb *et al.* 1997; Nicol *et al.* 2000) which ultimately influence population structure, demographics and foraging behaviour of marine top predators (Croxall *et al.* 2002; Weimerskirch *et al.* 2003; McIntyre *et al.* 2011; Weimerskirch *et al.* 2012). In light of these changes, it is important to understand how and at what scales marine top predators' foraging strategies are influenced by physical processes and environmental factors.

Telemetry data provided us with an abundance of information on animal movements, diving behaviour and their limitations (e.g. Gentry & Kooyman 1986). More recently, marine predators were used to measure *in situ* environmental variables, which is applied to map and characterise areas in the Southern Ocean otherwise sparsely visited (e.g. Biuw *et al.* 2007; Padman *et al.* 2010). In light of climate change issues, telemetry studies provided a means to characterise foraging behaviour in terms of the biotic and abiotic factors that influence it (e.g. Nel *et al.* 2001; Lea & Dubroca 2003; Weimerskirch *et al.* 2003; Lea *et al.* 2006; Péron *et al.* 2010) as well as how species respond to climate change (e.g. McMahon & Burton 2005; McIntyre *et al.* 2011; Weimerskirch *et al.* 2012).

Several top predators revealed an extraordinary flexibility in foraging tactics and behavioural strategies (Staniland & Boyd 2003; Lea *et al.* 2006, 2008; Biuw *et al.* 2007; Tosh *et al.* 2009; Staniland *et al.* 2010). In some otariid seals, heterospecifics occurring on the same island show more similarities in foraging behaviour than conspecifics from distant populations (e.g. Georges & Guinet 2000; Georges *et al.* 2000a,b; Beauplet *et al.* 2004; Bailleul *et al.* 2005; Luque *et al.* 2007).

Otariid seals

Otariid seals (Order Carnivora, Family Otariidae: fur seals and sea lions) are central-place foragers (Orians & Pearson 1979; Rice *et al.* 1998). Lactating females alternate between an "at-sea" foraging phase and an onshore "attendance phase" where the female is nursing her pup. Collectively this is known as the foraging cycle (Gentry & Kooyman 1986). All the nutrients required for milk production are acquired during females' foraging trips. How they apportion their time at sea and nursing ashore directly influence their maternal investment (Trillmich 1996). As income breeders (Stearns 1992) they are therefore more limited in terms of how far and for how long they can forage. Failure of a female to accurately process information from its environment at the aforementioned hierarchy of scales could lead to foraging failure and ultimately breeding failure. Prior knowledge of consistently good foraging areas is therefore imperative to the survival of their pups. Logic dictates that females visit preferred foraging areas with a high likelihood of energetic pay-off, rather than going to unknown areas and ultimately risk breeding failure.

The Subantarctic fur seal

One of the most widespread species of the *Arctocephalus* genus, the Subantarctic fur seal, has breeding populations north of the Subtropical Front on the temperate islands of Tristan da Cunha, Saint Paul and Amsterdam, with Gough Island just to the south of it (Bester 1981; Riedman 1990). Within the PFZ breeding populations co-occur with Antarctic fur seals *(Arctocephalus gazella)* on at least four islands, namely Macquarie Island, Île de la Possession (one of the Îles Crozet), Prince Edward Island and Marion Island, the largest sympatric population of the four (Condy 1978; Bester 1981; Kerley 1987; Guinet *et al.* 1994). Females give birth to single pups over a six week period which, on Marion, is centred around 17 December (Hofmeyr *et al.* 2007). Within 6-10 days of giving birth, females undergo a post-partum oestrus lasting *c.* 1 day. Similar to other otariids, Subantarctic fur seals experience delayed implantation of the blastocyst on the uterine wall until March/April, approximately 3-5 months after mating (Bester 1995). Gestation lasts 360 days and lactation last *c.* 300 days (Kerley 1983, 1987; Bester 1995). This lengthy pup-rearing period makes them ideal study species to observe how top marine predators deal with the decrease in food resources during the subantarctic winter (Knox 2007). Akin to this, one is able to compare foraging behaviour between summer and winter.

Prey of the Subantarctic fur seal

Throughout its distribution, Subantarctic fur seals prey mainly on mesopelagic fish of the Myctophidae family (a.k.a lanternfish; Klages & Bester 1998; Robinson *et al.* 2002; Luque *et al.* 2007; de Bruyn *et al.* 2009). The species composition of prey taken does, however, differ somewhat between the different islands, albeit superficially (de Bruyn *et al.* 2009). As mesopelagic fish, myctophids occupy the middle depth of the water column in the Southern Ocean (Knox 2007). They undertake both diel and seasonal vertical migrations between the epipelagic and mesopelagic regions (Catul *et al.* 2011). During the spring and summer months they are found higher up in the water column than during the winter, when they migrate down and inhabit the top layer of the Circumpolar Deep Water (300-500 m) (Knox 2007). At night they ascend to the surface to feed, which also puts them within the diving limits of shallow diving predators such as the Subantarctic fur seal (e.g. Gentry & Kooyman 1986). At dawn the lantern fish descend to the bottom layers of the ocean again (Catul *et al.* 2011). In some areas, during the day (i.e. areas with deep bottom topography) myctophids are beyond the diving capabilities of fur seals (George *et al.* 2000a; Georges & Guinet 2000). As a result, Subantarctic fur seals are nocturnal foragers and at most of their locations follow the diel vertical migrations of their prey closely by performing deeper and longer crepuscular dives (Georges *et al.* 2000b; Robinson *et al.* 2002; Luque *et al.* 2007). Cephalopods are also taken on occasion (Bester & Laycock 1985; de Bruyn *et al.* 2009). However, their contribution to the diet of Subantarctic fur seals might be grossly underestimated as determined by scat analyses (Klages & Bester 1998; Ferreira & Bester 1999).

Geographic disparities in foraging behaviour

The Subantarctic fur seal is another example of a top marine predator with a wide geographical distribution which, recently, revealed fascinating disparities in their foraging behaviour (de Bruyn *et al.* 2009). Lactating females from temperate Amsterdam Island undertake extended foraging trips lasting on average 11 days in the summer and 23 days in the winter during which they travel >100 km from their breeding colony towards the northern parts of the STF (Georges *et al.* 2000 a, b). In contrast, Subantarctic fur seals from Île de la Possession (Îles Crozet), and Macquarie Island mostly perform short overnight foraging trips (~40-50% within 10 km of the island). Longer foraging trips were still shorter than 10 days and rarely exceeded 60 km and 100 km from Macquarie Island and Île de la Possession respectively (Robinson *et al.* 2002; Bailleul *et al.* 2005; Luque *et al.* 2007). It is suggested that the location of Îles Crozet and Macquarie Island within the productive PFZ (see above), determine the distance travelled during a foraging trip (Georges *et al.* 2000a; Luque *et al.* 2007; Goldsworthy *et al.* 2010).

Individuals from the different populations also exhibit different diving behaviour. Females from Amsterdam Island dive to a mean depth of 19 m and 29 m during the summer and winter respectively (Georges *et al.* 2000b). Despite the similarities in their foraging cycle parameters, individuals from Macquarie Island and Île de la Possession differ greatly in their diving behaviour. Macquarie Island females perform the shallowest mean diving depths recorded for the species so far (9.9 m; Robinson *et al.* 2002) whereas females from Île de la Possession perform on average the deepest dives for the species. They dive to a mean depth of 37.8 m and 45.7 m during over-night and long foraging trips respectively.

Similarly, Marion Island is also located within the ostensibly productive PFZ (fig. 1). However, lactating females seem to follow a similar foraging strategy to that of females from Amsterdam Island. Studies on flipper-tagged lactating females and their pups suggest that females from Marion Island perform extended foraging trips but no overnight foraging trips (Bester & Bartlett 1990; Kirkman *et al.* 2002). However, methods used in these studies made the results equivocal. More recently, telemetry data confirmed that lactating females from Marion Island behave more like conspecifics from Amsterdam Island than females from Île de la Possession and Macquarie Island (de Bruyn *et al.* 2009). Females mainly travelled north-east of Marion Island, with some individuals foraging to the west of the island (de Bruyn *et al.* 2009). This previous at-sea data is limited to a single foraging trip per female. Whether females travel consistently in the same direction, to the same areas on consecutive foraging trips or vary their foraging localities between foraging trips is still unknown. Thus far, no diving data has been collected for the species at Marion Island.

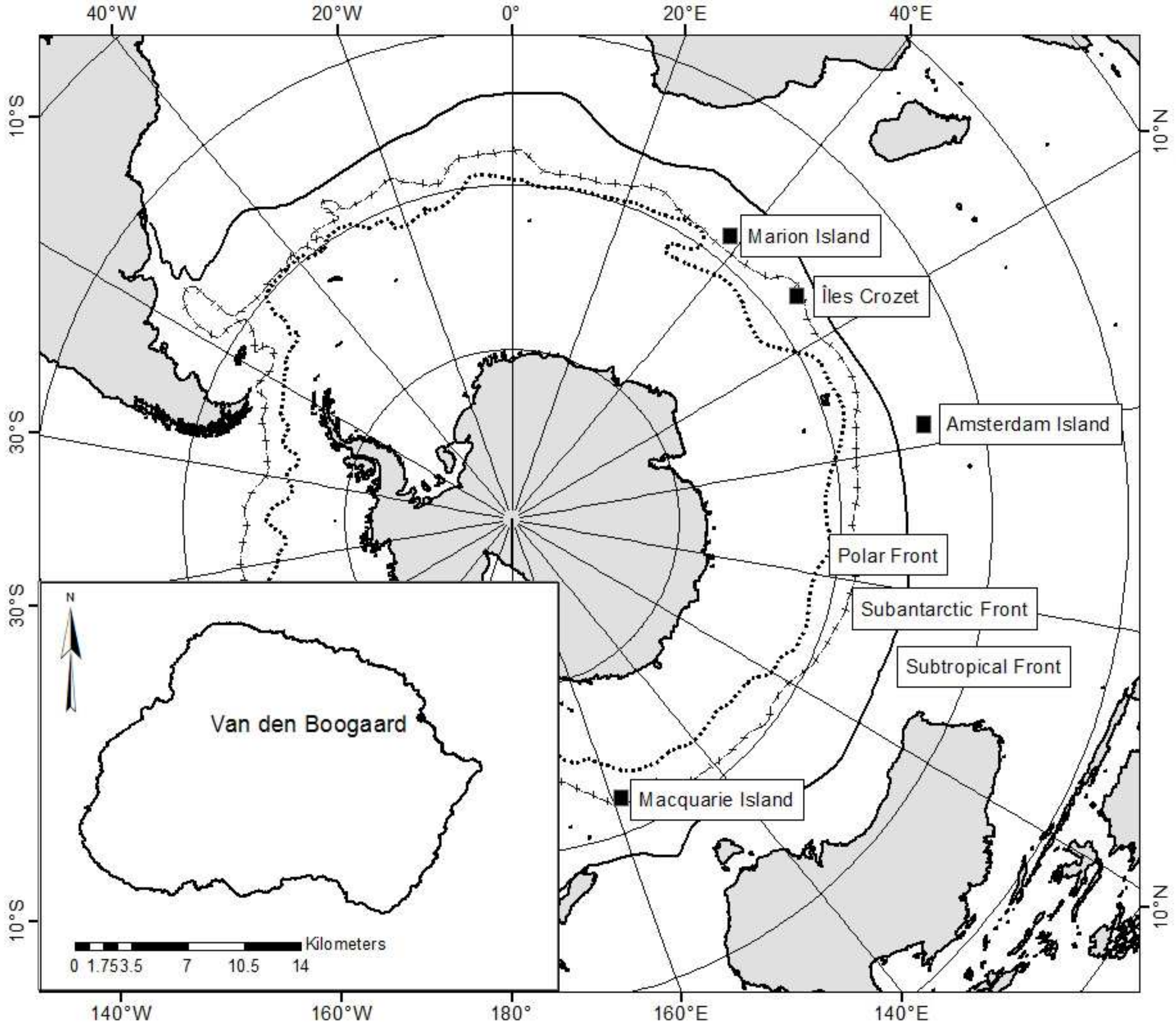

Figure 1.1: *The position of Marion Island in the Southern Ocean in relation to Île de la Possession (Îles Crozet), Amsterdam Island and Macquarie Island as well as the Antarctic Polar Front, Subtropical Front and the Subantarctic Front. The location of Van den Boogaard beach (study beach) on Marion Island is indicated (inset).*

Study Area

The Prince Edward Islands are situated in the Indian sector of the Southern Ocean. It lies in the path of the “roaring forties” and the accompanying currents and fronts (see previous sections; Ansorge & Lutjeharms 2002). The islands are volcanic outcrops that rise steeply from the ocean floor and have no peri-insular shelf or plateau. Prince Edward Island is the smaller of the two (46 km^2; Boelhouwers *et al.* 2008) and lies 19 km to the northeast of the larger Marion Island (300 km^2; Meiklejohn & Smith 2008). They are separated by a shallow saddle, which is between 40 and 200 m deep. The nearest landfall is Îles Crozet, *c.* 950 km to the east. South Africa is *c.* 2000 km to the northwest. Towards the west of the islands lies the South West Indian Ridge (SWIR) and to the northwest, the Del Caño Rise (DCR) (Fig. 2). Within the SWIR lies the Andrew Bain Fracture Zone (ABFZ). Here the ACC splits, most of the water is deflected upward and the rest is funnelled through the fracture zone (Fronemann *et al.* 2002). This gives rise to a high number of both cyclonic and anti-cyclonic mesoscale eddies (Ansorge & Lutjeharms 2003, 2005).

Like most other subantarctic islands, Marion Island was subjected to sealing from the 17th century which continued intermittently until 1931 (Marsh 1948; Kerley 1987). Subantarctic fur seals were nearly hunted to extinction; small populations survived on Gough Island (Bester 1987), Amsterdam Island (Roux 1987a) and Marion Island (Kerley 1987). Starting in 1974 (Condy 1978), population censuses were conducted regularly at Marion Island (Wilkinson & Bester 1990; Hofmeyr *et al.* 1997, 2006; Bester *et al.* 2003, 2011) and are ongoing.

Recolonisation, or recovery of a severely depleted population, occurs in four distinct phases (Roux 1987b). Phase 1, survival, is characterised by few breeding pairs and a low rate of increase (< 5% per annum). During the second phase, establishment, the annual intrinsic growth rate is still lower than 10% but increases as the population grows. Pup mortality decreases with population growth. Recolonisation is the third phase where population density reaches a near-maximum at the original breeding colonies. Subsequently, a rapid recolonisation of the remainder of the coastline occurs. Intrinsic growth rates now reache values as high as 17% per annum and the duration of this phase depends on the number of remaining sites suitable for recolonisation. The fourth and final phase is known as "maturity". All available sites have been colonized and population density reaches high values. Annual growth rates are expected to drop, pup mortality increase and density dependent factors limit growth (Roux 1987b).

Between 1951 and the late 1970s the Subantarctic fur seal population on Marion Island followed the classical population recolonisation trajectory: First a period of survival, where population numbers remained low and increased slowly. During the 1980s and early 1990s it went through a phase of rapid recolonisation and increased exponentially. From the late 1990s up to present (last census 2003/04) the population entered and now remains in the maturity phase, with a mean annual intrinsic growth rate of 5.2% (Hofmeyr *et al.* 1997; Hofmeyr *et al.* 2006). Given the high weaning mass of pups from Marion Island in comparison to that at Gough Island (Bester & Van Jaarsveld 1994) and the increase in colony size in areas outside the main rookeries (Hofmeyr *et al.* 1997), the decrease in the rate of population growth is most likely due to lack of preferred breeding terrestrial habitat rather than a lack of marine resources (Hofmeyr *et al.* 2007). Today, Subantarctic fur seals at Marion Island number nearly 80 000 individuals and together with Prince Edward Island (Bester *et al.* 2003), support a population of *c.* 150 000 Subantarctic fur seals (Hofmeyr *et al.* 2007).

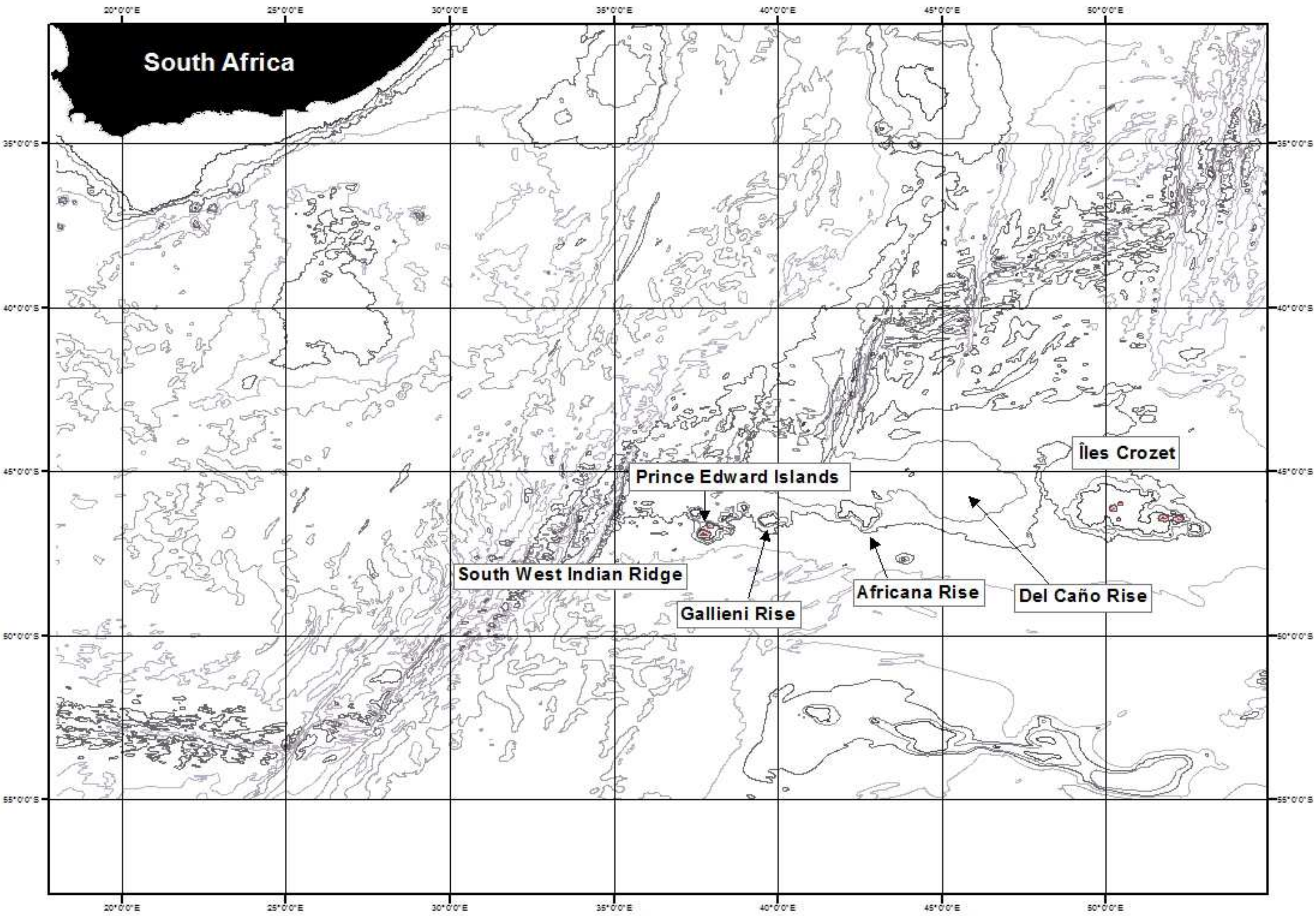

Figure 1.2: *The location of the Prince Edward Islands in relation to surrounding bathymetrical features.*

Objectives of this study

Despite the breadth of research on Subantarctic fur seals at Marion Island, the at-sea foraging behaviour of the species is still largely understudied. At-sea movements of 16 lactating females during one foraging trip each, over two years of study at one site on the northeast of the island, were investigated (de Bruyn *et al.* 2009). Furthermore, the diving behaviour of Subantarctic fur seals has never been studied at Marion Island. De Bruyn *et al.* (2009) suggested that the lack of a peri-insular shelf around Marion Island overshadowed the importance of the proximity of productive frontal systems in terms of foraging cycle durations. Identifying the causes of the disparity in foraging behaviour of the species between geographic locations will not only increase our understanding of foraging ecology (Staniland *et al.* 2004), but could also help to predict changes in populations' structures in the event of natural and human-induced climate variations. Such understanding could also potentially be useful in designing Marine Protected Areas (Lombard *et al.* 2007; Louzao *et al.* 2011). To fully understand the disparity in foraging behaviour, we need to know how females change their foraging behaviour temporally.

If we were to fully understand this disparity in foraging behaviour amongst populations and indentify the physical oceanographic features that drive such foraging behaviour, we need to know whether these preferred foraging areas stay the same between consecutive foraging trips for an individual, and even at a larger temporal scale: summer to winter and year to year.

The overall objectives of this study were therefore to:

1. describe and characterise the diving and ranging behaviour of lactating Subantarctic fur seals from Marion Island.
2. describe and characterise the attendance cycles of lactating Subantarctic fur seals from Marion Island.

These objectives were addressed in three sections:

1) To describe and quantify the timing and depth distribution of diving behaviour of Subantarctic fur seals from Marion Island:
    a. Are females from Marion Island nocturnal foragers and do they follow the diel

vertical migration of their myctophid prey?

b. What parameters measured would accurately describe diving behaviour best (i.e. mean depth, dive duration, bottom time, ascent and descent rates, etc.)

c. How do these values change across several temporal scales, i.e. diel cycles, daily variation within a foraging trip and between summer and winter?

d. How does the diving behaviour of lactating females from Marion Island compare to those of conspecifics from other islands?

2) Investigate foraging site fidelity and tactics at an individual and colony level of Subantarctic fur seals from Marion Island:

a. What is the mean foraging trip duration and distances travelled from the breeding colony beach in the period 2009-2011 and how does it compare with that of 2006 - 2007?

b. How does colony-wide preferred foraging areas change annually and seasonally?

c. Do individual females show preference for specific foraging areas at sea over consecutive foraging trips?

d. How is individual foraging site fidelity influenced by annual and seasonal change?

e. Do females exhibit different foraging tactics based on the direction of foraging from Marion Island?

f. How does temporal variation influence the curvilinearity (i.e. straightness) of a female’s foraging trip?

3) To determine the foraging cycles (at-sea foraging trip and attendance period) for lactating Subantarctic fur seals from Marion Island using presence/absence data of flipper-tagged individuals:

a. What is the mean foraging trip duration and attendance period?

b. How does it differ seasonally and annually?

c. Is it influenced by pup sex?

d. How does this compare with conspecifics from other islands?

e. Is attendance cycle behaviour influenced by El Niño Southern Oscillation and anomalous sea-surface temperatures (measured over multiple temporal scales)?

f. Is observed presence/absence data sufficient to accurately calculate foraging cycle durations?

g. How is the onshore sighting probability of a female influenced by observer-bias?

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Chapter 2:

Diving behaviour of lactating Subantarctic fur seals from Marion Island

Abstract

The first records of diving behaviour in 9 (summer n=4, winter n=5) lactating Subantarctic fur seals *(Arctocephalus tropicalis)* from Marion Island are presented. Simple descriptive statistics are used to explain the diving and depth distributions as well as diving effort across several temporal scales. Females increased their mean diving depths, dive durations and diving effort throughout the lactation period which is consistent with findings from other populations. Females dive exclusively at night and during the summer performed deeper and longer crepuscular dives, presumably to follow the diel vertical migration of their myctophid fish prey. Counter intuitively, during winter females performed shallower and shorter dives at dusk and dawn. This is related to seasonal downward vertical movement of myctophid prey during winter making them inaccessible during dusk and dawn. Females cyclically increased and decreased diving effort throughout a foraging trip. This may represent encounters with prey-patches or females intermittently working harder or taking it easier in terms of dive effort. The diving behaviour of lactating females from Marion Island is most similar to conspecifics from Île de la Possesion (of the Îles Crozet) despite their differences in foraging trip duration and distance travelled offshore. Large differences exist between Marion and Amsterdam island individuals, notwithstanding similarities in foraging trip durations.

This is likely related to underwater bathymetry and distance of a bathymetric feature from the island. Despite Marion Island's location in the productive Polar Frontal Zone, lactating Subantarctic fur seal females work harder at foraging than at any other island population of conspecifics.

Key words: *Arctocephalus tropicalis*; diving behaviour; diving effort; diel variation; seasonal variation; Marion Island

Introduction

With the development of the time-depth recorder (TDR) over the past few decades, came the ability to extensively study the diving behaviour of marine predators (e.g. Gentry & Kooyman 1986; Bonadonna *et al.* 2000, 2001; Lea *et al.* 2002; Staniland *et al.* 2004, 2007; Georges *et al.* 2000b; Luque *et al.* 2007, 2008). Foraging behavioural traits were previously thought to be genetically linked or species bound. It is now known that seals show considerable plasticity with regards to their foraging behaviour (e.g. Goldsworthy *et al.* 2010) and the foraging behaviour of top marine predators are supposedly linked to two major limiting factors.

