The diet of the Subantarctic fur seal *Arctocephalus tropicalis* at Marion Island.

by

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Submitted in partial fulfilment of the requirements

for the degree of

Master of Science (Zoology)

in the

Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

South Africa

February 2010

The diet of the Subantarctic fur seal *Arctocephalus tropicalis* at Marion Island

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Picture by Mashudu Phalanndwa

Declaration:

I, **Azwindini Justice Ramunasi** declare that the thesis/dissertation, which I hereby submit for the degree **Master of Science in 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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Abstract

Faecal analysis (n = 806 scats) was employed to examine the diet of the Subantarctic fur seal *Arctocephalus tropicalis* at Marion Island (46˚ 54’S, 37˚ 45’E) over a period of six years (April 2000 – March 2006). Identifiable prey remains (fish otoliths, cephalopod beaks) were extracted from the faeces and analyzed. The number of individuals of each prey group identified was determined, and the size of individuals was estimated by applying appropriate regression formulae to measurements of the prey remains. Despite the biases associated with the method, useful information was gained on seasonal and inter-annual fluctuation in the presence of prey species in the diet. The indices used to investigate these variations were percentage numerical abundance, percentage frequency of occurrence and reconstituted body size (mass and length) of prey species taken. The diet was diverse and myctophid species predominated. Cephalopods were minor prey species in scats (n = 39). The five main prey species were *Gymnoscopelus bolini*, *G. piabilis*, *G. fraseri*, *G. nicholsi* and *Protomyctophum tenisoni*. In all respects *G. bolini* predominated throughout the study period, although in most comparisons no statistically significant differences in the relative contribution amongst the main prey species in the diet were found. Seasonal and inter-annual variations in the contributions of these species to the diet presumably resulted from changes in the relative abundance and distribution of prey.

Layout of this dissertation

There are six chapters in this dissertation of which three are arranged as independent papers for submission to journals, so there are some repetitions. Although I tried to limit these, some repetition will be encountered in different chapters. There is an inclusive chapter on methods and materials, to which all main chapters will refer to. Tables and figures follow the text of a particular chapter.

Now you can fold your arms and chilax **(**Picture by Mashudu Phalanndwa**)**

Acknowledgements

This study continued the “Pinniped Monitoring Programme” within the South African National Antarctic Programme (SANAP) and would not have been possible without the assistance of many individuals who were involved from the beginning of this study. I would like to thank the Department of Science & Technology (DST) for my salary while at Marion Island and the National Research Foundation (NRF) for providing a bursary during the laboratory and write-up phase of this study. Sincere thanks to Dr PSO Fouche, my Honours Supervisor at the University of Venda (UNIVEN); you have been like a father to me during my undergraduate and subsequent Honours level studies. I have extracted so many skills from you, starting from social to academic. It was not easy to train us in an institution without ideal resources, however, we learned to improvise and be creative. I gratefully acknowledge Steven Kirkman and Dr Silvia Mecenero for training me in prey identification. I would like to thank Bruce Dyer for providing valuable otolith reference materials. Thanks are due to all the field assistants who helped with scat collection. I would like to thank crazy Dumile Tshingana (aka “Majola”) for entertainment and sympathizing with me during 14 months of solitude on Marion Island. Special thanks to my supervisor Prof M.N. Bester (aka “The Captain”) for sailing with me from Marion Island through two years of my M.Sc; You gave me the platform to stretch my wings so that one day I will be able to fly beyond the sky. Greg Hofmeyr and Michelle du Toit’s guidance, encouragement and constructive criticism are gratefully appreciated. I would also like to thank my parents Reineth and Benard Ramunasi, my uncle Samson Ramunasi and Mr Nelson Mudau, you have been on my side throughout. I shall not be doing justice to myself if I do not include in my book of gratitudes, my family members who are no longer within their flesh, those I know and the ones I never saw, thanks for your mercy. I have known the Almighty God through you, may God in turn have mercy upon you. I am especially grateful to my only daughter Azwihangwisi Ramunasi, nangoho a zwi hangwisi nwananga zwe ra fhira khazwo, zwihulusa zwa u fhambanyiswa hanga na ene nwananga u vhuya u swika namusi ri tshi vho nga vhanwevho.

Mukololo wa Thengwe u nala dza vhathu!

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Chapter 1

General Introduction

The Southern Ocean has a rich, high productivity with large populations of whales and millions of penguins, fishes, seals, and cephalopods, depending on the near surface productivity (Knox 2007). Consequently the ocean provides an abundant and diverse range of food resources, such as zooplankton, fish, squid, crustaceans, mollusks and even birds, and mammals (Riedman 1990). The carnivorous pinnipeds have taken advantage of each type of food resource, consuming a wide variety of organisms found on or beneath the surface of the ocean (Riedman 1990).

There are 16 otariid species which comprise seven genera (Rice 1998). The family Otariidae comprises the sea lions (Otariinae) and the fur seals (Arctocephalinae) (Rice 1998; Robinson *et al*. 2002). Fur seals are distinguished from sea lions by the presence of dense underfur, consisting of 30 or more secondary hair associated with each primary hair, in the pelage of fur seals (Repenning *et al*. 1971). Moreover, the sea lions are typically much larger and have a broader, blunter nose compared to fur seals.

The subfamily Arctocephalinae, the southern fur seals, began diversifying 3 million years ago (Repenning 1975). Speciation is likely to have occurred in environments varying in seasonality and predictability of prey resources, which has resulted in the evolution of different breeding strategies, each suited to a particular combination of environmental variations (Gentry & Kooyman 1986, Robinson *et al*. 2002). The genus *Arctocephalus* embraces eight species, i.e. southern fur seals (Rice 1998). Two species from the Arctocephalinae, the Subantarctic fur seal *Arctocephalus tropicalis* and the Antarctic fur seal *A. gazella*, breed at the Prince Edward Islands, Southern Indian Ocean (Condy 1978). One of the two islands in the group, Marion Island (46° 54'S, 37° 45'E) (Fig. 1), is the study site. Subantarctic fur seals breed mainly on the exposed west coast, while Antarctic fur seal colonies are found on the south coast (Wilkinson & Bester 1990). The total size of the Prince Edward Islands' populations was estimated at approximately 150 000 Subantarctic fur seals and 5 800 Antarctic fur seals in the 2001/ 2002 and 2003