The first is extrinsic environmental factors that influence the distribution and abundance of prey (Franks 1992; Olson *et al.* 1994). Marine ecosystems are spatio-temporally heterogeneous habitats. Seasonal, physical and geographical variation is considered the main driving force behind the patchy distribution of resources. Hydrographical features such as oceanic fronts and eddies are associated with predator prey distributions (Moore & Abbott 2000; Abbott *et al.* 2000). Where currents meet bathymetric features, upwelling occurs and the subsequent formation of eddies and/or phytoplankton blooms ensue (Ansorge & Lutjeharms 2005). Any variability in primary production is passed up the food chain to higher levels and inevitably influences top marine predators (e.g. Georges *et al.* 2000a; Nel *et al.* 2001; De Bruyn *et al.* 2009; Bailleul *et al.* 2010). The ability of predators to find and utilise these heterogeneously distributed resources will ultimately affect their survival and breeding success.

The second limiting factor – intrinsic limitations or strategies (Lea *et al.* 2002; McDonald *et al.* 2009; Lea *et al.* 2010) influences the ability of top marine predators to deal with the aforementioned spatio-temporal heterogeneity in distributed resources. Intrinsic limitations or strategies range from major physiological inter-species variations to individual variation between or within populations caused by variation in age, body mass (condition) or experience.

Otariid seals (fur seals and sea lions) are central-place foragers (Orians & Pearson 1979). During their breeding season lactating females alternate between pup provisioning periods on land (attendance bouts) and foraging trips at sea (collectively called foraging cycles; Gentry & Kooyman 1986). The distance that females have to travel between their foraging grounds and breeding sites, together with the repetitive diving to catch prey are energetically constraining to them.

The Subantarctic fur seal (SAFS) is one of the most widely distributed fur seals and have breeding populations north of the Subtropical Front (STF) on temperate Gough, Tristan da Cunha, Saint Paul and Amsterdam islands. Within the Polar Frontal Zone (PFZ), SAFS co-occur with Antarctic fur seals (*A. gazella*) on four Subantarctic islands, namely Île de la Possession (of the Îles Crozet), Macquarie and Marion islands (Condy 1978; Bester 1981; Kerley 1987; Guinet *et al.* 1994). Females give birth to single pups over a six week period centred on mid-December (Hofmeyr *et al.* 2007). Pups are weaned ~10 months later in October (Kerley 1983, 1987). The extensive distances between the different island breeding colonies in both geographical longitude and latitude mean they are subjected to a considerable range of geographically different environmental conditions. This allows us to study and understand how lactating females alter their diving behaviour under variable conditions. Their extended lactation period with attendant foraging trips additionally allows for comparisons between summer and winter diving behaviour.

A range of data on the foraging ecology of this species is available, which exhibits flexibility in foraging tactics and behavioural strategies (e.g. Bester & Bartlett 1990; Kirkman *et al.* 2002; Georges & Guinet 2000; Georges *et al.* 2000a, b; Beauplet *et al.* 2004; Bailleul *et al.* 2005; Luque *et al.* 2007, 2008). Disparities in foraging trip duration, distance and diving behaviour of female Subantarctic fur seals from geographically distant island populations are apparent (see de Bruyn *et al.* 2009). Lactating females from temperate Amsterdam Island (AI) undertake extended foraging trips (summer average = 11 days, winter average = 23 days) during which they travel >100 km from their breeding colony towards the northern parts of the STF (Georges *et al.* 2000a,b). In contrast, Subantarctic fur seals from Île de la Possesion (IP) and Macquarie Island (MAC) mostly perform over-night foraging trips (of which ~40 - 50% are <10 km from each island). Even longer foraging trips extended for less than 10 days and rarely exceeded a distance of 60 km and 100 km from MAC and IP respectively (Robinson *et al.* 2002; Bailleul *et al.* 2005; Luque *et al.* 2007). It is suggested that the locations of IP and MAC within the productive PFZ determine the distance travelled during a foraging trip (Georges *et al.* 2000a; Luque *et al.* 2007; Goldsworthy *et al.* 2010). The PFZ is an area characterised by intense mesoscale activity, enhanced biological productivity and biodiversity (Lutjeharms

& Valentine 1984; Park *et al.* 2002; Kostianoy *et al.* 2004) and might be considered an oceanic ecotone. Several studies link top predator movements to this ostensibly rich environment (e.g. Guinet *et al.* 2001; Lea *et al.* 2002, 2006; Lea & Dubroca 2003).

Despite MI's seemingly favourable location within the PFZ, females undertake long foraging trips similar to females from AI and do not perform over-night foraging trips like conspecifics from IP and MAC (de Bruyn *et al.* 2009). De Bruyn *et al.* (2009) suggested that regional bathymetry overshadowed the proximity of productive frontal systems in their influence on movement behaviour of lactating Subantarctic fur seals, but exactly how this is achieved remains untested in the absence of diving data.

The diving behaviour of Subantarctic fur seals has not been studied at Marion Island. Here we present novel data for Marion Island lactating females. We compare their diving behaviour with conspecifics at other islands. In particular those islands that are situated in the same latitudinal band as Marion Island, where females show markedly shorter foraging trip durations and shorter travel distances. Simple descriptive statistics were used to quantify the timing and depth distributions of dives and diving effort. Variations in diving behaviour across multiple temporal scales are investigated.

Methods

Deployment details:

Argos-linked satellite platform transmitter terminals (PTT; Kiwisat 101, Sirtrack, 120g, 110 x 42 x 14 mm, 57 cm^2 cross-sectional area) and time-depth recorders (MK 9

TDR, Wildlife Computers, 30 g, 67 mm x 17 mm x 17 mm) were simultaneously deployed on lactating Subantarctic fur seals between April 2009 and January 2011 at Marion Island (46°54'S, 37° 45'E) on Van den Boogaard beach located on the north-eastern side of the island (fig. 2.1). Van den Boogaard is a low density rookery (Hofmeyr *et al.* 2006) and is characterised by large boulders bounded by 2-7 m high cliff faces and backed by a vegetated area. Five PTT/TDR combinations were deployed during the winter of 2009, 4 combinations during the winter of 2010, and five combinations during the summer of 2011.

Females seen suckling a pup were individually caught in a hoopnet and physically restrained for approximately 30 min during device attachment. TDRs were set to only sample when wet at a sampling interval of 1 sec for depth and temperature readings. All TDRs had a depth reading resolution of 1 m. The MK 9 TDR was fastened with a hose-clamp to a nylon shade-netting strip. This assembly was attached to the fur on the dorsal midline of the seal just anterior to the scapulae. Simultaneously a PTT, linked to the ARGOS Collection and Location System, was attached a hand's length posterior to, and in line with, the TDR. Both the PTT and TDR were attached by means of a double-component, quick-setting epoxy resin (Araldite AW2101, CIBA-GEIGY Ltd.). The device assemblies were removed when the instruments approached the limit of their battery life (~4 months) by carefully cutting the fur underneath the devices while the female carriers were restrained as explained above.

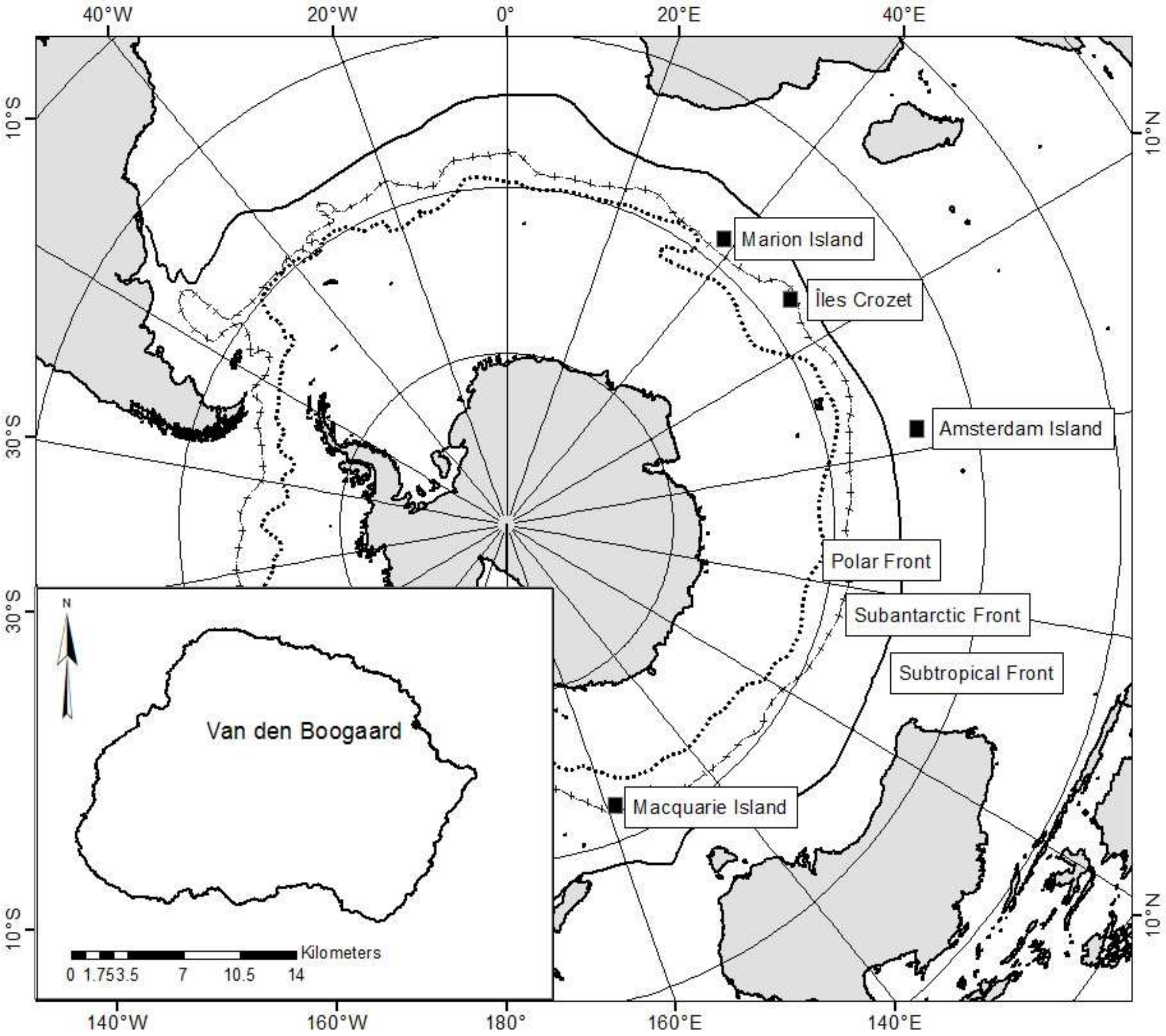


Figure 2.1: *The position of Marion Island in the Southern Ocean in relation to Île de la Possession (Îles Crozet), Amsterdam Island & Macquarie Island as well as the Antarctic Polar Front, Subtropical Front and the Subantarctic Front. The location of Van den Boogaard beach (study beach) on Marion Island is indicated (inset).*

Dive analysis:

Of the 14 females fitted with TDRs we retrieved diving records from 9 females; including devices that were redeployed, one device malfunctioned, 5 females never returned and 2 devices were lost at sea. (see table 2.4 in appendix for a summary of deployment details).

TDR data was extracted with "Hex Decoder V2.02.0030" software of Wildlife Computers. All dive analyses were performed using the R package diveMove (Luque 2007; R Development Core Team 2011). Zero-offset correction was performed using the "offset" method and using a correction factor of one. A minimum dive depth of 4 m and dive duration of 20 sec were chosen to exclude travelling and prey-handling behaviour and make the study comparable with others (e.g. McDonald *et al.* 2009). Summary statistics for each dive was calculated using the "diveStats" function in diveMove (Luque 2007). Daily averages from location data were used to calculate local apparent time of each dive. Local sunrise and sunset times were calculated using the maptools package in R (Lewin-Koh & Bivand 2011, R Development Core Team 2011).

Diving variables:

A combination of previously described dive variables were chosen for analysis (Lea *et al.* 2002; Goldsworthy *et al.* 2010; Staniland *et al.* 2010). These 9 variables were chosen to (i) accurately describe the timing and depth distribution of dives performed by lactating females (i.e. dive depths and durations) and (ii) to evaluate the influence of several temporal scales on dive variables. These temporal scales are: hour of the night, day of the foraging trip since departure from the island, and the difference between winter and summer on the diving effort (see below) expended by each individual. The variables tested are: (1) maximum depth per dive, (2) mean distance travelled at the bottom of the dive (i.e. sum of dive wiggles' distance; Lea *et al.* 2002) (3) mean dive duration, (4) mean bottom time per dive, (5) mean post dive duration, (6) mean dives per hour, (7) mean number of dives per trip, (8) % night spent diving per foraging night and (9) vertical distance travelled per hour. Variables 1-5 were used to describe timing and depth distribution of dives whereas variables 6-9 were used as a measure of diving effort.

Data manipulation:

Annual variation in prey abundance has been linked to changes in females' foraging strategies and trip durations. During years of 'normal' food availability, females performed short foraging trips and maximised time spent diving while reducing travelling and resting time (e.g. Boyd *et al.* 1994; Arnould *et al.* 1996; Boyd 1996). When resources were scarce, females exhibited longer foraging trips and spent comparatively more time diving per trip (Goldsworthy 1995; Beauplet *et al.* 2004). During the winter and summer seasons between 2009 and 2011 there were no significant differences in foraging trip and onshore attendance durations (chapter 4). This observed lack of annual variation in foraging cycles allowed the assumption of little or no annual variation in diving behaviour in the lactating females from this study. Diving data from the winters of 2009 and 2010 were subsequently pooled into "winter data". The "summer data" refers to diving records obtained during the summer of 2011.

Night groups:

At some islands, Subantarctic fur seals are nocturnal foragers (e.g. Georges *et al.* 2000a, Robinson *et al.* 2002, Luque *et al.* 2007). To assess whether MI females dive nocturnally, and to account for the seasonal changes in day length, we calculated the mean ± standard error (SE) of each dive variable and plotted it against one of 5 night time groups as follows: “Dusk” included all dives performed within one hour before and after sunset. “Evening” all dives performed one hour after sunset to 23h00, “Midnight” all dives between 23h00 and 02h00, whereas “morning” included dives between 02h00 and one hour before sunrise. Lastly, “dawn” represents dives performed within one hour before and after sunrise. The particular cut-off times for “dusk” and “dawn” coincided with the diel vertical migration of fur seal myctophid fish prey (Klages & Bester 1998, Knox 2007, Catul *et al.* 2011). We tested differing delineations of evening, midnight and morning by shifting cut-off times by 1 and 2 hours in each direction. Exploratory plots revealed no observable differences. Means and standard errors were calculated for each variable within each night group, separately for ‘winter’ and ‘summer’.

Daily variation throughout a foraging trip:

For each day after departure from the island, daily averages (± SE) were calculated of each of the nine dive variables. This was done to determine how females’ daily foraging effort fluctuated throughout a foraging trip. In other words, did it remain constant throughout the trip or did they, e.g. only dive towards the middle or end of the foraging trip.

Results

General attendance behaviour:

During winter, females (n = 4 in 2009 and n = 1 in 2010) collectively performed eight foraging trips that were on average 40.1 ± 32.8 days long. This was significantly longer (Kruskal-Wallis $\chi^2 = 16.26$, $P < 0.0001$) than the summer foraging trip lengths (mean foraging trip duration = 10.76 ± 3.5 days) of 21 foraging trips by four lactating females.

General diving behaviour:

We recorded 73496 dives during the winter of which 99.97% (73476) were performed at night. Table 2.1 provides a breakdown of the total number of dives, night dives and daily dives performed by each of the instrumented females. The absolute maximum depth reached was 163.5 m for a dive lasting 3.5 min while the longest dive by any individual took 5.7 min to a depth of 88 m. The mean maximum dive depth (±SE) recorded for all seals in the winter (n = 5) was 53.5 ± 28.6 m and mean dive duration was 1.7 ± 0.77 min. In the summer, 99.9% (37310) of dives occurred at night. The deepest dive was 144.5 m and lasted 3 min, while the longest dive lasted 4.1 min to a maximum depth of 93 m. The mean maximum dive depth recorded for all seals during summer 2011 (n = 4) was 34.06 ± 19.08 m and mean dive duration was 1.16 ± 0.62 min (table 2.2). A total of 20 and 37 day-time dives were recorded for the winter and summer respectively, and all occurred within an hour of sunrise and sunset. Since we only used daily average locations, and not an exact point location for each dive, it is possible that these dives might have occurred between dusk and dawn.

Table 2.1: *Summary of the total number of dives, night dives and daily dives performed by each of the instrumented lactating Subantarctic fur seals from Marion Island.*

Seal tag nr	**TDR number**	***N* of day dives included**	**Total *n* of night dives**	**Total *n* of dives used**
Winter 2009				
GW495	0890425	0	6736	6736
GW522	0890438	0	3726	3726
FB515	0890439	20	10794	10814
	0890440	0	6959	6959
FB513	0990062	0	27526	27526
Winter 2010				
A184	0990466	39	17735	17774
Summer 2011				
A188	0990473	9	11645	11654
A142	0990474	17	11126	11143
LB504	0990476	1	8440	8441
GW503	0990471	10	6099	6109

Table 2.2: *Quantitative summary of diving behaviour of lactating Subantarctic fur seals from Marion Island, comparing winter to summer. Means ± SE are shown.*

Dive Variable[a]	**Summer**	**Winter**
Total *n* of dives	37347	73496
Night Dives	37310	73476
Mean dive depth ± SE	34.5 ± 2.2 m	45.2 ± 4.8 m
Median dive depth ± SE	31.5 ± 2.1 m	44.4 ± 5.1 m
Mean bottom depth ± SE	28.1 ± 2.0 m	36 ± 3.3 m
Deepest dive	144.5 m	163.5 m
Mean dive duration ± SE	70.2 ± 3s	104.3 ± 7.8 s
Median dive duration ± SE	63.8 ± 4.5s	103.3 ± 9.7 s
Mean bottom time ± SE	49.1 ± 2.1s	72.2 ± 7.8 s
Longest dive	245 s	340 s
Dives per hour at night ± SE	19.1 ± 1.7	17.7 ± 1.6
% Night spent diving ± SE	32.2 ± 2.9 %	43.9 ± 1.8 %
Mean post dive duration ± SE	317.6 ± 67.1 s	284.86 ± 39.8 s
Median post dive duration ± SE	34.8 ± 3.5 s	39 ± 6.3 s
Mean foraging trip length ± SE	12.1 ± 1.2 days	39.4 ± 10.1 days
Mean dives per trip ± SE	1829.1 ± 287.1	8886 ± 2383.7

[a] The mean was used for each individual to avoid pseudoreplication.

Histograms revealed two modes when plotting maximum dive depth (first mode ~6-20 m and second mode ~45-55 m), dive duration (first mode ~20 sec and second mode ~95 sec) and bottom time (first mode ~10 sec and second mode ~50-70 sec) during the winter, and a unimodal distribution for bottom distance (mode ~5 m) (see fig. 2.2). Summer showed a less distinct bimodal distribution for maximum dive depth (first mode ~20 m; second mode ~35 m) and dive duration (first mode ~20 sec; second mode ~75 sec) with the modes closer together than during the winter. Bottom time and distance both had a unimodal distribution (modes at 20 sec and 20 m respectively). When plotting each of the variables separately for each foraging trip the first three foraging trips in the summer retained a unimodal distribution with the highest number of dives to shallower depths and with shorter durations. Foraging trips four to six, however, showed bimodal distributions for maximum dive depth (first mode range: 8-12 m and second mode range: 30-50 m) and dive duration (first mode range: 25-50 sec and second mode range: 75-80 sec). A visual inspection of diving depth in winter plotted against time of day revealed several clusters of shallower dives in between deeper dives. No clear pattern is apparent as to when a female performed such bouts (clusters) of shallower dives.

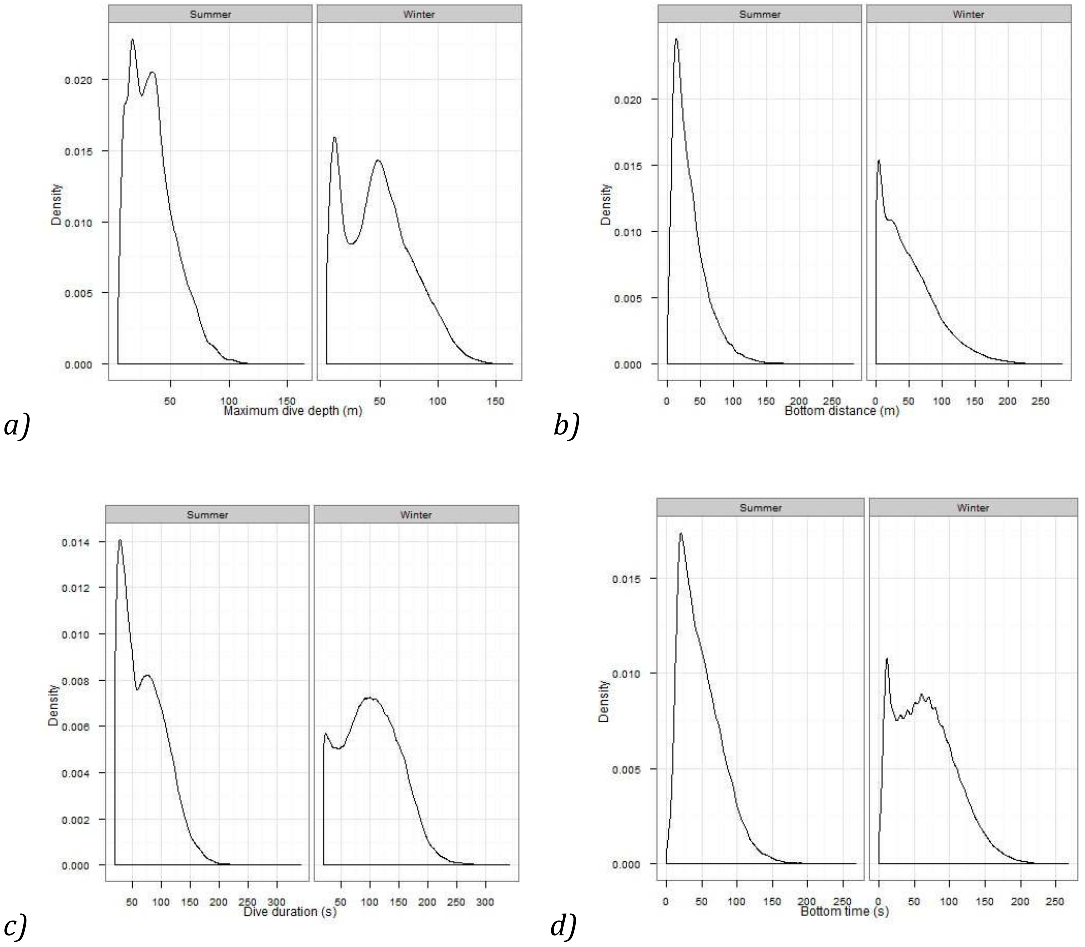
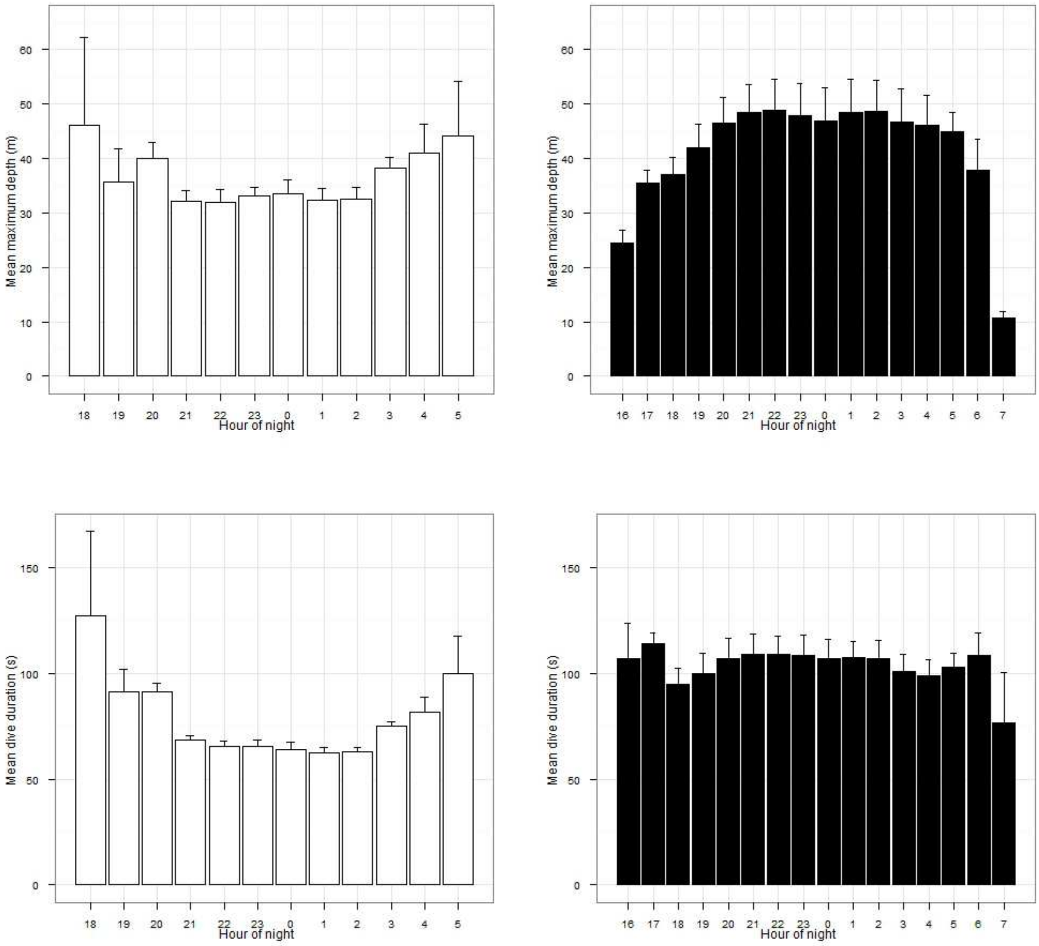


Figure 2.2: *Density plots revealing a difference between summer and winter in the distribution of a) maximum dive depth (m), b) vertical distance travelled at the bottom of the dive (m), c) dive duration (s) and d) bottom time (s) recorded for lactating Subantarctic fur seals from Marion Island.*

Diving behaviour across night groups:

Overall, summer and winter differed greatly in terms of how nocturnal diving effort changed for the seals (figures 2.3 & 2.4). In the summer, females started to dive later in the evening and stopped earlier in the morning as compared to winter, which is consistent with shorter nights in summer than in winter. Figures 2.5 a-b illustrates the inverse relationship in females' nocturnal diving depth distributions between summer and winter. For summer and winter, dusk and dawn diving times were equal, but during the remainder of the night winter and summer females showed no overlap in timing and depth distribution of dives (figures 2.5 c-d). However, diving effort between summer and winter was more similar throughout the night, with smaller differences during the middle of the night as compared to timing and depth distribution of dive variables (figure 2.6).



a)

b)

Figure 2.3: *Hourly changes in a) maximum dive depth (m) and b) dive duration (s) by lactating Subantarctic fur seals from Marion Island. Variables illustrate differences between summer (□) and winter (■). Values represent means + SE.*

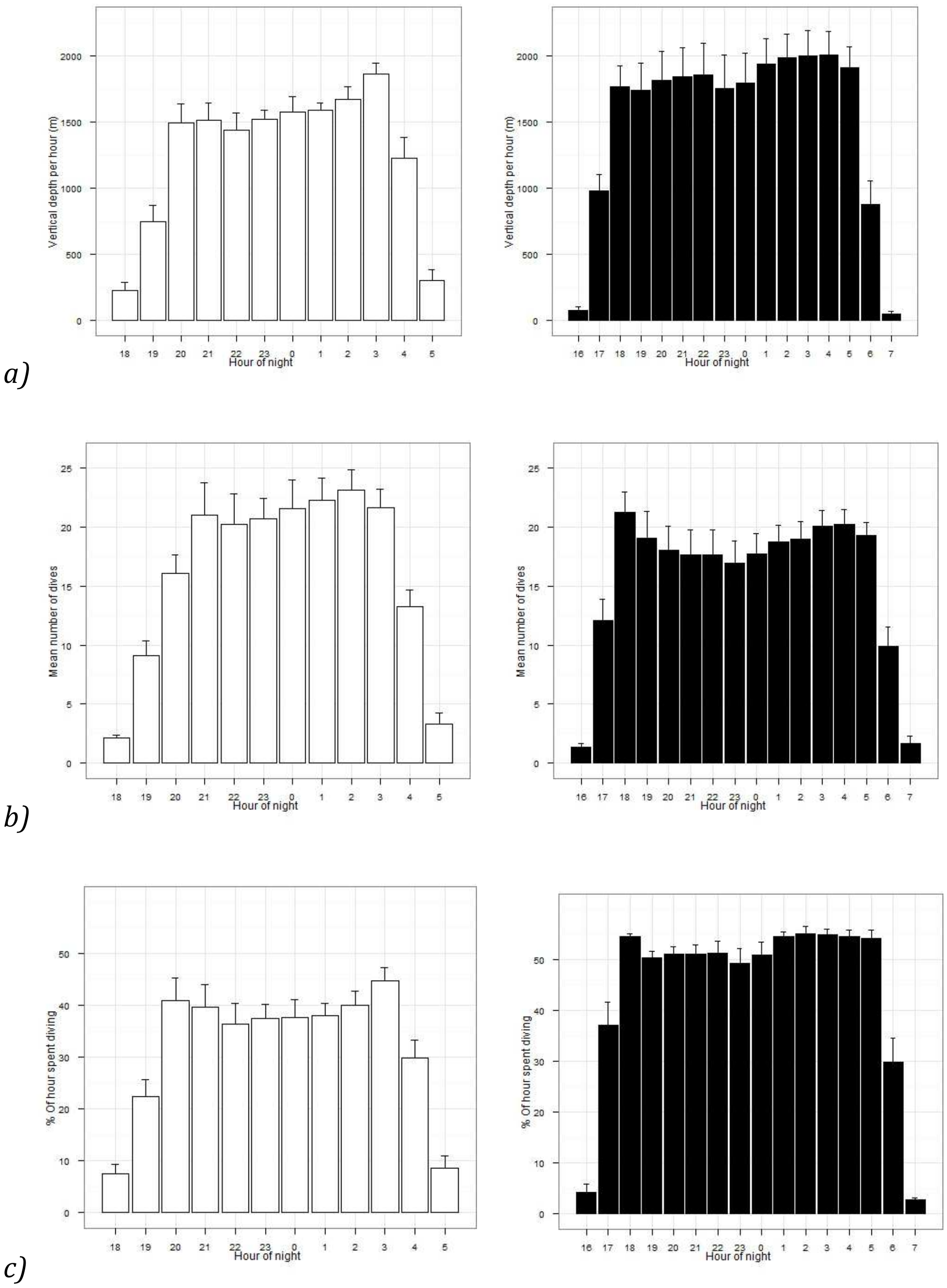
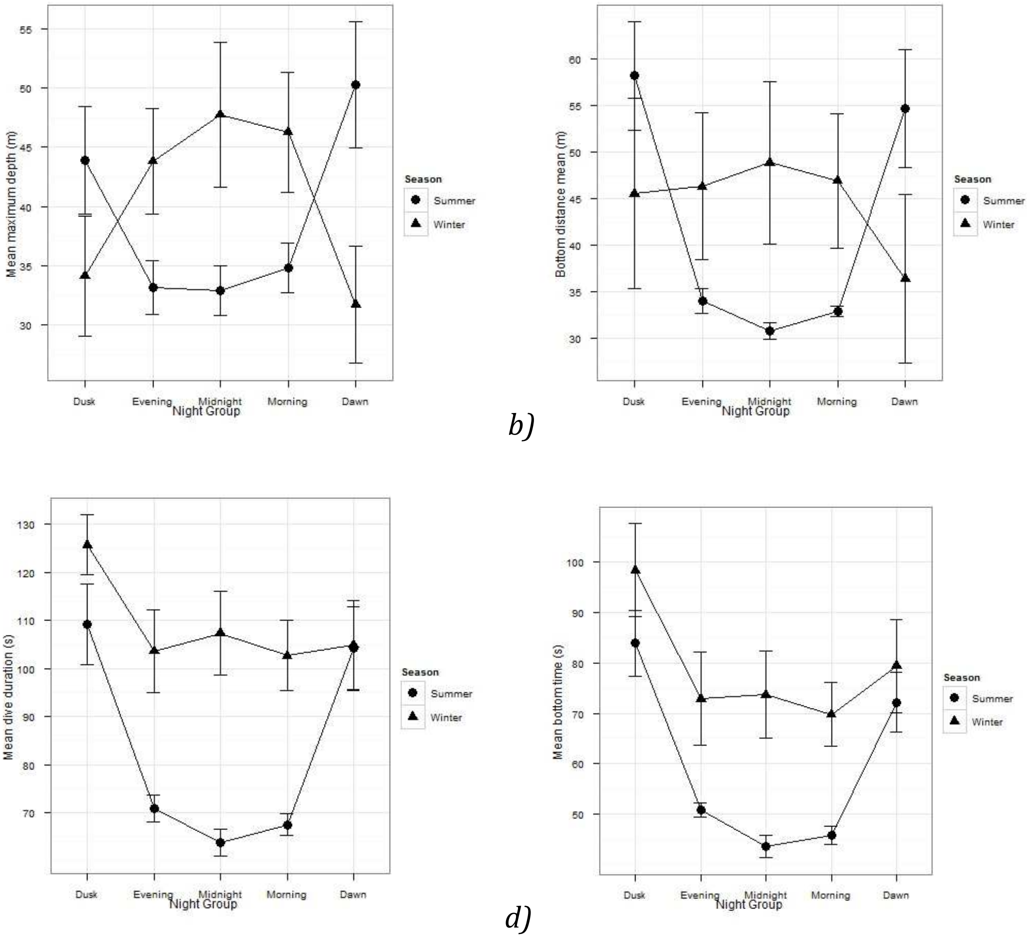


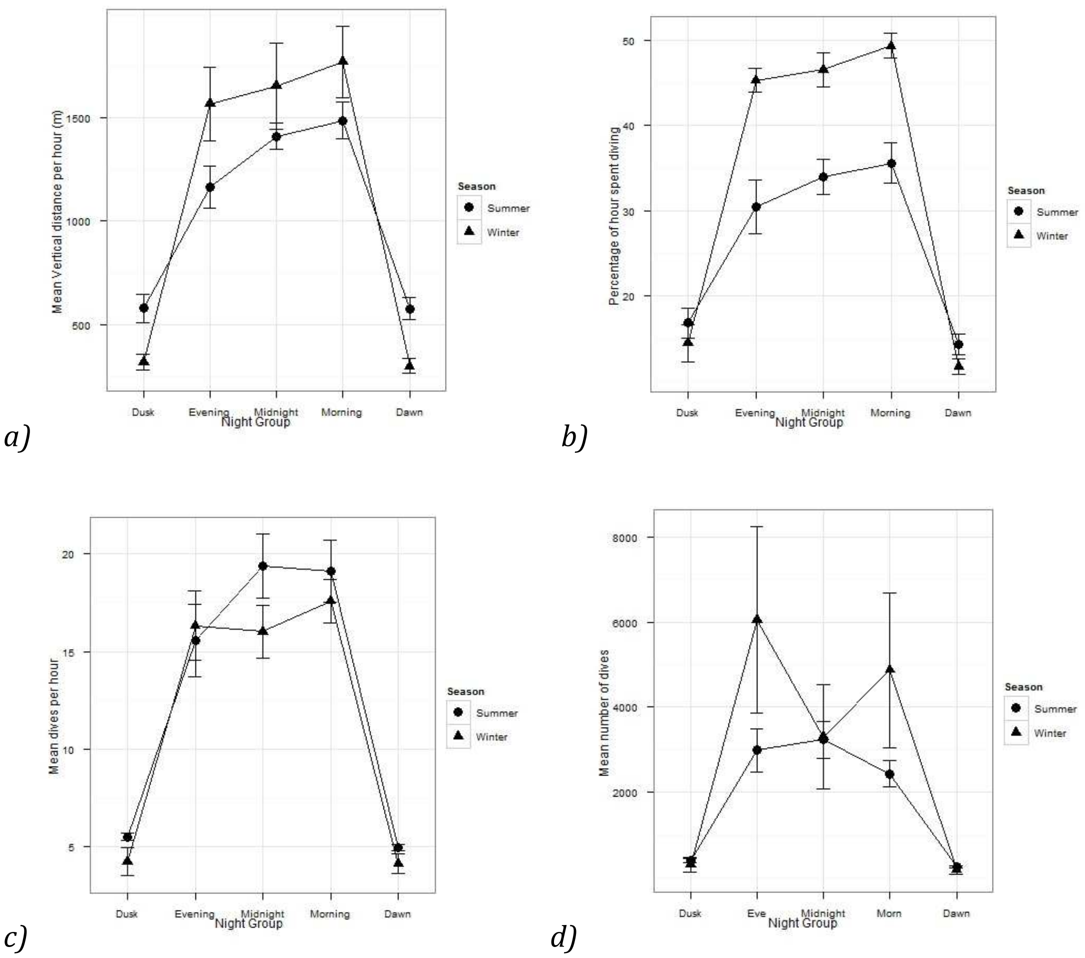
Figure 2.4: *Hourly changes in dive effort indicated by a) vertical distance travelled per hour (m.h^{-1}), b) dives per hour, and c) percentage of hour spent diving by lactating Subantarctic fur seals from Marion Island. Variables illustrate differences between summer (□) and winter (■). Values represent means + SE.*



a) *b)*

c) *d)*

Figure 2.5: *Diurnal change in a) maximum depth (m); b) bottom distance travelled (m); c) dive duration (s), and d) bottom time (s) between the different night groups of lactating Subantarctic fur seals from Marion island. Values presented are means ± SE.*



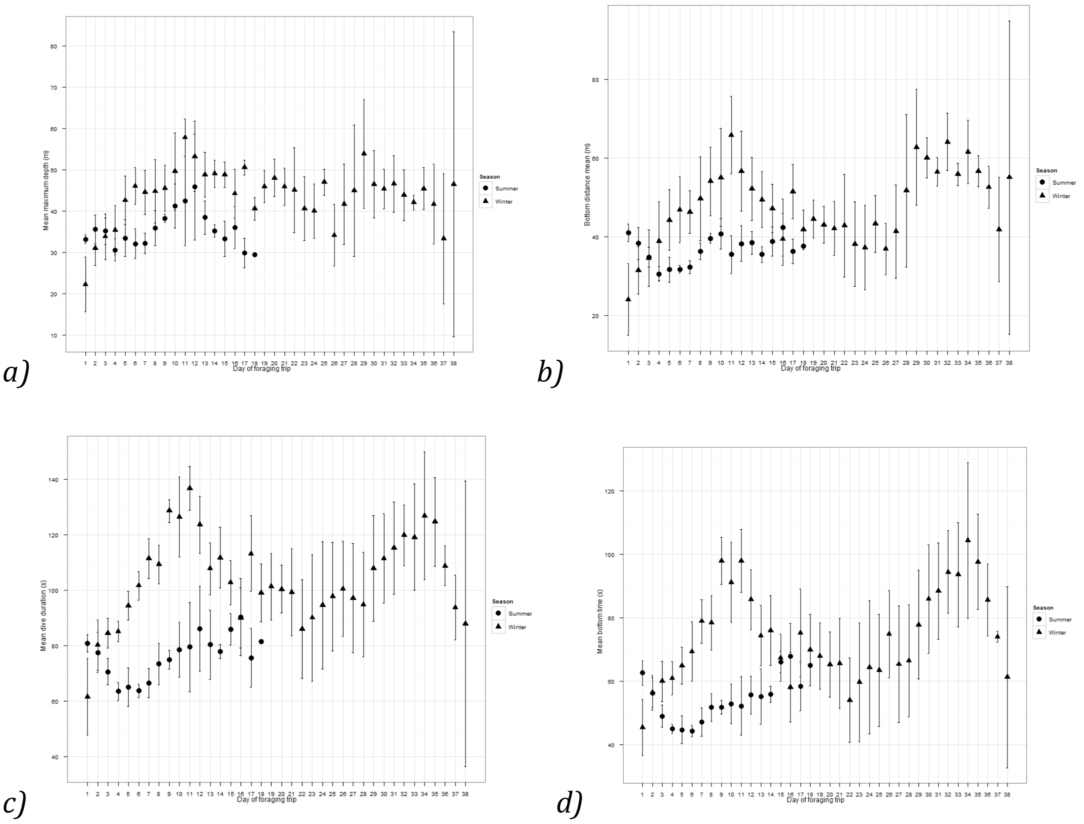
a) *b)*

c) *d)*

Figure 2.6: *Diurnal change in diving effort of lactating Subantarctic fur seals from Marion Island as measured by a) vertical distance per hour (m.h^{-1}); b) percentage of hours spent diving, c) dives per hour performed, and d) the total number of dives recorded within each night group. Values presented are means ± SE.*

Daily variation throughout a foraging trip:

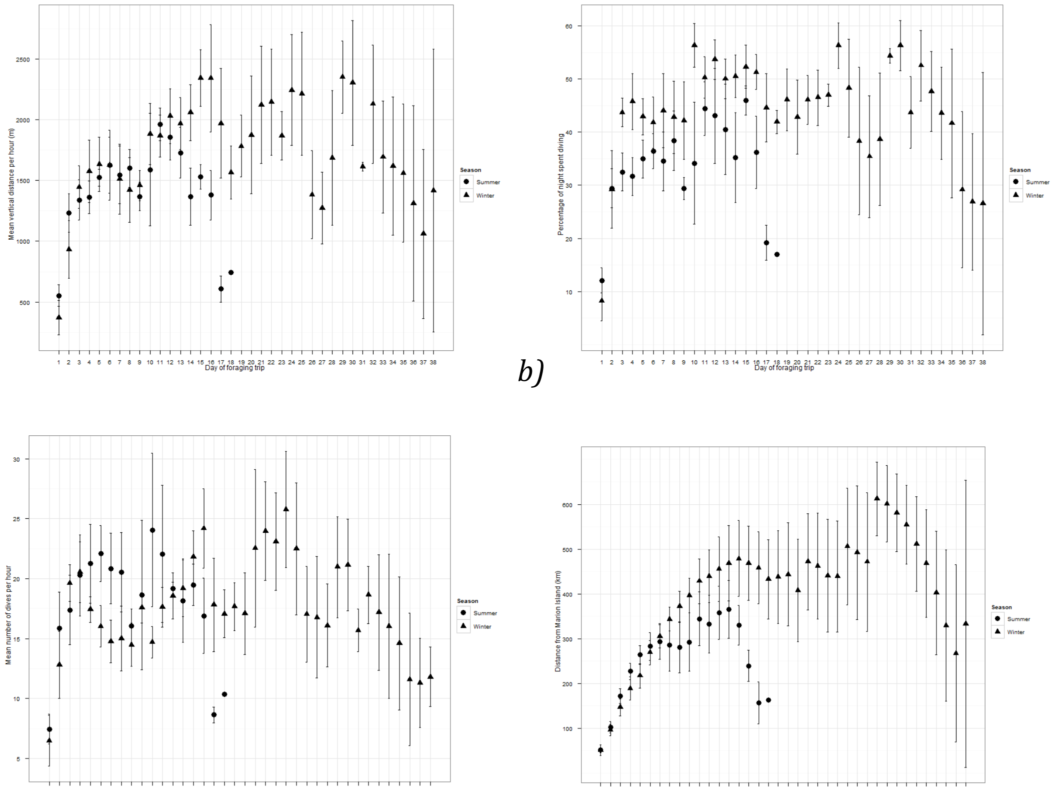
There is a cyclic change as the days elapse after departure from the island in each of the variables. During both the summer and the winter diving depth and duration variables of the females peaked on day 11 or 12 (fig. 2.7; fig. 2.8 a-c). On days 11 and 12 after departure from MI, summer and winter females were approximately at the same distance from the colony (fig. 2.7d). There was no overlap between winter and summer related to the bearing at which females travelled from the island. Additional comparisons of each of the variables to the distance at which females were from the island on each day showed no patterns, daily fluctuations or groupings and appeared to vary at random.



a) *b)*

c) *d)*

Figure 2.7: *Daily change in a) mean maximum depth (m); b) bottom distance travelled (m); c) dive duration (s), and d) bottom time (s) recorded for lactating Subantarctic fur seals after departure from Marion Island. Values presented are means ± SE.*



a)

b)

c)

d)

Figure 2.8: *Daily change in diving effort of lactating Subantarctic fur seals as measured by a) vertical distance per hour (m.h^{-1}); b) Percentage of the night spent diving c) dives per hour performed, and d) the total distance from Marion Island (km) after departure of the island. Values presented are means ± SE.*

Table 2.3: *Summary of dive variables from lactating Subantarctic fur seals, comparing Marion Island with Île de la Possession, Amsterdam and Macquarie islands. For Île de la Possession overnight foraging trips (OFT) and long foraging trips (LFT) are separated (Luque et al. 2007). At Macquarie Island no differences exist between OFTs and LFTs, but inter-annual differences (Robinson et al. 2002) occur. Female dive statistics from Marion and Amsterdam islands are separated into winter and summer (Georges et al. 2000b; this study). Values presented are means ± SE.*

Island	**Amsterdam**		**Possession**		**Marion**		**Macquarie**	
Dive Variable	**Summer**	**Winter**	**OFT**	**LFT**	**Summer**	**Winter**	**1995/96**	**1991**
Mean dive depth (m)	19±0.4	29±1	37.8±0.35	45.7	34.5±2.2	45.2±4.8	9.9	14.2
Median dive depth (m)	n/a	n/a	37.4±0.46	43.7±0.48	31.5±2.1	44.4±5.1	8	10
Mean max depth (m)	110	183.2	99.9	89.3	131.4	137.2	n/a	n/a
% Dives performed at night	99	100	98	98.5	99.9	99.7	98.9	94.9
Mean dive duration (sec)	64.8±1	91.2±2.2	88.1±	103	70.2±3	104.3±7.8	39	41.4
Median dive duration (sec)	n/a	n/a	88.3±0.66	108	63.8±4.8	103.3±9.7	30.6	30.6
Mean bottom time (sec)	33±0.8	48.1±1.9	34.9	39.5	49.1±2.1	72.2±7.8	n/a	n/a
Dives per hour	8.9	10.2	n/a	n/a	19.1±1.7	17.7±1.6	11.2±4.8	14.4±2.8
% Night spent diving	15.6	27.8	33.1	33.1	32.2±2.9	43.9±1.8	13±7.1	14.6±3.4
Mean foraging trip length (days)	11	23	0.48±0.02	5.23±0.51	12.1±1.2	39.4±10.1	0.2-9.6*	0.4-8.5*
Deepest dive (m)	n/a	208	141	134	144.5	163.5	95	108
Longest dive (s)	n/a	390	310	255	245	340	180	184.2
Vertical distance per hour ($m.h^{-1}$)	330	591	1105.8	10824	1306.5±63.8	1600±146.7	107.2±46.8	195.9±44
Ascent rate	1.31	1.18	1.23	1.22	2.8	2.8	n/a	n/a
Descent rate	1.27	1.26	1.07	89.3	2.5	2.5	n/a	n/a

* For Macquarie Island, this represents the range of foraging trip length from OFTs to LFTs

Discussion

This study illustrates how the diving behaviour of lactating Subantarctic fur seals from MI is more similar to that of females from neighbouring IP despite their disparity in foraging trip durations and distance of foraging locations from their colonies. These islands are on similar latitude and distance north of the APF. MI females' diving behaviour differed markedly from conspecifics at MAC and AI and also showed variation in their diving behaviour across several temporal scales. However, a small sample size precludes any definitive hypothesis testing. Furthermore, winter data remains lacking for IP and MAC.

Diel variation:

Subantarctic fur seals from MI are nocturnal foragers (99.7% of dives), as at other islands (Georges *et al.* 2000a, Robinson *et al.* 2002, Luque *et al.* 2007). During the summer, females also change their diving behaviour throughout the course of the night. They perform deeper and longer crepuscular dives as they evidently follow the diel vertical migration of their myctophid prey. These crepuscular movements are in congruence with animals from MAC (Robinson *et al.* 2002), and other Arctocephaline populations that forage on pelagic species (e.g. Croxall *et al.* 1985; Gentry & Kooyman 1986; Goebel *et al.* 1991; Boyd & Croxall 1992; Lea *et al.* 2002). At AI females dive deeper, longer and have longer bottom times at dusk. At dawn, however, they only perform appreciably longer dives, spending more time at the bottom of dives but do not follow their prey to increased depths (Georges *et al.* 2000b).

Diving to shallower depths at dusk and dawn and performing deeper dives during the night, as shown for MI females, is not new to the species. Luque *et al.* (2007) found a similar pattern in females from PI when they performed short over-night foraging trips, and diving data from two winter females coincided as well. No explanation as to why the females dive deeper during the night than at dusk and dawn is proposed (Luque *et al.* 2007). At AI, winter females dive longer and spend more time at the bottom of their dives than at MI; however, they show no significant change in dive depth throughout the night (Georges *et al.* 2000b). Explanations for these observed differences are confounded by our limited sample size. During the winter, productive layers in the ocean move down in the water column (at 40°S below 520 m; Metzl *et al.* 1999) and myctophid prey descend to greater depths (350-500 m) and inhabit the top layer of the Circumpolar Deep Water (Knox 2007). Thse layers would be inaccessible to diving females during dusk and dawn (Georges *et al.* 2000a & b). We suggest that the deeper dives performed during dusk translate to either searching behaviour (iterated by longer bottom times) or females targeting a different prey type.

Myctophid fish constitute the main diet of Subantarctic fur seals (Klages & Bester 1998), however, cephalopods are also taken, albeit in small numbers (Bester & Laycock 1985; de Bruyn *et al.* 2009). Importantly, however, scat analyses misrepresent the importance of cephalopod abundance in the diet of fur seals in general (e.g. Klages & Bester 1998; Ferreira & Bester 1999; Staniland 2002; de Bruyn *et al.* 2003). At night the females would forage on myctophids because the prey is within their reach. At dawn when prey migrates down to the bottom layers and are presumably once again beyond their reach, females may concentrate their diving and foraging in search of prey (e.g. cephalopods) that remain in shallower depths (Georges *et al.* 2000b). Georges *et al.* (2000b) alluded that females also might be satiated at dawn and may not unnecessarily expend energy to follow the vertical migration of their prey. However, this seems an unlikely explanation considering that during the winter, food resources are scarcer (Mann & Lazier 1991; Knox 2007), the demands of the growing pup are higher and females may also be pregnant with next season's pup (Bester 1995; Georges *et al.* 2000a).

Antarctic fur seals *(Arctocephalus gazella)* use two different dive types – "shallow" dives averaging 8.6 m, and "deep" dives averaging 48.6 m (Goldsworthy *et al.* 2010). In the present study, Subantarctic fur seal females also prefer two dive depths in the summer (shallow = 15-20 m, deep = 35-40 m) and winter (shallow = 6-20 m, deep= 45-55 m). Goldsworthy *et al.* (2010) relate this disparity in dive depths to differences in diving locations in terms of ocean depth. In our case, visual inspection of dives provides no clear pattern. Further analysis of spatial data is required to provide an answer for MI animals.

Daily variation throughout a foraging trip:

Females change their diving behaviour daily with periods of increased foraging effort, diving to deeper depths for longer, or spending more time at the bottom of a dive. Diving effort increased daily after leaving the island, after which it fluctuated throughout the rest of the foraging trip. Georges *et al.* (2000a) identified three foraging phases throughout a trip for lactating female Subantarctic fur seals from AI. During the first phase, females swim directly towards the subtropical front foraging grounds, performing no foraging dives along the way. The second phase is characterised by intensive diving and very little travelling and the last phase by a decreased diving effort and increase in travelling. They suggest that during the first phase females swim directly to a known foraging location, phase two is intensive foraging and phase 3 is the return phase to the island when females forage opportunistically when encountering prey-patches. Contrary to females from AI, MI females start diving within hours of departure from the island.

Even though diving effort was lower during the first few days after departure from MI, dives per hour, vertical depth change per hour and percentage of an hour spent diving remained higher when compared to AI and MAC (table 2.3). Prey-searching behaviour therefore seems an unlikely explanation for diving effort during the first days of a foraging trip.

Perhaps resources are indeed available close to the island, but not abundant enough to meet female energetic requirements. Large SE values and fluctuations in diving variables across days after departure from MI could be interpreted as encountering prey-patches (Georges *et al.* 2000a). However, the lack of any such peaks and dips in dive variables with distance from the island suggests that females tire and after maximising their diving behaviour for a few days, rest more on subsequent days.

Inter-island comparisons:

Subantarctic fur seal females from MI surpass those from AI and MAC in all dive variables (table 2.3). Conversely, the majority of dive variables of lactating females were similar between MI and IP. Mean dive depth of females at IP is only slightly higher than those from MI (39.7 m vs. 34.5 m at MI). The same is true for mean dive duration but the percentage of the night time spent diving is the same for females from the two localities. MI females exceed those at all other islands in terms of vertical distance travelled per hour (i.e. dive rate), ascent and descent rate, bottom time and mean maximum depth. However, these differences between the MI and IP female populations are small in comparison to those between MI, AI and MAC. The mean dive depth and duration for the two females from IP measured during winter decreased (Luque *et al.* 2007), in contrast to the current study and to that of Georges *et al.* (2000b) where females increase their diving effort from summer to winter. However, because Luque *et al.* (2007) collected this type of data for only two females, the comparison is preliminary.

Research on other fur seal species relates changes in diving behaviour to changes in prey species and geographic region (Beauplet *et al.* 2004; Page *et al.* 2005; Goldsworthy *et al.* 2010). Klages & Bester (1998) hypothesized that local bathymetry influence available prey species which in turn dictates diving behaviour. Evidence suggests that at islands with a narrow shelf (e.g. MI, MAC and AIs) fur seal females feed off-shore on mesopelagic open ocean prey species (e.g. myctophid fish, e.g. de Bruyn *et al.* 2009) whereas at islands with an underwater shelf or plateau (i.e. Îles Crozet) they predominantly forage near-shore on benthopelagic species (e.g. channichthyid fishes) (*c.f.*

Goldsworthy *et al.* 2010). However, Subantarctic fur seals forage on myctophid fish prey at IP (Luque *et al.* 2007), MI (Klages & Bester 1998), AI (Beauplet *et al.* 2004) and MAC (Robinson *et al.* 2002). Although the prey-species composition in their diets differ; for those females at IP it is only superficially different to that at MI (de Bruyn *et al.* 2009). Females from MI and IP show no overlap in their summer foraging areas. Therefore, it seems that prey species availability dictates diving behaviour and effort, which is in turn affected by the bathymetry over which foraging patches are found (Reid *et al.* 2006). Pelagic oceanographic sampling of known foraging areas for both populations are required to identify available prey before any definitive conclusions could be drawn.

In summary, although lactating females from MI and IP differ in foraging trip duration and distance travelled (de Bruyn *et al.* 2009; this study), they share most similarity in diving behaviour as compared with AI or MAC. The absence of a peri-insular shelf or nearby plateau at MI appears to dictate foraging locations which necessitates long distance travel, whereas the water depth and available prey at the foraging sites determine diving behaviour (this study).

Appendix

Table 2.4: *Summary of time-depth recorder (TDR) deployments on lactating Subantarctic fur seals at Marion Island from the winter of 2009 to the summer of 2011.*

Seal tag nr	TDR number	Deployment date	Retrieval date	Data corrupted (Y/N)	Comments:
Winter 2009					
	0890425	2009/04/24	2009/06/06	N	0890425 is replaced by 0990066
GW495	0990066	2009/06/09	Did not retrieve		Not replaced
GW524	0890429	2009/04/24	Did not retrieve		Not replaced
	0890438	2009/04/24	2009/05/21	N	0890438 is replaced by 0990061
GW522	0990061	2009/05/21	2009/09/10	Y	Not replaced
	0890439	2009/04/28	2009/06/09	N	0890439 is replaced by 0890440
FB515	0890440	2009/06/09	Did not retrieve		Not replaced
	0890440	2009/04/28	2009/05/27	N	0890440 is replaced by 0990062
FB513	0990062	2009/05/27	2009/09/27	N	Not replaced

Table 2.4 (continued): *Summary of time-depth recorder (TDR) deployments on lactating Subantarctic fur seals from the winter of 2009 to l the summer of 2011.*

Seal tag no	TDR number	Deployment date	Retrieval date	Data corrupted (Y/N)	Comments:
Summer 2010					
OO455	0890438	2010/03/07	Did not retrieve		Not replaced
OO7478	0990062	2010/03/21	Did not retrieve		Not replaced
Winter 2010					
A184	0990466	2010/05/02	2009/07/23	N	Not replaced
OO456	0990467	2010/05/05	Did not retrieve		Not replaced
Summer 2011					
A188	0990473	2011/01/02	2011/03/20	N	Not replaced
A142	0990474	2011/01/03	2011/03/24	N	Not replaced
GW503	0990471	2011/01/02	2010/03/13	N	Not replaced
LB504	0990476	2011/01/03	2011/03/07	N	Not replaced
A187	0990475	2011/01/04	Did not retrieve		Not replaced

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Chapter 3:

Colony-wide and individual foraging site fidelity of lactating Subantarctic fur seals from Marion Island

Abstract

This study examines both inter- and intra-individual foraging site fidelity of lactating Subantarctic fur seals from Marion Island. Eighteen individuals were tracked between the winters of 2009 and 2011 and produced 59 foraging trips. Analogous with previous at-sea data from Marion Island, a colony-preferred foraging area lies north-east of the island and the fur seals foraged over the Del Caño Rise, Africana Rise and Gallieni Rise. In the summer, trips were due east from Marion Island, with females staying closer to the island and concentrating foraging efforts over the Gallieni Rise. Trips were also more direct with females supposedly swimming to patches of known prey quality. In the winter females foraged north-east and further afield, over the Del Caño Rise. A few individuals travelled west of Marion Island but only one female travelled west on more than one occasion. Trips to the west of Marion Island are most likely a short-term response to an inability to find sufficient prey, rather than a long-term consistent foraging tactic. Winter foraging trips were more indirect, indicating that females spent more time searching for quality foraging patches. Individuals showed a high degree of foraging site fidelity in all years and seasons. This study highlights individual and colony preferred foraging locations of a top predator. This is crucial for identification of highly productive marine areas and the development of marine protected areas.

Key words: Foraging site fidelity; directional preference; foraging tactic; satellite telemetry; Subantarctic fur seal; Marion Island.

Introduction

The survival and reproductive success of an animal is, amongst others, determined by its foraging success. The high degree of heterogeneity in the distribution of nutrients and prey availability in the ocean, both spatially and temporally, shapes the foraging behaviour of marine apex predators. Individuals have to be able to respond to changing conditions and prey availability at multiple hierarchical scales. Furthermore, during the breeding season lactating females have the added burden of obtaining resources for their progeny. In income breeders, such as otariid seals, females have to commute between foraging grounds and their rookery. They are therefore both spatially and temporally restricted by the fasting capabilities of their pups, and the physiological cost to a female increases with distance and duration of a foraging trip. As a result, this limits a female's capacity for searching behaviour. Individuals might encounter areas of low prey quality (or quantity) but would have to decide whether to stay and forage or leave the patch in search of higher quality and quantity patches. Unsuccessful females would consequently risk breeding failure through starvation of the pup. Prior knowledge of consistently good foraging areas is therefore imperative to the survival of their pups. It is expected that females visit preferred foraging areas with a high likelihood of energetic pay-off, rather than going to unknown areas and risk breeding failure.

Few studies have reported on patterns of foraging site fidelity in lactating fur seals both at a colony level (Bonadonna *et al.* 2000; Beauplet *et al.* 2004) and at an individual level (Bonadonna *et al.* 2001; Boyd *et al.* 2002; Biuw *et al.* 2009). Nonetheless, some individuals still show a high degree of variation in foraging locations between consecutive trips (e.g. Biuw *et al.* 2009). In Antarctic fur seals (*Arctocephalus gazella)* foraging routes stay very similar on consecutive foraging trips, but it is the availability of prey encountered along the way that determines foraging habitats (e.g Bonadonna et al. 2000; Staniland & Boyd 2003; Staniland *et al.* 2004). Generally, a combination of coastline orientation and oceanographic factors determine directionality of foraging from the respective islands (Goldsworthy *et al.* 2010). However, the actual oceanographic features that drive preferred foraging locations vary markedly between different populations and conspecifics from different islands exhibit a high degree of plasticity in foraging site choice tactics (Georges *et al.* 2000a; Arnould & Hindell 2001; Lea & Dubroca 2003; Kuhn *et al.* 2010). Even within a population different females vary the distances travelled to foraging areas as well as diving behaviour in response to varying physical oceanic features (Staniland & Boyd 2003; Staniland *et al.* 2004).

Subantarctic fur seal *(Arctocephalus tropicalis)* at-sea foraging behaviour has been studied at Amsterdam Island (Georges *et al.* 2000a, b; Beauplet *et al.* 2004); Macquarie Island (Goldsworthy 1999; Robinson *et al.* 2002); the Crozet archipelago (Bailleul *et al.* 2005; Luque *et al.* 2007, 2008) and Marion Island (Bester & Bartlett 1990; Kirkman *et al.* 2002; de Bruyn *et al.* 2009). Recently, disparities in foraging strategies of *A. tropicalis* between these islands raised some important questions. Subantarctic fur seal females (SAFS) from Marion Island (MI) take long extended foraging trips and do not make short over-night foraging trips like conspecifics from nearby Îles Crozet and at Macquarie Island. As such they behave more like females from distant temperate Amsterdam Island (Georges *et al.* 2000a) as shown by de Bruyn *et al.* (2009). It appears that foraging tactics are governed by different environmental pressures at different localities. Females from Amsterdam Island mainly forage in the sub-tropical front and sea-surface temperature played a major role in determining foraging locations (Georges *et al.* 2000a).

At Macquarie Island the proximity of the nearby Macquarie Ridge seemed to dictate foraging behaviour (Robinson *et al.* 2002) whereas the presence of the Crozet plateau around the archipelago played a commanding role in Île de la Possession female foraging tactics (Bailleul *et al.* 2005; Luque *et al.* 2007). Lactating females from Marion Island preferred an area NE of the island in the vicinity of the Del Caño Rise (de Bruyn *et al.* 2009). However, in the aforementioned studies sampling was done cross-sectionally, i.e. multiple trips per individual were excluded to balance datasets. To date no study has reported on intra-individual foraging site fidelity, or a directional preference for foraging from an individual's breeding beach, for this species. To fully understand this disparity in foraging behaviour and identify the physical oceanographic features that drive such foraging behaviour, we need to know whether these preferred foraging areas stay the same between consecutive foraging trips for an individual and at the colony-level scale.

Although de Bruyn *et al.* (2009) highlighted the Del Caño Rise as an area of foraging importance, some individuals travelled west from MI and foraged over deeper water, based on one foraging trip that was collected per female. Understanding whether the aforementioned relates to two different long-term foraging tactics, or simply short-term responses to changing resource availability was beyond the scope of thatstudy. It is not known whether females travel consistently to the same foraging areas as they gain knowledge of profitable sites over consecutive trips. Furthermore, diving data for lactating SAFS from MI (chapter 2) illustrates that females dive every night after departure from the island. Is this opportunistic sampling and foraging on their way to a known foraging patch or do females simply head out in a direction (with no knowledge of, or preference for, good foraging areas), forage throughout their trip and return when they have gained sufficient energy?

Improving our knowledge on intra-individual foraging plasticity is key to understanding inter-island variation in foraging strategies and could aid identification of environmental variables that drive foraging behaviour. I therefore pose the question whether lactating SAFS females from MI follow two different foraging tactics by either consistent travel in a westerly or easterly direction from the rookery? Secondly, within the broad-scale preferred travelling direction, do females show some form of foraging site fidelity (fine scale preferences)? Lastly, how does this vary in response to seasonal environmental fluctuations? These questions were addressed using spatial data from 18 individuals, collected over a 3–year-period (2009-2011), with multiple trips recorded per individual.

Methods

Device deployments:

An Argos-linked satellite platform transmitter terminal (PTT; Kiwisat 101, Sirtrack, 120g, 110 x 42 x 14 mm, 57 cm^2 cross-sectional area) and time-depth recorder (MK 9 TDR, Wildlife Computers, 30 g, 67 mm x 17 mm x 17 mm) combination was deployed on each of 18 lactating Subantarctic fur seals between the austral winters of 2009 and 2011 at Marion Island (46°54’S, 37° 45’E) at Van den Boogaard beach (see table 3.1 for a summary of deployment details). Van den Boogaard is located on the north-eastern coastline of the island (fig. 3.1) and is characterised by large boulders bounded by 2-7 m high cliff faces with a vegetated area to the back. It is also a low density rookery of Subantarctic fur seals (Hofmeyr *et al.* 2006).

Females seen suckling a pup were caught in a hoopnet and physically restrained for approximately 30 min during device attachment. The PTT was attached on the dorsal midline just below the scapulae of the animal with the TDR one hand's length anterior of the PTT, slightly above the scapulae (refer to chapter 2 for details on TDR sampling protocol). Both the PTT and TDR were attached by means of a double-component, quick-setting epoxy resin (Araldite AW2101, CIBA-GEIGY Ltd.). Females were recaptured and the devices together with accompanying attachments were removed when the PTTs approached the limit of their battery life (~4 months). This was done by carefully shaving the guard hairs of the fur underneath each device with a scalpel.

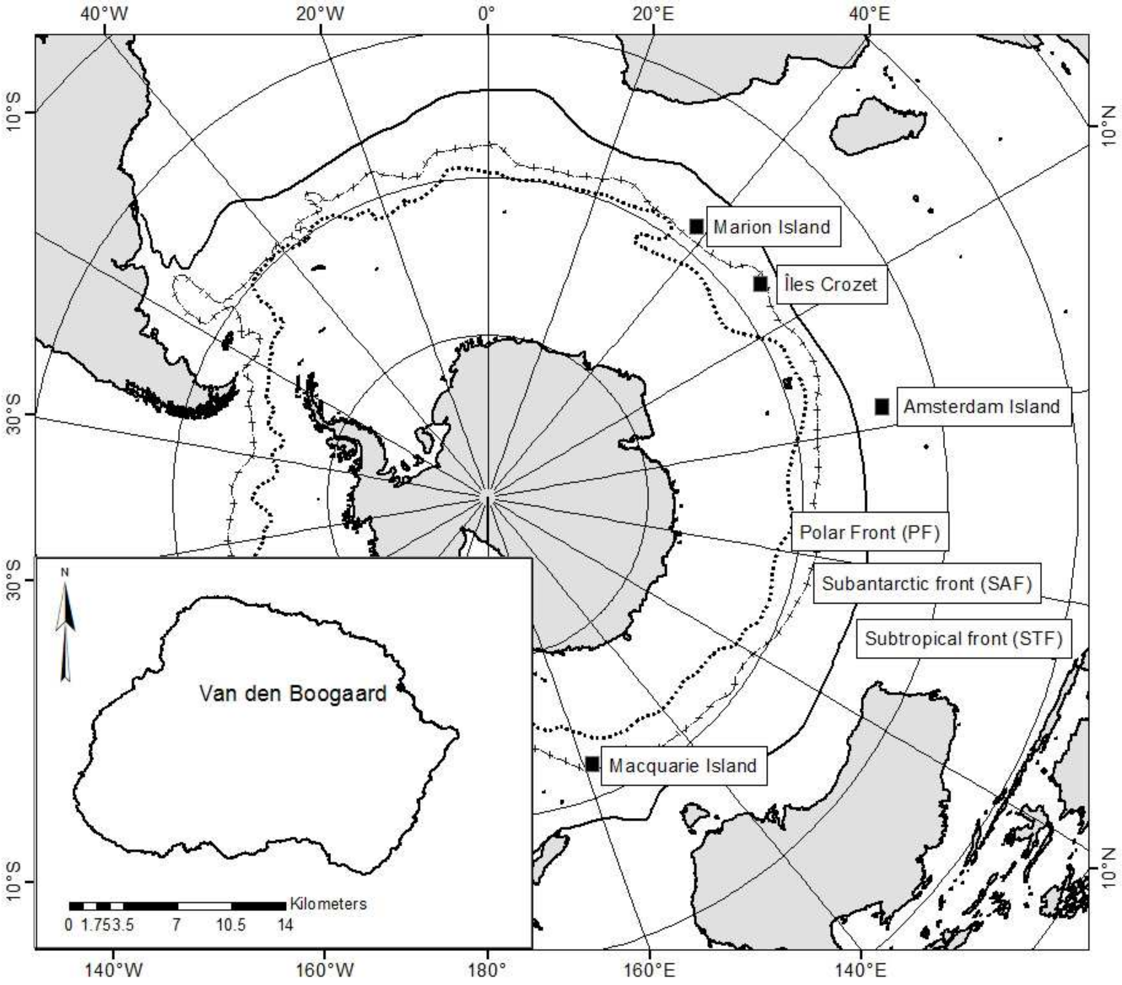


Figure 3.1: *The position of Marion Island in the Southern Ocean in relation to Île de la Possession (Îles Crozet), Amsterdam Island and Macquarie Island as well as the Antarctic Polar Front, Subtropical Front and the Subantarctic Front. The location of Van den Boogaard beach (study beach) on Marion Island is indicated (inset)*

Data handling:

Raw ARGOS data was extracted using the ARGOS-tools extension in ArcView (v 3.3). Location data is assigned a location class (LC) based on the number of satellite messages received and is given an accuracy estimate. LC 3 is accurate to 150 m, LC 2 to 350 m, LC 1 to 1 km, LC 0, A and B have no estimate and LC Z is an invalid location.

To distinguish foraging areas from non-foraging areas in the tracks, a state-space model (SSM) was fitted using a two-state switching correlated random walk model in R (R Development Core Team 2012) and WinBUGS (available online: http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml) as described in Breed *et al.* (2009). To fit the model, two Markov Chain Monte Carlo chains (MCMC) were run for 10 000 iterations, with a burn-in of 7000, sampling all model parameters and each regularized location estimate (which are estimated like parameters). Every fifth point of the 3000 remaining samples was retained for a net of 600 MCMC samples in each chain. From these 600 samples a mean and variance for each location estimate and model parameter was calculated. SAFS from MI only dive at night (chapter 2), therefore multiple interpolation time-steps were tested to see how foraging and non-foraging areas within the interpolated SSM tracks compared with night (foraging) and day (non-foraging) location fixes from the original tracks. Using a time-step of 120 min searching/foraging locations compared the best to night-time locations from the original tracks and was subsequently used to interpolate points. Distance travelled (km) and bearing (radians) from MI as well as between consecutive points were calculated with the 'argosfilter' package in R (Freitas 2010; R Development Core Team 2012).

General analyses:

Due to the unbalanced design of the data, a linear mixed-effects model was used to determine the effect of foraging trip duration (predictor variable) on total distance of the foraging trip and maximum distance reached from MI respectively (response variables). Individual and foraging trip number were used as random effects. Individual or number of foraging trip had no effect on the results and a simple linear model was subsequently used. To stabilise error variance in the models the response variables (maximum distance from MI and total foraging trip distance), a spread-stabilizing power transformation of -0.053 was used. Analysis of variance (ANOVA) was used to find differences in foraging trip duration between different seasons. Foraging trip duration (in days) was $\log_{10}$ transformed to stabilise heteroscedasticity.

Following Bailleul *et al.* (2005), a "curvilinear index" (CI) was calculated for each foraging trip. This makes it possible to determine whether or not the female went directly to the foraging area, swam in a loop or followed a complex swimming pattern akin to searching behaviour (Bonadonna *et al.* 2000). The index was calculated using the following equation:

$$CI = (2 \text{ x maximal distance}) / \text{total duration of trip} \qquad [1]$$

Higher CI values refer to straighter trips, with a value of 1 being a trip directly to a foraging site.

Influences on the straightness of foraging trips were tested with linear mixed-effects models using CI as the response variable. The effects of foraging trip duration, the number of the foraging trip since device deployment, their interaction term and mean trip direction from MI were included as fixed effects, and animal and season as crossed, non-nested random effects. Individual animal identification (i.e. tag number) and season were treated as non-nested random effects because there is no data for females in multiple seasons. In order to include mean trip bearing, which is a circular variable, in the model it was converted to a linear variable. On this linear scale the overall mean travel direction from MI was set as 0 with each degree difference smaller than the mean bearing as -1 units and each degree larger than the mean bearing as +1 units. A maximum likelihood method was used to fit all models. Autocorrelation plots did not reveal any significant autocorrelation. The final model of covariates was chosen by means of a backwards stepwise selection, starting with the most complex model. Initial model fitting revealed that tag number had no influence on the model and was subsequently excluded as a random effect. The small sample size corrected Akaike's Information Criterion (AICc) was used to select the most parsimonious model (Burnham & Anderson 2002) and several plot types were used to assess model fits (Pinheiro & Bates 2004). A marginal hypothesis test (*F*-test) was carried out on the final model to distinguish the significance of the various mixed effects (Bolker *et al.* 2009). The percentage of the variance explained by the random effect (i.e. season) was calculated by means of a variance component analysis (Crawley 2007). Mixed-effects models were fitted using the "lme4", "nlme", "MuMIn" and "car" libraries in R (Barton 2011; Bates *et al.* 2011; Fox & Weisberg 2011; Pinheiro *et al.* 2011; R Development Core Team 2012).

Directional data analysis:

All points within a 10 km radius from MI were discarded to exclude location fixes obtained while the female was on land or swimming in the shallows for thermoregulatory reason. For each of the remainder of the points a compass direction in degrees from MI was calculated and per foraging trip a first order circular mean was calculated to identify the mean direction of travel from the island. From this a second order mean and vector length was computed for each individual and each season (given by *Rho*). Moore's modified Rayleigh test (Zar 1998) determined whether mean foraging direction, both within individual (i.e. multiple trips per individual) and within seasons (multiple trips within a season), from MI was randomly distributed in relation to the island or if it was in a specific direction. I used circular analysis of variance (cANOVA; Jammalamadaka & SenGupta 2001) to examine whether the mean foraging trip direction from MI differed between and within individuals, and also between and within years. The response variable was the radian of the mean bearing from MI and the explanatory variable was tag number and season respectively (see Biuw *et al.* 2009 for further details). First and second order means and Moore's modified Rayleigh test were performed in Oriana 4 for Windows (Kovach Computing Service, Pentraeth, UK) and cANOVA in the "circular" package available on the R platform (Agostinelli & Lund 2011; R Development Core Team 2012).

Results

In total, the 18 females produced 59 foraging trips of which 51 were complete and 8 were incomplete (table 3.1). Incomplete tracks occur when ARGOS cease to receive uplinks from the PTT device during its time at sea. These incomplete tracks were excluded from all trip summaries and further analyses (table 3.2).

Table 3.1: *Summary of tracks obtained from 2009 winter (200W), 2010 winter (2010W), 2011 summer (2011S) and winter (2011W) at Van den Boogaard beach.*

Seal ID	**Seal mass at deployment (kg)**	**Deployment date**	**Track duration (days)**	**Season**	**No of foraging trips**	**No of complete tracks**	**No of incomplete tracks**
GW522_90759	43.0 kg	2009/04/24	134	2009W	3	2	1
GW495_90760	44.0 kg	2009/04/24	89	2009W	2	1	1
GW524_90761	34.0 kg	2009/04/24	19	2009W	1	0	1
FB515_90762	37.0 kg	2009/04/28	96	2009W	2	1	1
FB513_90763	31.0 kg	2009/04/28	146	2009W	2	2	0
OO455_90759	31.0 kg	2010/03/07	149	2010W	4	3	1
OO478_90763	35.0 kg	2010/03/21	142	2010W	4	4	0
A160_97807	22.0 kg	2010/04/29	85	2010W	2	2	0
A184_97808	30.0 kg	2010/05/02	78	2010W	3	3	0
OO456_97809	-	2010/05/05	100	2010W	2	1	1
A164_74368	40.0 kg	2010/06/02	130	2010W	4	3	1
A142_97803	38.5.0 kg	2011/01/03	76	2011S	6	6	0
GW503_97804	23.5 kg	2011/01/02	65	2011S	6	6	0
A188_97805	27.5 kg	2011/01/02	70	2011S	5	5	0
LB504_97806	25.5 kg	2011/01/03	62	2011S	4	4	0
LB491_93532	40.0 kg	2011/04/29	119	2011W	4	4	0
OO440_97808	36.0 kg	2011/04/29	131	2011W	3	3	0
A160_65641	35.0 kg	2011/05/15	24	2011W	2	1	1

Table 3.2: *Foraging trip summaries for each individual trip.*

Season	Tag	Foraging trip	Foraging trip duration (days)	Maximum distance reached from MI (km)	Total foraging trip distance (km)	Complete foraging trip?	Trip Curvilinear Index	Mean foraging trip direction (°)	Vector length (*Rho*)
2009W	GW522	1	20	387.74	1438.92	Yes	0.54	108.20	0.90
2009W	GW522	2	28	407.65	1635.01	Yes	0.50	48.01	0.98
2009W	GW522	3	68	1261.1	3541.67	No	0.71	70.08	0.90
2009W	GW495	1	36	487.72	1946.45	Yes	0.50	90.08	0.95
2009W	GW495	2	47	783.18	2517.62	No	0.62	31.14	0.91
2009W	GW524	1	19	435.01	1047.49	No	0.83	49.26	0.99
2009W	FB515	1	37	813.59	2839.71	Yes	0.57	-94.70	0.98
2009W	FB515	2	56	1474.64	3803.13	No	0.78	-18.43	0.52
2009W	FB513	1	25	460.54	1445.9	Yes	0.64	-114.65	0.95
2009W	FB513	2	117	1051.85	5349.78	Yes	0.39	-69.52	0.93
2010W	A164	1	27	510.12	1389.44	Yes	0.73	77.44	0.96
2010W	A164	2	48	575.66	2495.13	Yes	0.46	48.10	0.97
2010W	A164	3	32	577.42	1777.22	Yes	0.65	46.87	0.99
2010W	A164	4	18	493.07	1200.17	No	0.82	29.57	0.96
2010W	OO455	1	22	552.25	1584.11	Yes	0.70	108.31	0.96
2010W	OO455	2	20	267.82	1169.35	Yes	0.46	154.76	0.68
2010W	OO455	3	31	357.4	1759.59	Yes	0.41	134.92	0.93
2010W	OO455	4	64	799.85	4290.32	No	0.37	-69.99	0.88
2010W	OO478	1	28	664.24	1994.3	Yes	0.67	94.55	0.99
2010W	OO478	2	36	812.27	2380.15	Yes	0.68	85.96	0.98
2010W	OO478	3	12	211.46	774.61	Yes	0.55	72.44	0.97
2010W	OO478	4	57	692.55	3387.44	Yes	0.41	47.84	0.97
2010W	A160	1	36	858.72	2305.36	Yes	0.74	69.26	0.99
2010W	A160	2	47	678.65	2457.91	Yes	0.55	50.02	0.98
2010W	A184	1	17	246.59	1001.28	Yes	0.49	70.99	0.90
2010W	A184	2	23	390.17	1237.49	Yes	0.63	74.54	0.97
2010W	A184	3	27	405.34	1694.71	Yes	0.48	37.18	0.97
2010W	OO456	1	19	273.53	1024.67	Yes	0.53	123.02	0.96
2010W	OO456	2	77	1006.62	3537.14	No	0.57	72.79	0.99
2011S	A142	1	5	104.67	269.37	Yes	0.78	121.29	0.95

Table 3.2 (continued): *Foraging trip summaries for each individual trip.*

Season	**Tag**	**Foraging trip**	**Foraging trip duration (days)**	**Maximum distance reached from MI (km)**	**Total foraging trip distance (km)**	**Complete foraging trip?**	**Trip Curvilinear Index**	**Mean foraging trip direction (°)**	**Vector length (*Rho*)**
2011S	A142	2	9	340.79	778.73	Yes	0.88	94.10	0.99
2011S	A142	3	7	212.81	466.3	Yes	0.91	102.59	0.96
2011S	A142	4	8	217.37	1180.79	Yes	0.37	107.88	0.99
2011S	A142	5	12	335.73	849.83	Yes	0.79	98.72	0.98
2011S	A142	6	17	674.97	2545.38	Yes	0.53	120.55	0.97
2011S	GW503	1	9	308.4	750.32	Yes	0.82	66.60	0.99
2011S	GW503	2	9	291.46	723.49	Yes	0.81	83.60	0.99
2011S	GW503	3	8	193.45	505.8	Yes	0.76	75.69	0.99
2011S	GW503	4	6	212.87	530.8	Yes	0.80	79.66	0.99
2011S	GW503	5	11	304.36	934.28	Yes	0.65	105.31	0.98
2011S	GW503	6	10	300.26	722.94	Yes	0.83	91.01	0.99
2011S	A188	1	9	165.72	466.53	Yes	0.71	94.451	0.99
2011S	A188	2	9	179.56	499.76	Yes	0.72	103.661	0.99
2011S	A188	3	11	218.36	680.94	Yes	0.64	94.171	0.98
2011S	A188	4	13	249.95	731.4	Yes	0.68	110.28	0.99
2011S	A188	5	16	349.1	1069.92	Yes	0.65	103.32	0.96
2011S	LB504	1	8	220.37	516.74	Yes	0.85	78.13	0.98
2011S	LB504	2	13	424.22	1030.74	Yes	0.82	83.76	0.99
2011S	LB504	3	12	389.55	1030.48	Yes	0.76	78.44	0.93
2011S	LB504	4	18	541.77	2262.19	Yes	0.48	84.94	0.99
2011W	A160_2	1	14	318.09	2262.19	Yes	0.28	53.45	0.99
2011W	A160_2	2	4	289.7	867.38	No	0.67	50.86	0.55
2011W	LB491	1	16	307.18	1006.37	Yes	0.61	112.78	0.92
2011W	LB491	2	19	338.45	1324.87	Yes	0.51	83.19	0.99
2011W	LB491	3	22	252.85	1004.91	Yes	0.50	48.93	0.98
2011W	LB491	4	50	853.32	3167.98	Yes	0.54	52.95	0.99
2011W	OO440	1	17	331.62	1173.34	Yes	0.57	102.20	0.98
2011W	OO440	2	33	687.33	2447.98	Yes	0.56	58.04	0.93
2011W	OO440	3	67	632.57	4650.9	Yes	0.27	27.03	0.70

Both the maximum distance reached from MI and the total trip distance were positively correlated to duration of the foraging trip ($F_{1,49}$ = 56.93, $P < 0.0001$, r^2= 0.528). ($F_{1,49}$ = 148.2, $P < 0.0001$, r^2= 0.74). There were significant differences in foraging trip duration between seasons (ANOVA, $F_{3,47}$ = 24.957, $P < 0.0001$) and a post-hoc Tukey's HSD revealed that between the winters of 2009, 2010 and 2011 there were no significant differences in foraging trip duration. However, in summer (2011S) females performed significantly shorter foraging trips compared to each of the winters (see figures 3.3 & 3.4).

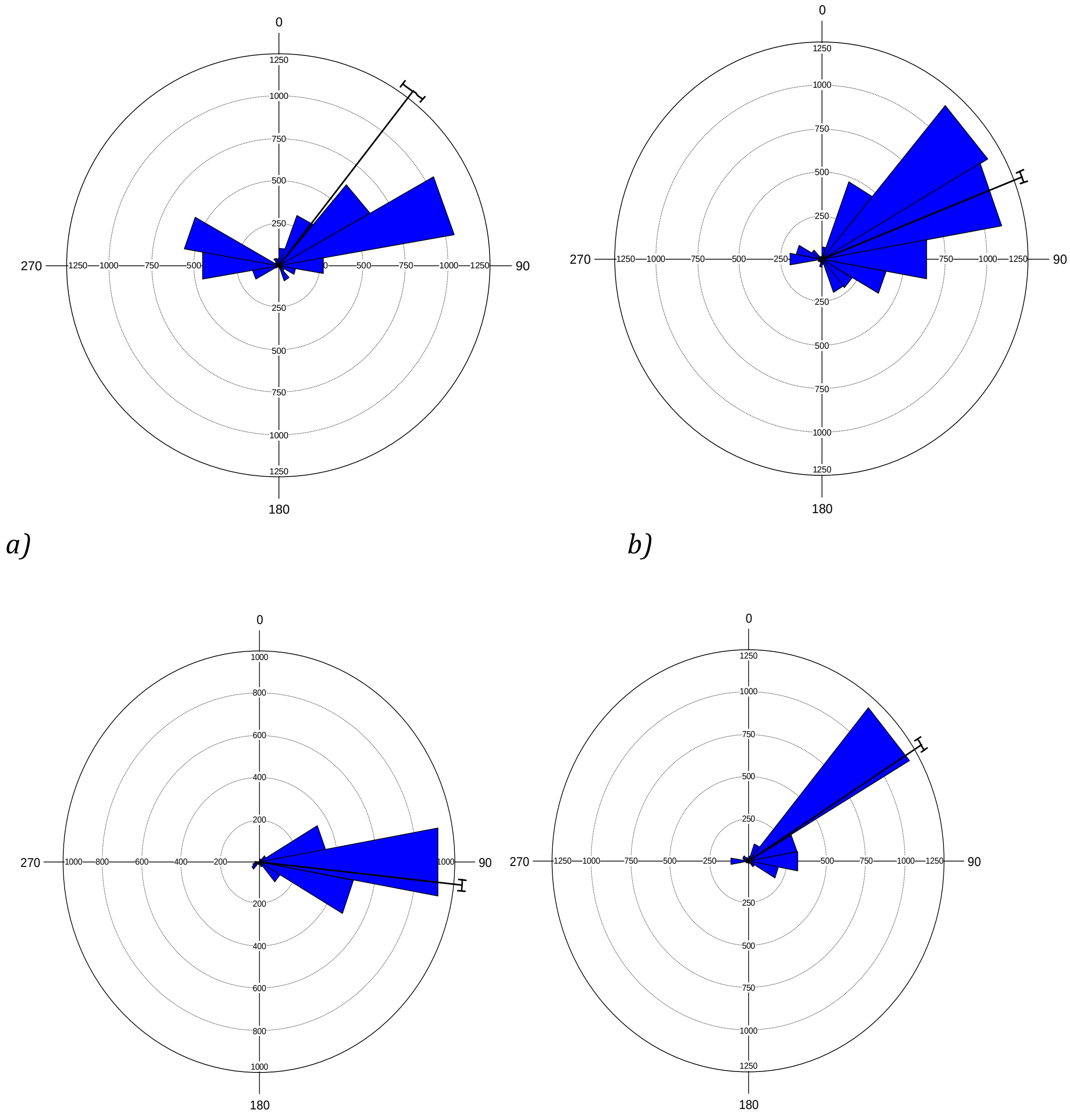
Directional data and the curvilinear index:

There were some differences in mean foraging trip directions between the years and seasons, but most of the trips in all seasons were north-east to east from MI (fig. 3.2). Moore's modified Rayleigh test indicated that during 2009W females did not travel in a specific direction from MI (R = 0.253, $P > 0.05$), whereas females foraged in a preferred direction (mean direction = 347.96°, *rho* = 0.075) from MI during 2010W (R = 1.258, $P < 0.01$; mean direction = 83.42°, *rho* = 2.35), 2011S (R = 1.23, $P < 0.005$; mean direction = 93.37°, *rho* = 5.15) and 2011W (R = 1.14, $P < 0.025$; mean direction = 64.40°, *rho* = 2.65). Of the 18 females tracked, there is more than one complete trackline for 13 females. Moore's modified Rayleigh test indicated that of those 13, only 4 did not swim in a preferred foraging direction on consecutive trips (see table 3 for summary) but the other 9 females showed preference in foraging direction from MI. Variation in mean bearing from MI was greatest between individuals and significantly different when compared to variation within an individual (cANOVA: $F_{12,34}$ = 9.636, $P < 0.0001$). There were no significant differences in mean bearing from MI between or within years (cANOVA: $F_{3,9}$ = 0.4789, $P > 0.05$).

Table 3.3: *Results summary of the Moore's modified Rayleigh test for females performing more than one foraging trip. Grand mean presents the second order mean foraging direction from Marion Island,* rho *is the resultant vector length,* n *is the number of foraging trips.*

Season	**Tag No**	***n***	**Grand mean**	***Rho***	***R***	***P-value***
2009W	GW522	2	76.688°	0.81	0.935	> 0.05 N.S.
2011W	OO440	3	66.261°	0.75	1.011	> 0.05 N.S.
2009W	FB513	2	267.69°	0.869	0.989	> 0.05 N.S.
2010W	A160	2	59.708°	0.977	1.047	> 0.05 N.S.
2010W	A184	3	60.833°	0.904	1.097	< 0.05
2011S	A142	6	107.388°	0.958	1.409	< 0.001
2011S	GW503	6	83.564°	0.97	1.41	< 0.001
2011S	A188	5	101.186°	0.977	1.332	< 0.001
2011S	LB504	4	81.374°	0.975	1.249	< 0.001
2011W	LB491	4	73.48°	0.878	1.17	< 0.025
2010W	A164	3	57.242°	0.943	1.133	< 0.025
2010W	OO455	3	130.188°	0.812	1.099	< 0.05
2010W	OO478	4	75.454°	0.932	1.212	< 0.005

Of the 59 foraging trips, only six were to the west of MI, and of these six only four were complete foraging trips (i.e. female made it back to MI). All six of these foraging trips were performed in a winter (4 in 2009W, 1 in 2010W and 1 in 2011W). Two females, FB513 and FB515, performed more than one foraging trip to the west of MI. The first trip of FB513 was NW of the island and the second more to the SW (fig. 3.5). FB515 travelled west on trip 1, but on her second trip swam NE but when she was ~630 km away from the island, she turned west where the track stopped ~1400 km from MI (fig 3.5). Female OO440 in the winter of 2011 also travelled NE from MI at first, turned around ~580 km from MI and started travelling west. The overall mean bearing of that foraging trip was still eastwardly (fig 3.5). The small number of trips to the west of Marion Island, precluded the use of any sensible significance tests to compare trip duration, distance travelled and the curvilinear index between trips performed to the east and west of Marion Island. Visual interpretation shows some differences (fig. 3.6). Foraging trips to the west of Marion Island were also over longer distances and durations (fig. 3.6a, b); these were also not direct and westbound trips showed lower curvilinear index values than eastbound trips (fig. 3.6c).



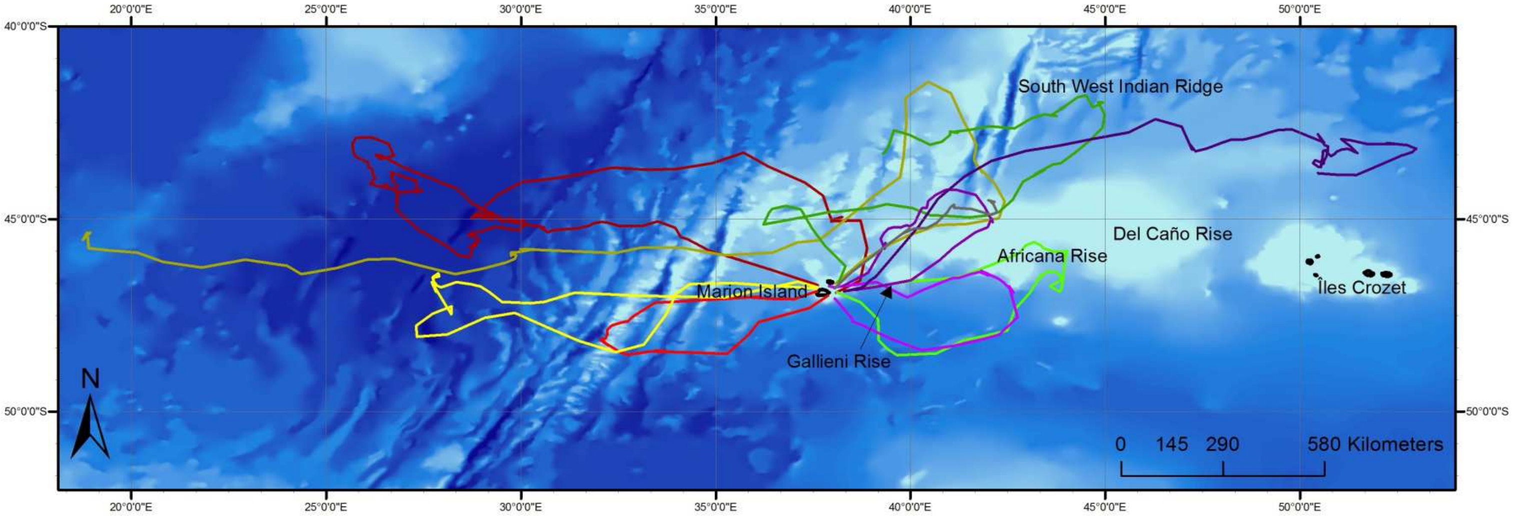
a)

b)

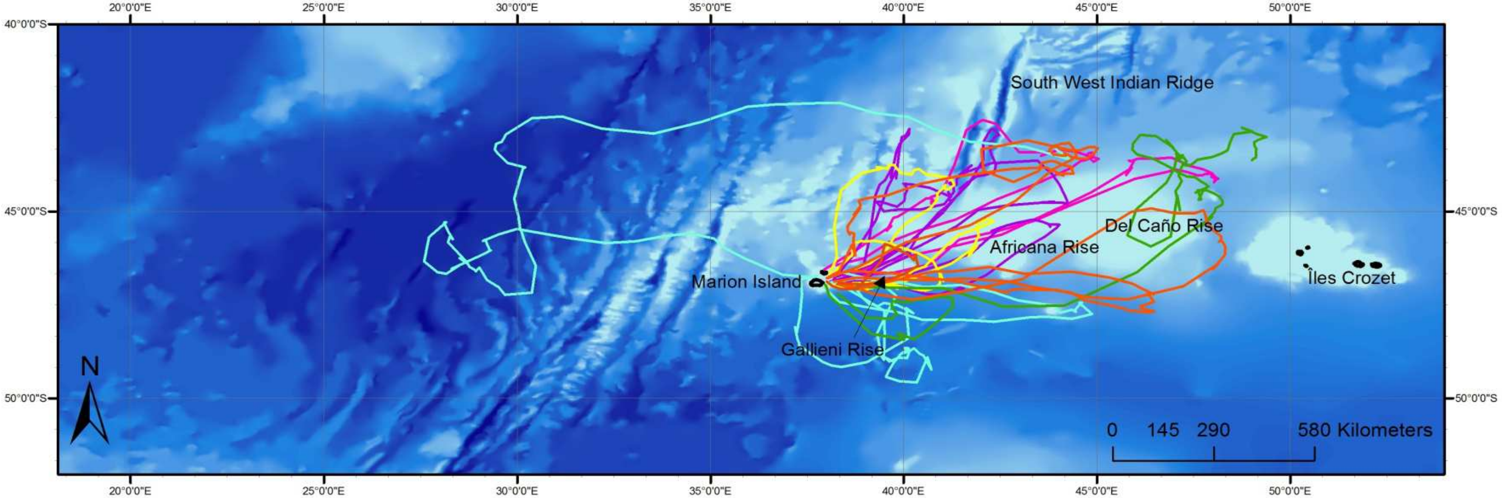
c)

d)

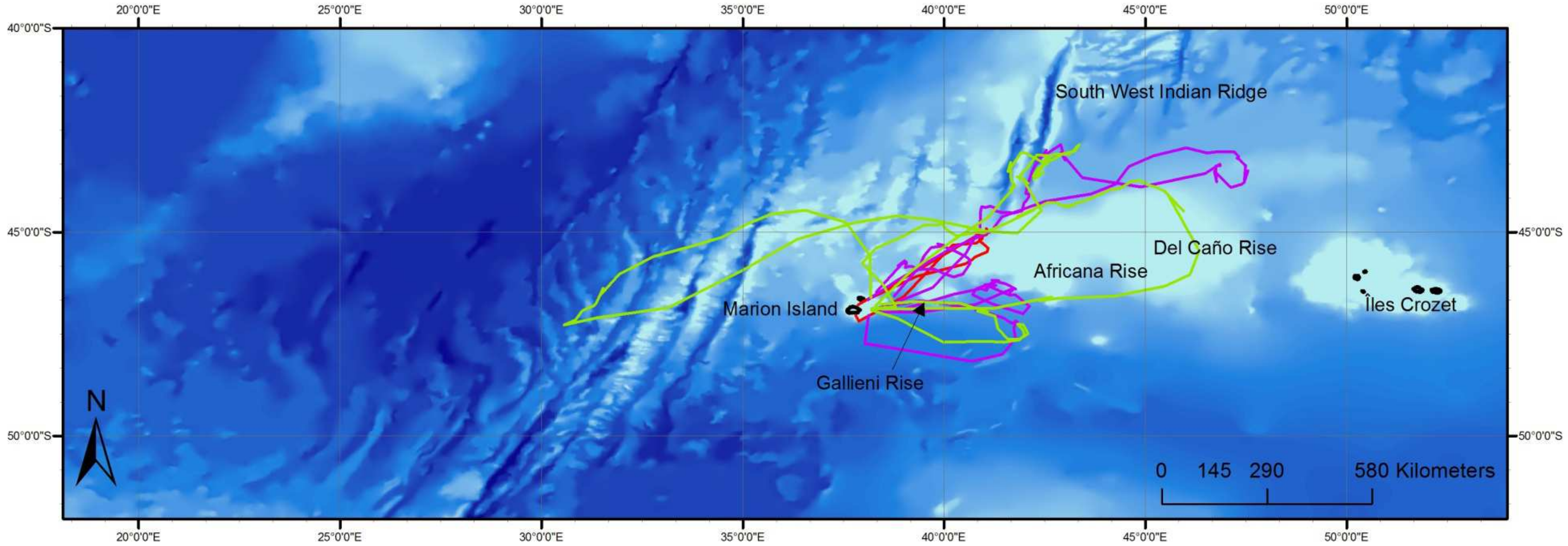
Figure 3.2: *Mean swimming direction of each individual foraging trip for a) Winter 2009; b) Winter 2010; c) Summer 2011 and d) Winter 2011. North is 0º and the seasonal grand mean is given by (-). Marion Island is central in each circle.*



a) Winter 2009

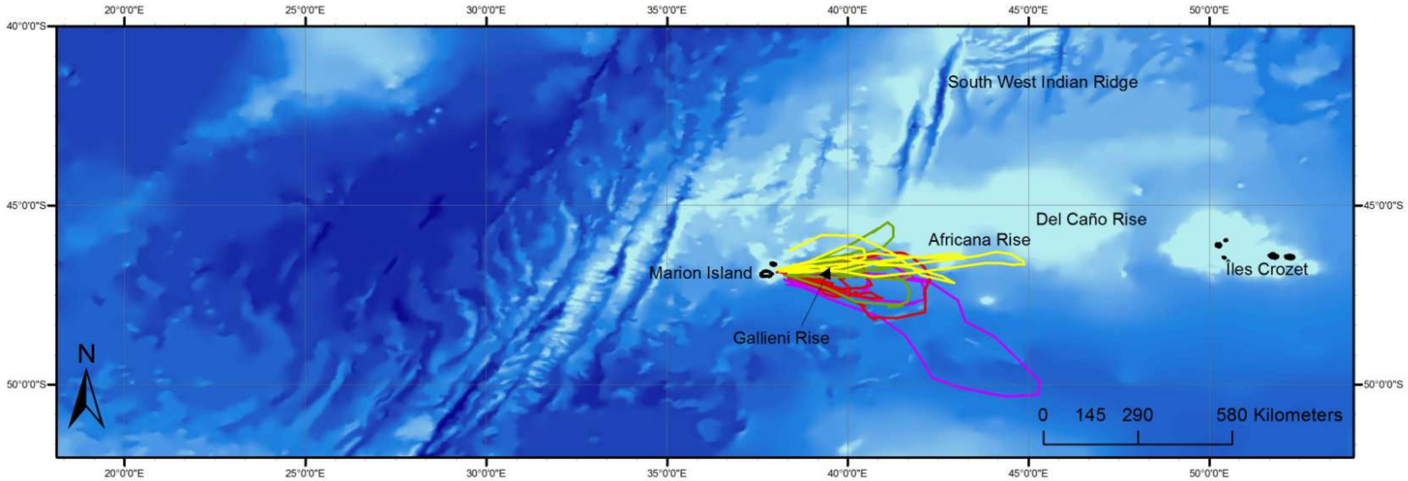


b) Winter 2010

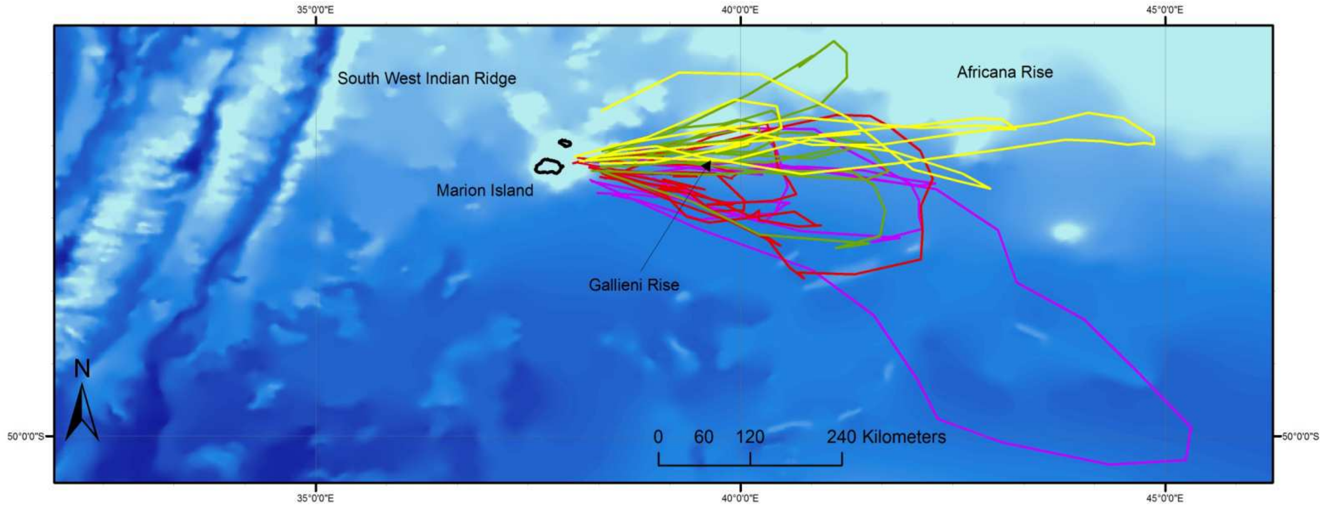


c) Winter 2011

Figure 3.3: *At-sea movement of lactating Subantarctic fur seals in relation to Marion Island during a) winter 2009; b) winter 2010 (previous page) and c) winter 2011. Tracks are presented with a one arc-minute bathymetry overlay (IOC IHO, BODC 2003). Different colours represent different individuals.*



a) Summer 2011



b) Summer 2011 (zoomed in)

Figure 3.4 (previous page): *At-sea movement of lactating Subantarctic fur seals in relation to Marion Island during the summer of 2011 a) presented at the same scale as the previous season and b) presented at a larger scale. Tracks are presented with a one arc-minute bathymetry overlay (IOC IHO, BODC 2003). Different colours represent different individuals.*

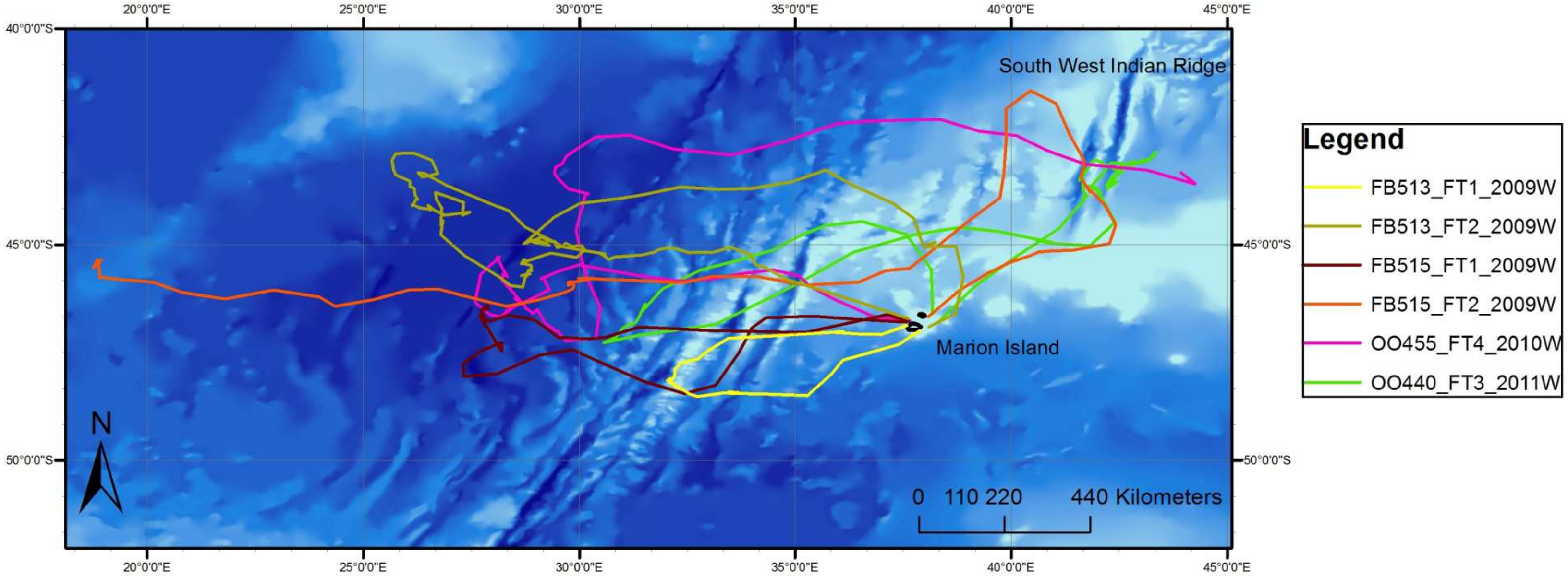


Figure 3.5: *Six foraging trips performed by four lactating females that travelled west of Marion Island in the winters of 2009 (2009W), 2010 (2010W) and 2011 (2011W). Tracks are presented with a one arc-minute bathymetry overlay (IOC IHO, BODC 2003). In the legend key the first 5 characters is the female's tag number and FT1 refers to foraging trip 1.*

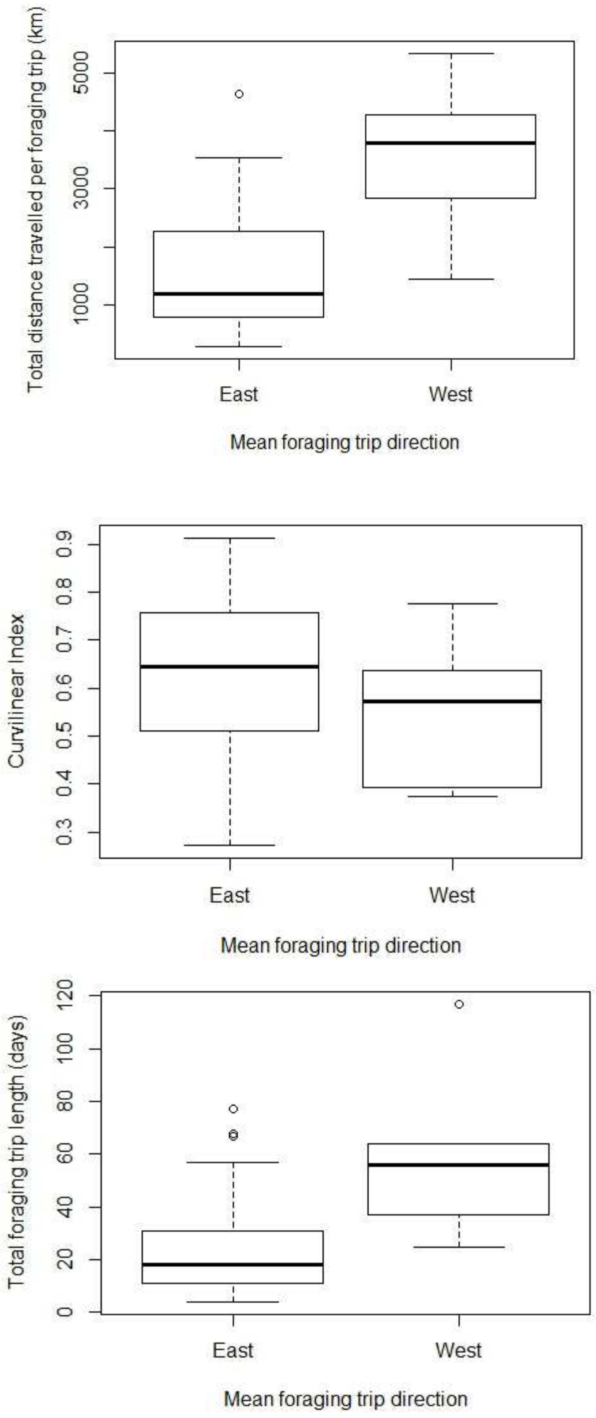


Figure 3.6: *Differences in total foraging trip distance travelled; a) foraging trip duration b) and curvilinear index c) compared between eastward and westward mean foraging trip directions from Marion Island.*

For the curvilinear-index mixed-effects models, the most parsimonious (i.e. the model with the lowest AICc score) retained both foraging trip number and foraging trip duration. The *F*-test, however, indicated that only the foraging trip number had a significant influence on the curvilinearity of a foraging trip. A negative relationship exists between the number and the curvilinear–index of the foraging trip (i.e. foraging trips earlier in the season were straighter). Season (random effect) explained 36% of the variation in the best model.

Discussion

This study presents the first data on intra-individual foraging site fidelity for lactating Subantarctic fur seals where inter-annual, -seasonal and -individual fidelity in foraging locations are elucidated.

On an individual scale, females maintained a preferred direction from the rookery on consecutive foraging trips. However, some variation persists and the exact foraging areas are not the same on consecutive trips. Longer duration foraging trips result in higher metabolic rates for lactating females (Arnould *et al.* 1996); they would therefore benefit from learning about quality and reliable foraging areas. The risk of not obtaining sufficient energy on consecutive trips would be lower and this could potentially reduce foraging trip duration. Consequently, energy lost to metabolic overheads by the female would also be lower if there is some foraging site fidelity. Changes in foraging areas by females on consecutive trips are most likely in response to tracking highly mobile prey, i.e. small scale fluctuations of available food patches within a larger area of predictable food resources (Fauchald *et al.* 2000). Areas that consistently yield prey in an almost predictable pattern are thought to drive this behaviour (Boyd *et al.* 2002). Considering that females dive every night after departure from the island (chapter 2); the assumption is that females swim to a known general preferred foraging area but sample or forage opportunistically *en route*.

Foraging trip duration was significantly different between individuals in this study. Other studies relate this variation to age-related experience and knowledge of preferred foraging areas (e.g. Fauchald *et al.* 2000; Staniland *et al.* 2004). As no information is available on the age of tracked seals, no inferences with regards to individual variation based on experience can be made in this study. Antarctic fur seal females from South Georgia have preferred foraging areas with dissimilar diets among different foraging areas (Staniland *et al.* 2007). At Marion Island no clear separation in diet seems to exist between animals foraging in different areas (Klages & Bester 1998; de Bruyn *et al.* 2009) although previous diet studies at Marion Island did not focus on identifying such differences. The exact reason behind this individual variation remains unknown.

Despite individual variation at a local scale, at a regional spatial scale females exhibited a preferred foraging area NE of the rookery in all years of the study (2009 to 2011). This is in agreement with previous at-sea distribution data from 2006 and 2007 (de Bruyn *et al.* 2009) and it seems that females from this particular rookery situated on the NE coast of Marion Island have a preferred foraging direction. Although there were no significant differences in mean foraging trip direction between years, in 2009 females did not have a preferred foraging direction from the rookery. This is perhaps indicative of annual changes in prey abundance and availability (McCafferty *et al.* 1998; Boyd *et al.* 2002). However, the lack of a colony-preferred foraging direction in 2009 is most likely an artefact of small sample size and should be interpreted with caution.

Colony-preferred foraging areas are not a new concept for central-place foragers (e.g. Georges *et al.* 2000a; Bonadonna *et al.* 2001; Beauplet *et al.* 2004), however, the ultimate force driving this is not yet fully understood. Coastline orientation (Lea *et al.* 2008; Goldsworthy *et al.* 2010), local competition (Bonadonna *et al.* 2001) and the most well-known: direction and distance to physical oceanographic features such as a front (Georges *et al.* 2000a) or continental shelf edge or ridge (Boyd *et al.* 2002; Staniland *et al.* 2004; Goldsworthy *et al.* 2010) appear to be important. At Marion Island, the most probable driving force for the preferred colony foraging direction is local bathymetry (de Bruyn *et al.* 2009), with certain bathymetrical features such as the Del Caño Rise, Africana Rise, Gallieni Rise and Discovery II Fracture Zone being the most prominent. To fully understand how seals interact with these features and how they are influenced by other environmental factors, such as sea-surface height and temperature, a finer-scale modelling approach is required.

Antarctic fur seals (*A. gazella*) breeding at Cap Noir (Îles Kerguelen) have two general preferred foraging areas (Bonadonna *et al.* 2001). Dissimilar foraging tactics, associated with different bathymetrical features, are employed at these two different foraging areas. Conversely, foraging trips to the west of Marion Island do not represent a different foraging tactic in lactating SAFS. Foraging trips to the west lasted longer and were further from Marion Island than those to the east; they were also less frequent. If it was indeed a different foraging tactic where females learn about good, consistent foraging areas to the west of Marion Island, females would conceivably forage there in a more consistent pattern and travel there on consecutive trips. These westward trips are most likely a short-term response to variable food resources in other preferred areas. Westward foraging trips by conspecifics from a similarly NE situated study colony at Amsterdam Island were only performed during the winter (Beauplet *et al.* 2004) when food resources are known to be scarcer (Knox 2007; Beauplet *et al.* 2004). The more indirect structure (i.e. lower curvilinear index) of the westward foraging trip could be related to searching for better prey patches. For instance, female FB515 in the winter of 2009 travelled NNE of Marion

Island toward the Bob Fischer Ridge, but then looped around and subsequently travelled west of Marion Island before returning to the rookery (fig. 3.5).

On a temporal scale, females also showed considerable variation in distances travelled, trip duration and foraging route structure. Although differences in foraging direction travelled by *A. tropicalis* from MI were non-significant, there was some variation. This may result from annual changes in prey abundance or distribution; thus variability in marine resources drive preferred foraging locations of seals (Lea *et al.* 2008). However, none of these changes were significant enough to alter the colony's preferred foraging areas (present study). Summer tracks were shorter both in maximum distance travelled from MI as well as trip duration. They were also more direct. Females focused their foraging over the Gallieni Rise (present study) rather than the Del Caño Rise further afield (de Bruyn *et al.* 2009). Antarctic fur seals from Îles Kerguelen that performed foraging trips with a more 'looped' structure, supposedly searched for food patches of better quality (Bonadonna *et al.* 2000). During trips of longer duration, these seals did not remain for longer in the same area, but instead covered greater distance in search of food. In the present study, the positive correlation between foraging trip duration, total distance travelled and maximum distance reached from MI would mean that in the winter, females spend more time searching for necessary resources to transfer to offspring. Even within a season, between consecutive foraging trips and as the season progressed, trips were less direct and slightly further than preceding trips; females probably spent more time tracking mobile prey within the moving Antarctic Circumpolar Current (Biuw *et al.* 2009). Aside from seasonal changes that influence foraging route structure, the growing demand of a pup could also affect foraging routes (Biuw *et al.* 2009). In the winter, females not only have to gain more energy for a larger and older pup, but have the added energetic burden of pregnancy (blastocyst implantation in March/April – Bester 1995).

In conclusion, lactating Subantarctic fur seals from Marion Island show both individual and colony-level foraging site fidelity. Deviation from this behaviour is brought about by both spatial and temporal variation at a range of scales. Spatially, bathymetrical features provide consistently good or preferred foraging areas. Temporally, movement behaviour is manipulated by short-term variation, as well as seasonal and annual fluctuations in prey abundance and availability. Foraging trips to the west of MI do not present a different long-term foraging strategy for lactating females from the north-easterly situated rookery on MI, but is most likely a short-term response to changing prey availability. If females in a colony all prefer the same general area, this would point to a highly productive zone. Over-exploitation of such areas by human activity would negatively influence fur seal foraging success and consequently their breeding success (e.g. Trites *et al.* 2007). Therefore, identifying colony preferred foraging areas of top predators could indicate important areas for conservation, not only in terms of marine predators such as seals but also to the prey they forage upon and links lower in the food chain (Hyrenbach *et al.* 2000; Lombard *et al.* 2007).

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Chapter 4:

Attendance patterns of female Subantarctic fur seals (*Arctocephalus tropicalis)* and environmental perturbations

Abstract

Possible influences of El Niño events and/or anomalous sea-surface temperatures were investigated using six years (2006 - 2011) of attendance cycle data from flipper-tagged lactating female Subantarctic fur seals from Marion Island. Observer-based procurement of attendance patterns over-estimate attendance durations and subsequently underestimate foraging trip duration because females are often missed by observers when present on land. I accounted for detection failures by means of multi-state capture mark-recapture (CMR) models and corrected attendance data accordingly. Although detection probabilities across the different seasons and years were never below 85%, foraging trip duration was slightly longer than previously recorded at Marion Island. Survival probability of pups from summer to winter was 0.72 ± 0.04. Neither El Niño nor sea-surface temperature anomalies influenced any of the attendance cycle parameters. This could either be because, 1) prior to and during the study period only weak El Niño and La Niña events occurred and females were not influenced by them, or 2) foraging trip duration is a poor predictor of environmental change. Only season and pup sex had a significant impact on female provisioning rates. In winter foraging trip duration was much longer (*t*-value = 28.38, $P < 0.0001$, $df = 182$) and attendance durations only slightly longer (*t*-value = -2.5, $df = 180$, $P = 0.01$) than during summer. Similarly, the proportion of time spent on land was higher than time spent at sea during winter. This is likely due to seasonal change in prey abundance, growing demands and increased fasting abilities of the pup as well as the increased demands of gestation on the female. Females spent a higher proportion of their time on land when they had female pups ($\chi^2 = 15.2830$, $df = 2$, $P < 0.001$). This might be related to ingestion capabilities due to body size differences between female and male pups, females being smaller and physically limited by the amount of milk they can ingest. Although observational attendance data remains useful it ideally requires concomitant data on pup growth, production and female body condition to elucidate changes in female provisioning rates.

Key words: Attendance patterns; Subantarctic fur seal; El Niño; observational-data; mark-recapture; sea-surface temperature anomalies; detection probability; transition probability; survival probability.

Introduction

Foraging strategies are central to an animal's life-history. However, "foraging strategy" is a term loosely applied in the literature. It could refer to genetically-linked, species bound behaviour shaped by natural selection and evolution (e.g. Stephens & Krebs 1986; Galimberti *et al.* 2000; Toïgo *et al.* 2007). Or it could refer to a more short-term tactic followed by an individual in response to local conditions (e.g. Bonadonna *et al.* 2001; Lea *et al.* 2002; Nøttestad *et al.* 2002; Caudron *et al.* 2009; Goldsworthy *et al.* 2010). In terms of evolutionary fashioned strategies, otariid seals (fur seals and sea lions) are known as central place foragers (Orians & Pearson 1979). Their strategy is characterised by a separation between foraging at sea (i.e. foraging trip) and nursing a pup on land (attendance period), collectively described as an attendance cycle. This also makes them income breeders, where the success of the pup depends on the ability of the female to locate prey and gain sufficient energy on consecutive foraging trips.

The adaptability and variation of attendance cycles in fur seals have received considerable attention over the last 3 decades (e.g. Croxall *et al.* 1985; Gentry & Kooyman 1986; Costa *et al.* 1989; Bester & Bartlett 1990; Lunn *et al.* 1993; Goldsworthy 1999, 2006; Kirkman *et al.* 2002, 2003). They draw interest because of the variety of strategies that are species-bound (inter-species comparisons) and flexibility within a species between populations (intra-species comparisons). Species-bound variation in lactation period is linked to latitude (Bester 1981). High latitude species, like the Antarctic fur seal *(Arctocephalus gazella)*, make work of the short summer and predictable prey distribution and wean their pups in 4 months (Arnould & Boyd 1995). Conversely, temperate species such as the Subantarctic fur seal *(A.*

tropicalis) typically have a lactation period of 10 months (Gentry & Kooyman 1986). Several studies indicated that despite disparities in lactation period, otariid seals are able to adapt and change their foraging tactics or “strategies” in response to changing local conditions. Differences vary from island to island (Goldsworthy 1999; Robinson *et al.* 2002; Luque *et al.* 2007; de Bruyn *et al.* 2009) and even colony to colony (Lea *et al.* 2008; Staniland *et al.* 2010; Lowther & Goldsworthy 2011).

How females apportion their time at sea and on land could be controlled in two contrasting ways: (i) females forage until they have gained the maximum amount of energy they can in that amount of time; or (ii) females forage until they have reached a net energy gain of some threshold. In reality this may actually be a combination of the two (Boyd *et al.* 1991). Females have a minimum energy gain threshold that needs to be achieved before returning to a pup. However, the females are also limited by the fasting abilities of their pups, their own storage capacity and several external environmental pressures acting on them (Boyd *et al.* 1991; Goldsworthy 1999; Verrier *et al.* 2009; Lowther & Goldsworthy 2011).

Costa (2008) in his seminal review illustrated that females would increase their foraging intensity and change prey taken first before increasing their foraging trip durations. The amount of energy a female can deliver to the pup per shore visit is relatively constant (Costa 1991a, b). An increase in foraging trip duration just means that females take longer to deliver the same amount of energy and results in an overall decrease in energy delivered. Increasing foraging trip duration should therefore be a last resort in times of reduced prey availability caused by climatic shifts or anomalies.

The El Niño Southern Oscillation (ENSO) is one of the best documented large scale environmental perturbations. Essentially, this decrease in strength of Pacific Trade Winds results in increased sea-surface temperatures in the Pacific Ocean with resultant massive die-offs of plankton and fish which subsequently influences their marine mammal predators (Stenseth *et al.* 2002). The influence of ENSO events on the provisioning patterns of marine predators is well studied, especially with regards to fur seals (e.g. Trillmich 1991; Guinet *et al.* 1994; Guinet *et al.* 1998; Forcada *et al.* 2005; Lea *et al.* 2006).

Here I use observational presence-absence data collected from flipper-tagged, individually identifiable lactating Subantarctic fur seals (*Arctocephalus tropicalis)* over a six year period to determine if there were annual differences in female provisioning rates and if so, whether they result from an ENSO event or anomalous sea-surface temperatures. Observer-based attendance pattern studies have been considered non-ideal in the past because females could be missed when present or short over-night foraging trips would not be accounted for (e.g. Goldsworthy 1999, Kirkman *et al.* 2002; Goldsworthy 2006). I account for detection failures by means of multi-state capture mark-recapture (CMR) models and subsequently correct attendance data. Influences of season, pup sex and presence of satellite tracking device on female attendance cycles are also explored.

Methods

Study site:

Marion Island (46°54’S, 37°45’E) is located in the Indian sector of the Southern Ocean. It lies directly in the path of the Antarctic Circumpolar Current (ACC) and is bounded to the north by the Subantarctic Front and by the Antarctic Polar Front to the south (Ansorge & Lutjeharms 2002). This study was conducted at Van den Boogaard and neighbouring Rockhopper Bay beaches (VdB, RhB; fig. 4.1), low-density rookeries on the north-eastern side of the island (Hofmeyr *et al.* 2006). On average 141 pups were born here annually during the 6-year study period (MN Bester, unpublished data). VdB and RhB are characterised by large boulders, typical of the preferred Subantarctic fur seal (SAFS) breeding haul-out sites (Bester 1982); bounded by 2-7 m high cliff faces and backed by a vegetated area (fig. 4.2a-c).

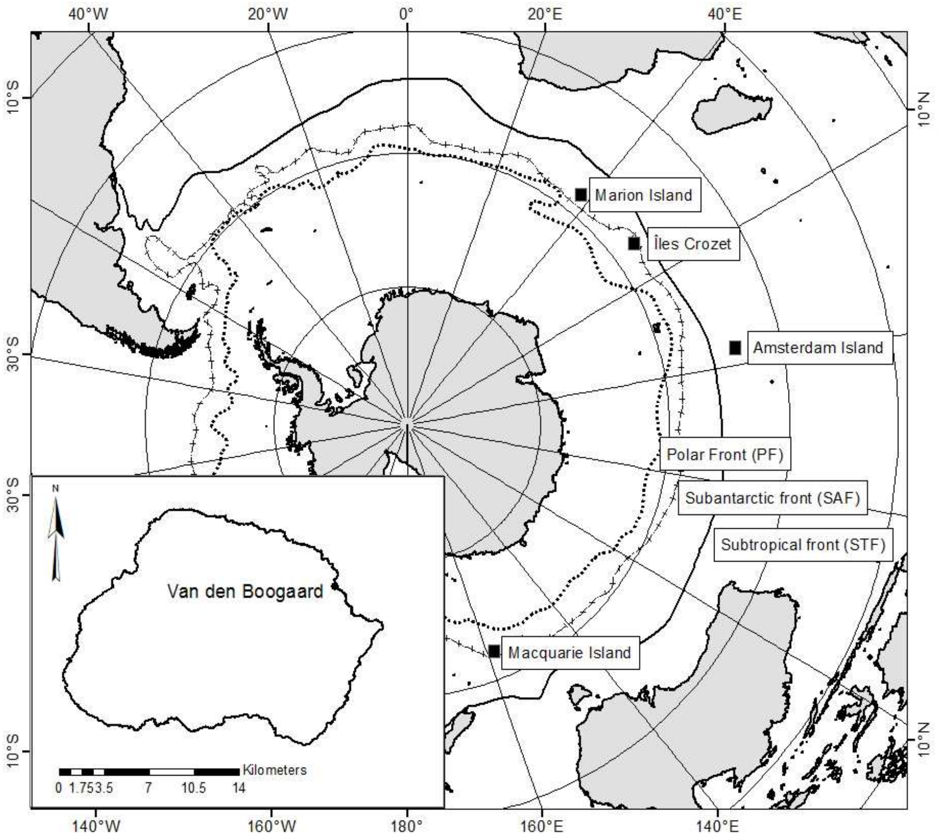


Figure 4.1: *The position of Marion Island in the Southern Ocean in relation to Île de la Possession (Îles Crozet), Amsterdam Island and Macquarie Island as well as the Antarctic Polar Front, Subtropical Front and the Subantarctic Front. The location of Van den Boogaard beach (study beach) on Marion Island is indicated (inset).*

Figure 4.2a: *Rockhopper Bay main beach as seen from the cliff top.*

Figure 4.2b: *Rockhopper Bay main beach as seen from the vegetated slope.*

Figure 4.2c: *Van den Boogaard beach as seen from the shoreline.*

Field methods:

Starting in the winter of 2006, females observed to suckle pups were captured using a hoopnet, while their respective pups were caught by hand. Females and pups were weighed and marked with uniquely numbered and colour-coded tags (Dalton Jumbo® Rototags, Henley-on-Thames, U.K.) in the trailing edge of each fore-flipper. The sex of the pup was noted. Experienced field personnel conducted attendance observations twice daily (1 - 2 hour sessions at approximately 09:00 and 16:00 (GMT+3)) by careful inspection of beach and vegetated areas at both study sites. Beach observations were often made from rock faces above the colony using binoculars to avoid disturbing the seals. The presence of all marked females and/or their pups was recorded together with their behaviour and subsequent indications of possible disturbance caused by the observers. This study includes data from the winter of 2006 up to and including the summer of 2011. Summer observations started on 15

January and lasted for two months until 14 March in each year. Winter observations were conducted from 15 May for 3 months until 14 August. For clarification, "season" refers to either a winter or summer season within a year (e.g. summer 2008). "Year" refers to the summer and winter seasons collectively within a given year (note that “year 2008” includes summer and winter data of pups born over a period of six weeks centred on mid-December 2007). A minimum of 30 mother-pup pairs were tagged during each year. Several females never returned from foraging bouts or for every breeding season or their pups died early in the season; consequently several untagged mother-pup pairs were caught and tagged at the start of each winter season to maintain/increase the sample size. An effort was made to capture and tag the pups of previously tagged study females that returned to pup again. However, this was not always possible as some females become wary of observers and tend to move into the water as field personnel approach. As a result the sexes of pups from 62 females in this study are unknown.

Data-handling and analyses:

Females were often seen on one day, absent on day two, and present again on day three, or sometimes absent for two or three days before located again. Given that SAFS from MI do not take short over-night foraging trips (de Bruyn *et al.* 2009; chapter 3), such females were regarded as present on day two. However, when females were absent for two or three days it became subjective to choose a cut-off point. To eliminate bias, detection probability was modelled by means of multi-state capture recapture (CMR) models and attendance bout durations corrected accordingly.

Multi-state Capture Recapture models:

Demographic parameters were estimated based on resight histories of lactating SAFS at RhB/VdB beaches from winter 2006 to summer 2011. This involved 217 individuals over 151 time steps (summer = 59 days; winter = 91 days). Capture *(P)*, Survival *(Φ)* and Transition *(ψ)* probabilities were estimated separately under a Conditional Arnason-Schwarz (CAS) multi-state capture-mark-recapture (CMR) framework (Lebreton & Pradel 2002) using the M-Surge software (Choquet *et al.* 2004). Under CAS models, *P* only relies on the current state in which the animal occurs. These parameters were modelled according to the following variables: season, year and pup sex. Since no age data is available for the females, age was not considered in the models. Two states were identified. The first is when a female was present and seen by the observer (i.e. “on land”) and the second when the female was absent (i.e. “at sea”). The aim was to obtain sighting probabilities to correct foraging cycle durations accordingly.

Survival probability:

If a female's pup died or she never returned in a season she was excluded from the analyses. If there is adequate attendance data for a female within one season but not the next or previous season within the same year, she was included in the model. In other words, if there is attendance data for a female in summer 2008, but she never returned in the winter of 2008, she was retained for analyses. I assumed a closed population within a season and *Φ* could therefore be set to a constant of one. Between seasons, within a year, the population was assumed to be open.

Transition probability:

Previous studies indicated that females' foraging trip durations increase as pups gets older (Georges & Guinet 2000, Kirkman *et al.* 2002). Pup sex also influences females' foraging cycles (Goldsworthy 2006). Yearly fluctuations in food availability caused by anomalous environmental events could potentially cause females to stay longer out at sea or return to the rookery sooner (e.g. Boyd *et al.* 1991). The probability for a female to move from land to sea or sea to land was modelled as the interaction between current state (i.e. at sea or on land), state moving to (sea or land), season, year and pup sex. The sex of very few pups were unknown and could therefore not be included in the interaction term. As such, I only included females with pups of known sexes in the interaction, and included females with an unknown sex pup as an additive effect. No attendance pattern data exists for the summer of 2006 and winter 2011, therefore in these seasons transition probability as a whole was constrained to zero.

Sighting probability:

Obviously the probability of sighting a female while in state two (i.e. "at sea") was set to a constant of zero. *P* in the summer of 2006 and winter 2011 were constrained to zero. All possible combinations for sighting probability while on land were tested. Akaike Information Criterion (AIC) was used to select the most parsimonious model, with models considered to be different when their AIC values differed by more than 2 (Burnham & Anderson 2002; Lebreton *et al.* 1992). The model with the lowest AIC value that could accurately estimate all the parameters was chosen.

Correction of attendance data:

To correct for days a female was present on land but missed, the total number of days a female was seen within a season was divided by the detection probability for that given season. For example, in the winter of 2008 the detection probability was 90.95%. Female LB573 was seen a total of 9 days, divided by 0.9095, which results in a corrected number of attendance days of 9.89. The corrected number of attendance days for each female was used in subsequent analyses of foraging trip parameters.

Calculation of foraging cycle parameters:

Traditionally only complete foraging cycles (foraging trip and subsequent attendance period) would be used in analyses. This would limit sample sizes and result in several days of observations being discarded (e.g. Kirkman *et al.* 2002, 2003). Furthermore, attendance observations were only conducted for sections of the lactation phase (summer attendance (15 January – 14 March) and winter attendance (15 May – 14 August)). Consequently, individual mean foraging trip duration (*f*) in days was calculated using the equation,

$$f = (A \text{ x } S) / (1\text{-}S) \qquad (1)$$

where A = mean attendance period (days), and S = proportion of time spent at sea over the entire observation period (Goldsworthy 2006). This approach enabled inclusion of all available data collected in each study period. If only foraging cycles were used, incomplete initial and final foraging trips, as well as first attendance observations would be excluded from analyses. The equation underestimates mean foraging trip duration but is more accurate estimate than using the length of a foraging trip of females for which only complete foraging trips were recorded (Goldsworthy 2006).

Environmental variables:

The Southern Oscillation Index (SOI) is the standardized difference in sea-level barometric pressure between Tahiti and Darwin (Australia) (available from the Bureau of Meteorology (Australia) http://www.bom.gov.au/climate/current/soihtm1.shtml). SOI values are often used as a proxy measure for the strength of ENSO events. Annual SOI anomalies were calculated by subtracting the mean annual value for period *x*, year *t*, from the 60-year (1950–2012) SOI mean measured over the same period. SOI anomalies purportedly show influence on several marine predators in the southern Indian and the Southern Ocean through, amongst others, a reduction in primary production and prey availability (Guinet *et al.* 1994; Guinet *et al.* 1998; Nel *et al.* 2002; Barbraud & Weimerskirch 2003; Lea *et al.* 2006). Reduced primary production is expected to operate with a lag-period. Four different periods over which SOI anomalies could influence pup condition were considered: 1) the period from the median pupping date (16 – 20 December, Hofmeyr *et al.* 2007) to weaning (mid-October, Kerley 1983) (= $\mathrm{SOI}_{\mathrm{LP}}$, December$_t$ to October$_{t+1}$; hereafter referred to as the lactation phase); 2) one year lag; 3) three year lag; 4) five year lag. These different time periods were based upon different duration of lag effects known to influence marine predators (Guinet *et al.* 1998; Barbraud & Weimerskirch 2003).

Monthly sea surface temperature anomalies (SSTa) were obtained from the Integrated Global Ocean Service System (Reynolds & Smith 1994: http://ingrid.ldeo.columbia.edu/SOURCES/IGOSS). The median maximum distance reached by lactating fur seals during foraging trips from Marion Island, obtained from satellite tracked females during the summer and winter (291 km and 502 km respectively, chapter 3) was used to draw separate radii around Marion Island. SSTa data were extracted at a monthly 1° scale and averaged within the respective "summer" and "winter" foraging areas for the following time periods: 1) lactation phase (explained above); 2) the preceding two months from mid-October to mid-December while foraging at sea to gain mass before giving birth to her next pup, having weaned her previous pup, and is no longer lactating (hereafter referred to as 'previous non-lactation phase'); 3) current attendance cycle season (e.g. summer 2008 = January to March 2008 average); 4) the previous season (for summer$_{(t)}$: April$_{(t-1)}$ - September$_{(t-1)}$ winter: Dec$_{(t-1)}$ - Mar$_{(t)}$; 5) one year lag; 6) three year lag; 7) five year lag. Figure 4.3 illustrates changes in anomalous SST values averaged over the 502 km radius drawn around Marion Island ("winter" foraging area) between January 2000 and May 2012. This timeframe captures temperature anomalies that might influence foraging trip duration at a lag effect.

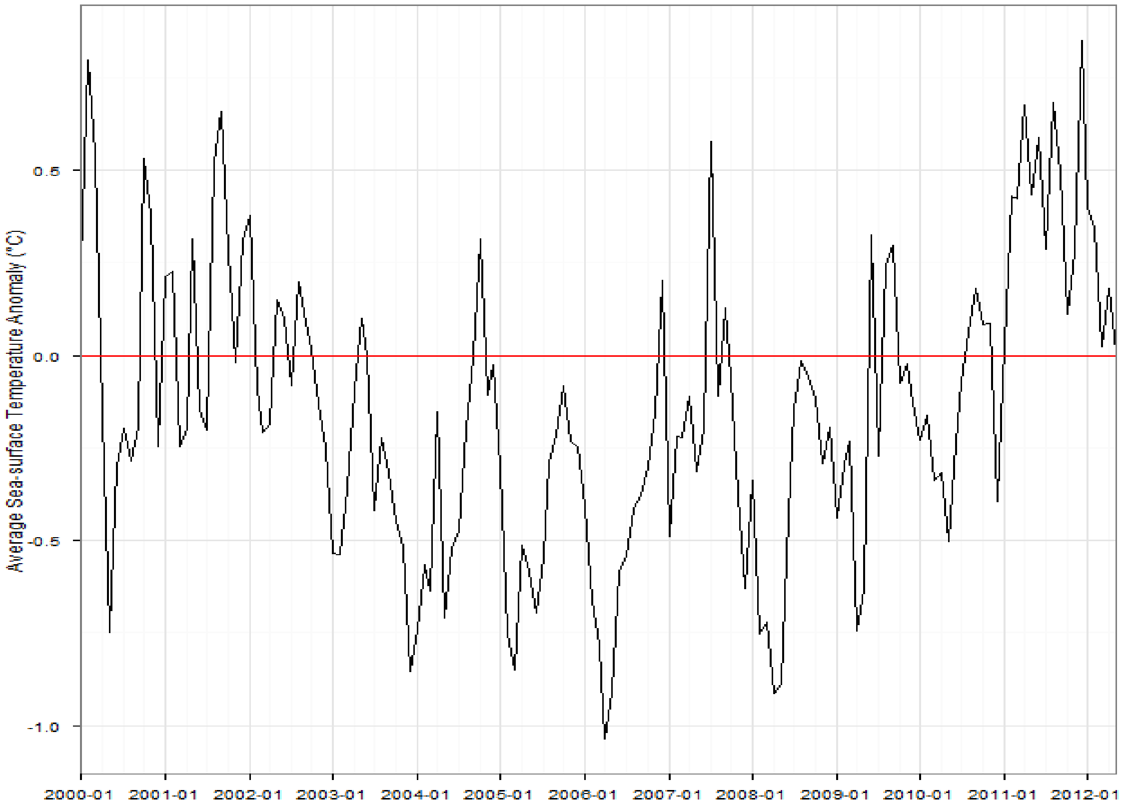


Figure 4.3: *Variations in anomalous sea-surface temperatures (^{0}C) in a 502 km radius around Marion Island from January 2000 to May 2012.*

Mixed-effects models:

Linear mixed-effects models were used to test the influences of several covariates on foraging trip duration and attendance period (in days) as well as proportion of time spent on land and at sea respectively. Mixed-effects models were fitted using the, “nlme” and “car” libraries in R (Fox & Weisberg 2011; Pinheiro *et al.* 2011; R Development Core Team 2012).

Proportions of time spent on land and at sea were square-root arcsine transformed prior to modelling. The initial starting covariates used in all models were: season, year, sex of the pup, whether or not a female carried a telemetry device (irrespective of the type of device), an interaction term between year and season, the interaction between season and device presence/absence as well as the five SOI and seven SSTa variables explained above. Individual identity (i.e. tag number) was the random effect. A backward stepwise selection method was employed by sequentially excluding covariates, however each possible combination of the covariates were tested as well as various interaction terms between the SOI and SSTa variables. A maximum likelihood method was used to fit all models. Autocorrelation plots did not reveal any significant autocorrelation issues. Small sample corrected Akaike's Information Criterion (AICc) was used for model selection (Burnham & Anderson 2002) together with several plot types to assess model fits (Pinheiro & Bates 2004). A marginal hypothesis test (*F*-test) was carried out on the final model to distinguish the significance of the various mixed effects (Bolker *et al.* 2009). The percentage of the variance explained by the random effect (i.e. season) was calculated by means of a variance component analysis (Crawley 2007).

Results

A total of 308 females were observed over the 6-year period with several females observed in more than one season and/or year. Taking this into account there is presence/absence data for 124 unique individuals (table 4.1).

Table 4.1: *Summary of foraging cycle parameters within each year and season. Values presented are means ± SE.**

Season	Number of mother-pup pairs	Number of device carrying females	Mean number of bouts	Mean attendance period (days)	Mean foraging trip length (days)	Mean % time at sea	Mean % time on land
2006W	14	4	3.071429	2.77 ± 0.28	30.21 ± 3.11	90.54 ± 1.23	09.46 ± 1.23
2007S	22	5	3.863636	3.20 ± 0.19	10.70 ± 1.09	74.84 ± 1.82	25.16 ± 1.82
2007W	24	1	2.916667	3.03 ± 0.25	30.61 ± 1.97	90.26 ± 0.92	09.74 ± 0.92
2008S	36	1	4.888889	3.18 ± 0.17	09.18 ± 0.54	73.05 ± 1.33	26.95 ± 1.33
2008W	25	0	3.2	2.73 ± 0.17	30.14 ± 2.28	90.82 ± 0.82	09.18 ± 0.82
2009S	39	0	5.153846	3.09 ± 0.15	09.00 ± 0.50	73.34 ± 1.24	26.66 ± 1.24
2009W	37	1	3.0	3.19 ± 0.14	29.57 ± 1.45	89.79 ± 0.52	10.21 ± 0.52
2010S	42	0	5.238095	3.27 ± 0.14	08.75 ± 0.45	71.79 ± 1.26	28.21 ± 1.26
2010W	31	1	3.193548	2.98 ± 0.17	27.93 ± 1.48	89.90 ± 0.58	10.10 ± 0.58
2011S	38	4	5.421053	3.21 ± 0.15	08.27 ± 0.47	70.94 ± 1.35	29.00 ± 1.35

*Standard Error

Capture-Mark-Recapture (CMR) models:

Tagged female survival for all years between seasons was estimated to be 0.72 ± 0.04 (confidence limits = 0.637 and 0.792). That is, on average only 72% of flipper-tagged females survived from summer to winter. The likelihood of a female remaining at sea (state two, i.e. remaining in a state of moving from land to sea, or sea to sea) was always higher than for a female to remain on land. Figure 4.4 presents estimates of females changing state by moving from, (a) sea to land; (b) from land to sea. Figure 4.5 illustrates estimates of females remaining in their current state by, (a) remaining on land, and (b) remaining at sea across the different seasons. Differences in these parameters according to pup sex are also illustrated.

Capture probability is best predicted by the interaction between season and year (fig. 4.6). AICc values decreased substantially when pup sex was also included in the model. Model estimates indicated that capture probability was only lower for females with pups of an unknown sex and there were no notable differences between having male or female pups. However, given the small number of females with pups of unknown sex, all years and seasons could not be estimated and pup sex was subsequently excluded from the final model.

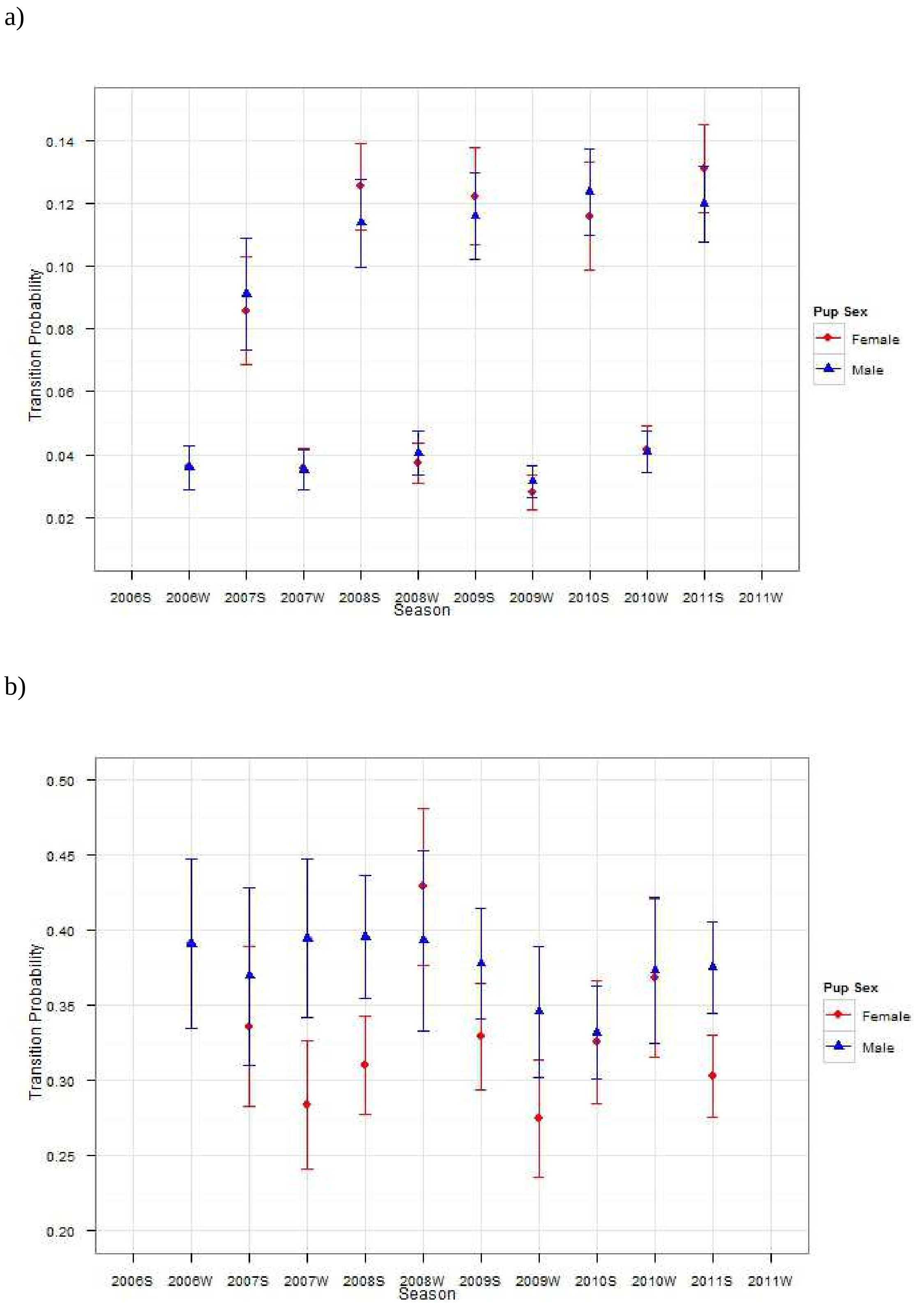
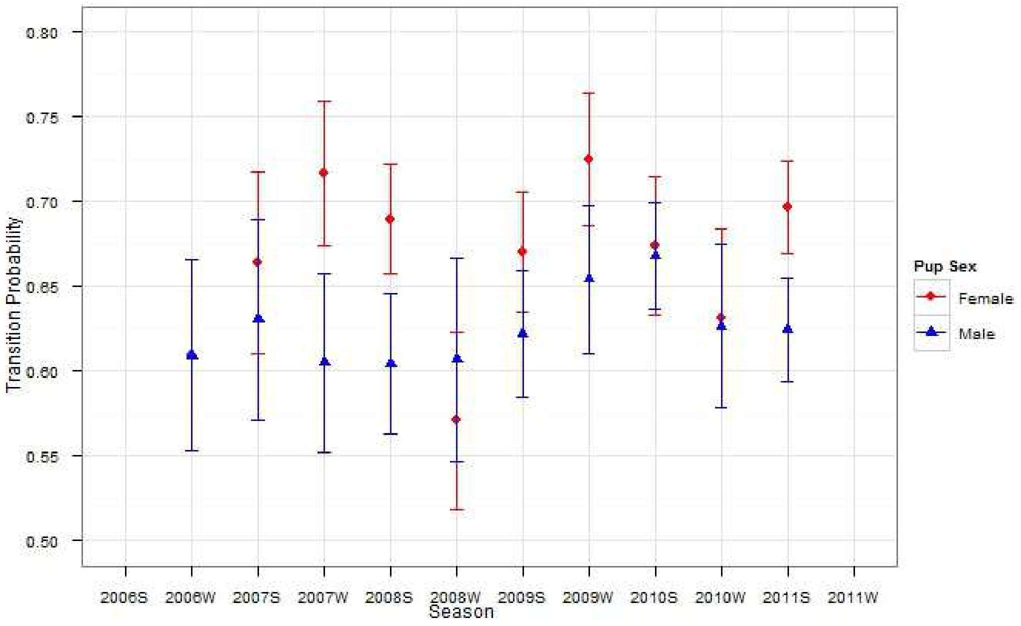


Figure 4.4: *The Transition probability (±SE) across the different seasons that females will a) move from sea to land and to b) move from land to sea. Differences associated with pup sex are also indicated.*

a)



b)

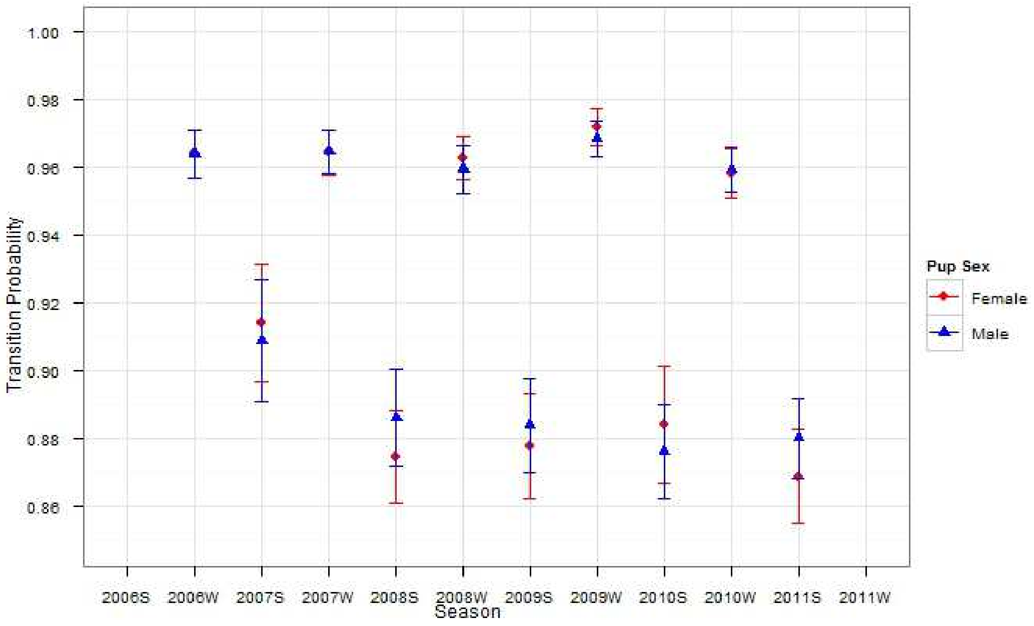


Figure 4.5: *The Transition probability (±SE) across the different seasons that females will a) remain on land and b) remain at sea. Differences associated with pup sex are also indicated.*

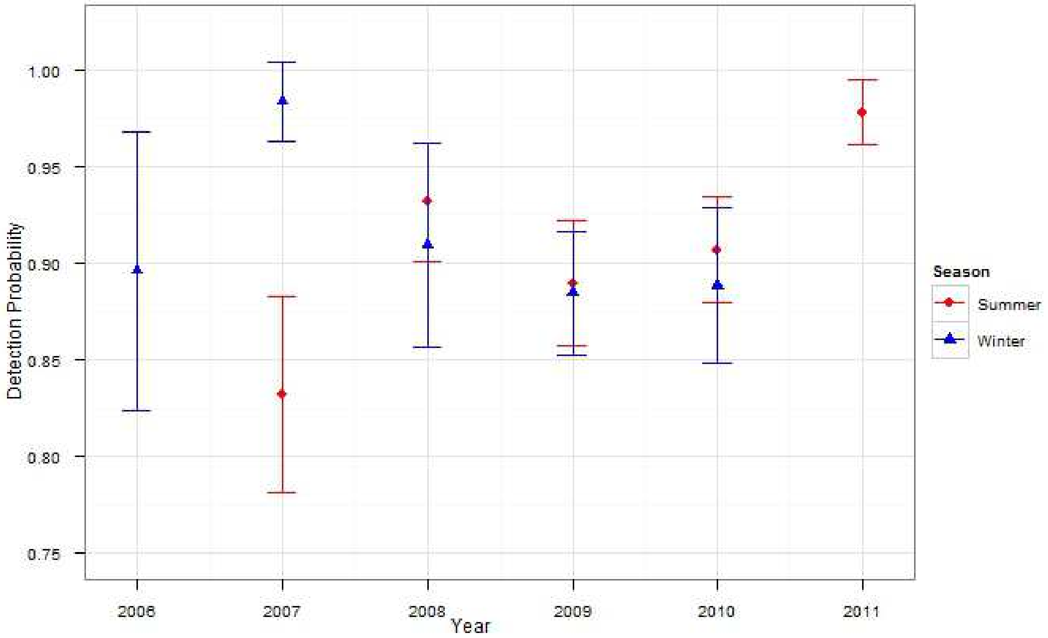


Figure 4.6: *Probability (±SE) of a female being detected and marked as present when she is on land; across different years, with differences between summer and winter shown.*

Mixed effects models: foraging trip duration

The best-fit model (i.e. the model with the lowest AICc score) retained both season and the presence/absence of a telemetry device. The *F*-test indicated that only season had a significant influence on the duration of a foraging trip (χ^2 = 813.66, *df* = 1, *P* < 0.0001) and that the presence of a device had no significant influence (χ^2 = 3.84, *df* = 1, *P* > 0.05). Model estimates indicate that foraging trip durations increased by 20.3 ± 0.7 days from summer to winter (*t*-value = 28.38, *P* < 0.0001, *df* = 182) and an insignificant 3.2 ± 1.6 days if the female carried a device compared to females not carrying a device (*t*-value = 1.95, *P* > 0.05, *df* = 182). Individual (random) effects explained 21.1% of the variation in the best model.

Mixed effects models: attendance period

Only season and pup sex were retained in the most parsimonious model and an *F*-test indicated both were significant. Females performed shorter attendance periods by 0.3 ± 0.12 days (*t*-value = -2.5, *df* = 180, *P* = 0.01) and 0.59 ± 0.14 days (*t*-value = -4.08, *df* = 180, *P* = 0.0001) when they had a male pup and pup of unknown sex, respectively. During the summer females stayed on land significantly longer (0.25 ± 0.1 days (*t*-value = -2.59, *df* = 180, *P* = 0.01)). Individual (random effect) explained 20.23% of the variation in the best model.

Mixed effects models: proportions of time spent on land and at sea.

When using the arcsine transformed percentage time at sea as explanatory variable, the most parsimonious model retained season, the presence/absence of a device and pup sex. Device presence was non-significant (χ^2 = 2.4432, *df* = 1, *P* > 0.05), with season and pup sex both being significant covariates (*F*-test: χ^2 = 766.86, *df* = 1, *P* < 0.0001 and χ^2 = 15.2830, *df* = 2, *P* < 0.001 respectively). Females with male pups spent 2.6 ± 1.1% more time at sea (*t*-value = 2.48, *P* < 0.005, *df* = 180) and females with pups of unknown sex 4.7 ± 1.3% (*t*-value = 3.76, *P* < 0.001, *df* = 180) spent more time at sea than females with female pups. In the winter females spent 23.4 ± 0.85% (*t*-value = 27.47, *df* = 18, *P* < 0.0001) more of their time on land compared to summer. Individual variation explained 21.53% of the model.

The best-fit model with the arcsine transformed proportion of time spent on land as explanatory variable, retained both season and pup sex. Across all seasons females with male pups spend 2.7 ± 1.1% less time on land (*t*-value = -2.54, *P* < 0.05, *df* = 181) and females with pups of unknown sex 4.7 ± 1.3% (*t*-value = -3.73, *P* <

0.001, *df* = 181) less time than females with female pups. In the winter, females spent 23.4 ± 0.85% (*t*-value = -27.31, *P* < 0.0001, *df* = 181) less of their time on land compared to summer. Individual variation explained 20.78% of the model.

Discussion

Although telemetry is the ideal platform to study attendance cycles, it is often subject to small sample sizes because of 1) the cost of these devices, 2) losses of devices due to animals not returning to deployment areas, loss or destruction of the device, or 3) simply failure of the device to record data. This limits the confidence in conclusions drawn from telemetry data as related to seasonal, annual or long-term climatic changes, as most variation within a year or season is explained by individual disparity (see Bonadonna *et al*. 2001). This is when observer-based studies, where obtaining larger sample sizes is less costly and often more easily accomplished, are useful for adding robustness to conclusions.

Previous studies on flipper-tagged lactating females and their pups suggest that females from Marion Island perform extended foraging trips (Bester & Bartlett 1990; Kirkman *et al.* 2002) but no over-night foraging trips for those that were satellite tracked (de Bruyn *et al.* 2009; chapter 3), similar to females from Amsterdam Island (Georges & Guinet 2000). However, in both these studies (Bester & Bartlett 1990; Kirkman *et al.* 2002) daily observations were only performed once a day, around midday. Females leaving at night, returning early the next morning, would subsequently be marked as present and the over-night foraging trip would not be detected. Females also often move into the shallows especially during midday for thermoregulatory reasons (Bester & Rossouw 1994) and as a result would be missed.

These studies were therefore considered inappropriate to detect over-night foraging trips. Goldsworthy (1999) also illustrated that observational methods underestimate foraging trip duration and overestimate attendance period for conspecifics at Macquarie Island, leading to erroneous results. Similarly, using twice daily observations and accounting for under-detection (this study), foraging trip durations and attendance periods were longer than what were previously estimated by Bester and Bartlett (1990) and Kirkman *et al.* (2002). Mean foraging trip duration is 29.55 ± 9.6 and 9.03 ± 3.4 days in the winter and summer respectively, over the entire study period. Kirkman *et al.* (2002) reported a mean foraging trip duration over their three year study period of 25.5 ± 2.4 and 7.0 ± 0.4 days for winter and summer respectively. Whether this difference is because of sampling protocol or caused by some form of external environmental pressure is unknown. Nonetheless, accounting for detection failures in the present study is a measurable improvement on previous methods of arbitrary assumptions of female presence-absences. It illustrates that, given appropriate data analyses, observer-based data could be useful in augmentation of costly telemetry studies.

The lack of differences in both foraging trip duration and attendance duration between years either indicates; (i) there has been no change in environmental factors that affect these, or (ii) females have been able to compensate for such change by means other than increasing foraging trip duration as suggested by Costa's (2008) proposed model. El Niño influences pinnipeds in the eastern Pacific (Trillmich 1991) as well as pinnipeds and other Southern Ocean top predators (e.g. Guinet *et al.* 1994, 1998; Vergani *et al.* 2001, 2004; Barbraud & Weimerskirch 2003; Inchausti *et al.* 2003; Lea *et al.* 2006). Populations are affected through changes in pup production

(Guinet *et al.* 1994), pup sex ratios (Vergani *et al.* 2004), breeding performances and body conditions of both parent and offspring (Guinet *et al.* 1998; Vergani *et al.* 2001; Inchausti *et al.* 2003; Lea *et al.* 2006). El Niño influenced pup production, growth rates and contributed to poor female and pup body condition of Antarctic fur seals one year after the ENSO event (Guinet *et al.* 1994; Lea *et al.* 2006). Seabirds, on the other hand, apparently respond to ENSO events 3 - 5 years after the fact on both the Crozet and Kerguelen Archipelagos (Guinet *et al.* 1998; Barbraud & Weimerskirch 2003). In 1997/1998 several bird species on Marion Island either showed a dramatic increase in breeding success or drastic failures (Crawford *et al.* 2003). They attributed this to the 1997/1998 ENSO event (one of the strongest ever recorded) based on anomalously high sea-surface temperatures around Peru and Ecuador (in agreement with ENSO events) and concomitantly around Marion Island. However, warm anomalous SST caused by ENSO events need to travel eastward via the Drake Passage before it could reach the Southern Indian Ocean (Stenseth *et al.* 2002) and consequently operate with a lag effect (discussed above). It is thus unlikely that the anomalous warm SST in 1997/1998 at Marion Island could be attributed to the 1997/1998 ENSO event and so quickly affect marine top predators. This does not mean that the anomalously warm SST did not influence breeding seabird populations through reduction in prey abundance or changes in prey availability as, e.g. variations in krill abundance influenced both seabird and seal populations at South Georgia (Boyd 1999; Croxall *et al.* 1999).

The SAFS from Marion Island did not change their attendance patterns over the six-year study period, nor did measurements of SOI and anomalous sea-surface temperatures influence this. These findings corroborate the prediction of the Costa

(2008) model whereby foraging trip duration is not a good estimate of changes in prey availability induced by external environmental perturbations. Previous studies where El Niño was found to affect Southern Ocean top predators, all included data from after intense and severe ENSO events. During the present 2006 to 2011 study period only weak ENSO events occurred from 2002-2003, 2006-2007 and 2009-2010. Two weak La Niña events occurred from June 2007 to February 2008 and August 2008 to April 2009 (http://www.bom.gov.au/climate/enso/). These weak events either did not affect females at all or not enough to force females to eventually increase their foraging trip duration. Other population parameters such as pup production, female and pup body condition and foraging effort at sea are required to determine whether any of these weak ENSO events influenced the foraging behaviour of lactating Subantarctic fur seals from Marion Island.

Guinet *et al.* (1994) found changes in pup production related to an ENSO event on Île de la Possession (Îles Crozet) for Antarctic fur seals, but not Subantarctic fur seals. On Marion Island Antarctic fur seal females increased their foraging trip duration and pup growth was lower in a year with high SST (Kirkman *et al.* 2003). However, in the same year SAFS females did not increase foraging trip duration (only shore visit duration in the winter) and pups had a higher weaning mass than other years (Kirkman *et al.* 2002). Furthermore, SAFS from Marion Island, similar to those on Amsterdam Island, have some of the longest foraging trip durations reported for any otariid (Georges & Guinet 2000; de Bruyn *et al.* 2009). Despite environmental changes, SAFS pups thrive where Antarctic fur seals do poorly. Given their long lactation period and the pups' extended period of fasting, SAFS pups have likely evolved methods to deal with extended periods of fasting and are therefore more robust to environmental change (Verrier *et al.* 2009). Weak environmental fluctuations, as described before, are thus unlikely to influence SAFS and would explain these results.

Other influences on attendance cycles:

Influences of satellite or archival tracking devices on animals have been studied extensively (e.g. McMahon *et al.* 2005) with some authors finding an influence (e.g. Bailleul *et al.* 2005) and others none (e.g. Boyd *et al.* 1991; Lea *et al.* 2006; McMahon *et al.* 2008). Even though females that carried a device undertook longer foraging trips, this relationship was non-significant in the present study. Given the small percentage of study females which carried a device (5.5%), the observed increase in foraging trip duration could purely be coincidental, and attendance cycle data stemming from observer based data may therefore be compared with attendance cycle data from telemetric methods.

In most otariid species, including Subantarctic fur seals (Georges & Guinet 2000; Kirkman *et al.* 2002; Beauplet *et al.* 2004; Luque *et al.* 2007), Antarctic fur seals (Boyd *et al.* 1991; Biuw *et al.* 2009); New Zealand fur seals (Goldsworthy 2006), Australian fur seals (Arnould & Hindell 2001) and the Northern fur seals (Gentry & Holt 1986) foraging trip duration increases from summer to winter. It is attributed to; 1) seasonal change in prey availability and abundance, 2) increase in pup demands (Georges & Guinet 2000) and 3) females are also pregnant in the winter (Bester 1995) which requires additional energy gain for the growing unborn pup. In the summer the fasting capabilities of young pups are considerably lower than when they are older during winter (Verrier *et al.* 2009) and pups are limited in the amount of milk they are able to ingest due to their small size. Consequently attendance patterns are dependent on pup demands (Georges & Guinet 2000). In the winter pups are able to fast for longer (Verrier *et al.* 2009) and are able to ingest more milk. Female attendance patterns are then controlled by female traits, such as body size and experience (Georges & Guinet 2000). However, unlike other studies where attendance period remains similar from summer to winter (e.g. Goldsworthy 1999; Georges & Guinet 2000; Kirkman *et al.* 2002, 2003), attendance durations increased in this study. Like their counterparts on Amsterdam Island, they undertake one of the longest, in distance and duration, foraging trips known for otariids (Georges & Guinet 2000; Kirkman *et al.* 2002; de Bruyn *et al.* 2009). However, unlike females from Amsterdam Island that dive to mean depths ranging between 19 and 29m, Marion Island females often exceed diving depths of 40 m (chapter 2). This means they work harder not only in terms of swimming distance but also foraging effort itself. Increased attendance period in the winter might therefore be related to resting behaviour. Females habitually arrive on land and spend a day resting before reuniting with her pup (personal observation).

New Zealand fur seal females spend a higher proportion of their time at sea when they have male pups and more time ashore for female pups (Goldsworthy 2006). Similarly, during the summer SAFS females at Marion Island spend 69.6 % of their time at sea if they have female pups compared to females with male pups (73.9 % of time spent at sea). During the winter this dissimilarity decreased and females spend 89.4 % of their time at sea when they have a female pup compared to 89.9 % for male pups. Milk-ingestion capabilities and sucking rates of larger male pups were suggested as possible explanations (Chilvers *et al.* 1995; Goldsworthy 2006).

However, on Amsterdam Island, foraging trip duration and attendance periods were not related to pup sex, but rather the weight of the pup (Georges & Guinet 2000). Marion Island SAFS pups show significant differences in body mass between male and female pups from as early as 30 d of age up to weaning (Kirkman *et al.* 2002). The difference in attendance patterns of mothers with male versus female pups on Marion Island is therefore probably a consequence of differences in pup mass and not gender. Notably, the degree to which females' attendance cycles differ between male and female pups from summer to winter decreases (4.3% vs. 0.3% for summer and winter respectively). This is despite the fact that differences in pup mass become larger from summer to winter (Kirkman *et al.* 2002). Reasons for this are not well understood; more data on sex differences in pup growth is required to explain this phenomenon.

Differences in capture probability:

Despite that field personnel are thoroughly trained, annual and seasonal variation in capture probabilities indicate that both, effort by - (annual variation) and experience of observers (seasonal variation), play a role in resighting a female. The annual relief voyage for Marion Island arrives mid-April and experienced field personnel have a month to train new field personnel. The ship departs mid-May leaving the new team behind, and therefore a Marion Island "team year" does not overlap with a SAFS breeding year, which starts mid-December (median pupping date for females) and ends October the next year (weaning of pups) (Kerley 1983; Hofmeyr *et al.* 2007). Therefore, summer attendance pattern observations would be performed by experienced field personnel that have been working on the island since April the previous year. Winter observations, however, are generally performed by less experienced field personnel that arrived at the island only a month prior to the start of the winter attendance pattern study. This might explain why capture probability was lower in the winter than in summer for most years, although the effect of comparatively more severe weather conditions (e.g. more snow-cover) cannot be discounted.

Conclusion:

This study illustrates that in ideal situations, given the correct data handling, observer based attendance cycle data could aid telemetry based studies. It also indicates that not only season but also pup sex influence the percentage of time females apportion to foraging at sea and suckling their pups on land. However, these observations are most likely linked to sex-related differences in pup mass rather than the sex of the pups. No annual changes in attendance cycle data were detected, nor did the El Niño Southern Oscillation or anomalous sea-surface temperatures influence attendance cycles. This could be because attendance cycle data is a poor predictor of weak El Niño or small environmental fluctuations as suggested by Costa (2008). The protracted weaning period and fasting capabilities of SAFS pups may also have evolved to compensate for weak environmental fluctuations. Attendance cycle data concomitant with information on pup growth, female body condition and population changes are required to further test for environmental influences on female foraging behaviour.

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Chapter 5:

Conclusions

Synthesis

The development of satellite telemetry over the past few decades resulted in an unprecedented increase in knowledge and understanding of the at-sea behaviour for top marine predators (e.g. Gentry & Kooyman 1986; Bonadonna *et al.* 2000, 2001; Lea *et al.* 2002; Bradshaw *et al.* 2004; Biuw *et al.* 2007; Tosh *et al.* 2009; Bailleul *et al.* 2010; McIntyre *et al.* 2011). Foraging forms the cornerstone of an animal's life-history. Successful synchronisation of foraging behaviour with reproductive costs, environmental fluctuations and seasonal cycles forms the boundary between success and failure of an individual or of whole populations. Understanding how top marine predators interact with their three-dimensional environment at a hierarchy of both spatial and temporal scales is imperative to understand how both long- and short-term climate fluctuations influence marine ecosystems and whole populations.

A population's survival and growth depend upon its breeding success, which in turn is directly influenced by its foraging success. During the breeding season lactating females have the added burden of obtaining resources for their progeny. Otariid seals (i.e. fur seals and sea lions) are income breeders which means females have to regularly commute between foraging grounds and their breeding colony. They are therefore both spatially and temporally restricted by the fasting capabilities of their pups, and the energetic cost to a female increases with distance and duration of a foraging trip (Arnould *et al.* 1996).

Recently, disparities in foraging strategies of *Arctocephalus tropicalis* amongst four islands raised some important questions. Subantarctic fur seal females from Marion Island take long extended foraging trips and do not make short over-night foraging trips like conspecifics from nearby Îles Crozet and at distant high latitude Macquarie Island. As such they behave more like females from distant low latitude temperate Amsterdam Island (Georges *et al.* 2000a) as shown by de Bruyn *et al.* (2009). It appears that foraging tactics are governed by different environmental pressures at different localities. Females from Amsterdam Island mainly forage in the sub-tropical front and sea-surface temperature played a major role in determining foraging locations (Georges *et al.* 2000a). At Macquarie Island the proximity of the nearby Macquarie Ridge seemed to dictate foraging behaviour (Robinson *et al.* 2002) whereas the presence of the Crozet plateau around Îles Crozet played a commanding role in female foraging tactics at Île de la Possession (Bailleul *et al.* 2005; Luque *et al.* 2007). At least some lactating females from Marion Island preferred an area NE of the island in the vicinity of the Del Caño Rise (de Bruyn *et al.* 2009). Individuals from the different populations also exhibit different diving behaviour. Females from Amsterdam Island dive to a mean depth of 19 m and 29 m during the summer and winter respectively (Georges *et al.* 2000b). Despite the similarities in their foraging cycle parameters, individuals from Macquarie Island and Île de la Possession differ greatly in their diving behaviour, including those from Amsterdam Island. Macquarie Island females perform the shallowest mean diving depths recorded for the species so far (9.9 m; Robinson *et al.* 2002) whereas females from Île de la Possession perform on average the deepest dives for the species. They dive on average 37.8 m and 45.7 m deep during over-night and long duration foraging trips respectively. In the hitherto absence of dive data, we did not know how lactating females from Marion Island compare in terms of their diving behaviour.

Here, I studied the foraging behaviour of a marine top-predator, the Subantarctic fur seal, at a range of both temporal and spatial scales. This was done using new dive data, longitudinal at-sea ranging data and observer based attendance pattern data.

Temporally, females vary their diving behaviour seasonally, diurnally during the foraging trip and even throughout the course of the day/night. They dive exclusively at night and during the summer perform longer and deeper crepuscular dives during dusk and dawn. This is to presumably follow the diel vertical migration of their myctophid prey and is in congruence with other populations of both conspecific and heterospecific otariid seals (e.g. Lea *et al.* 2002; Luque *et al.* 2007). Counter intuitively, during the winter lactating females performed shorter, shallower crepuscular dives as opposed to summer. This is most likely related to a seasonal downward vertical movement of myctophid prey, inhabiting lower depths in the water column during winter (Knox 2007). During dusk and dawn they are then inaccessible to diving fur seals. Overall diving behaviour of females from Marion Island is more similar to conspecifics from nearby Île de la Possession, despite disparities in attendance cycles. De Bruyn *et al.* (2009) suggested that extended foraging trips are related to Marion Island's distance to particular bathymetrical features. This study now suggests that underwater bathymetry also dictate diving behaviour. Although the sample size of nine individuals is very small, the diving data is new and forms a good foundation from which greater understanding of this disparity in foraging behaviour amongst islands can be gained.

In the aforementioned studies at Île de la Possession, Macquarie and Amsterdam islands sampling was done cross-sectionally, i.e. multiple trips per individual were excluded to balance datasets. To date no study reported on intra-individual foraging site fidelity, or a directional component to foraging by an individual from its breeding beach, for this species.

De Bruyn *et al.* (2009) found that most females travelled north-east of Marion Island, but a few travelled west. Determining whether foraging trips to the west of the island is undertaken consistently by a female, to form part of a specific 'foraging strategy' or in response to changing available resources and environmental cues, was beyond the scope of the data. Of the 18 females tracked in this study only two travelled to the west of Marion Island after they initially travelled eastward. All westward foraging trips were undertaken during the austral winter. This is supposedly not a foraging strategy but a short-term response to tracking prey in a highly heterogeneous environment. Despite the colony-level preferred foraging area to the NE of Marion Island (de Bruyn *et al.* 2009; this study), individuals also showed a high degree of foraging site fidelity by consistently travelling in the same general direction from the island. The actual foraging locations did change somewhat which, again, is presumably in response to tracking prey in a highly variable environment. Knowledge of preferred foraging areas in marine top predators is imperative in designing of Marine Protected Areas (Louzao *et al.* 2011).

Although telemetry studies are ideal to study temporal and spatial variation of foraging behaviour, it is expensive and often suffers from limited sample sizes. This could lead to erroneous conclusions drawn when extrapolating to whole colonies or populations. Observer-based studies, such as attendance pattern studies, could be used to augment telemetry data. However, observer-based studies are subject to human error, such as observers noting a female to be absent when she is in fact present. Using multi-state capture mark-recapture models (CMR), I accounted for detection failures and corrected attendance data accordingly. The resultant difference between measured attendance cycle data in this study and previous studies for the same species at Marion Island (Bester & Bartlett 1990; Kirkman *et al.* 2002), is most likely due to differences in sampling protocol and data analyses among studies. The use of CMR here makes the results of the present study more robust. Seasonal change again influenced female provisioning rates substantially with foraging trips increasing in duration as seasons progressed from summer to winter. This is conceivably in response to a seasonal reduction and availability of prey resources in winter, together with growing demands of the current pup (Georges & Guinet 2000) as well as of the foetus of the next pregnancy beyond the April implantation date of the blastocyst (Bester 1995). Pup sex influences on attendance cycles could have some potential implications in years of reduced prey availability and resultant sex ratios of pups that eventually wean. Attendance cycles are not a good predictor of weak El Niño events or of other sea-surface temperature anomalies. Given the Subantarctic fur seals' extended lactation period, pups have the ability to fast for long periods (Verrier *et al.* 2009) making them more robust against environmental perturbations. Combining attendance cycle data with concomitant data on female body condition, pup and population growth as well as pup sex ratios is the next step forward.

Although Marion Island is situated in the seemingly favourable location within a marine ecotone - the Polar Frontal Zone, lactating Subantarctic fur seal females work harder at foraging than at any other island population of conspecifics. This appears to be the result of a lack of any closely situated bathymetrical features associated with increased and predictable prey availability. Females compensate for this by consistently travelling to areas of supposedly known prey availability on consecutive foraging trips.

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Marion 66 Sealers

Marion 69 Sealers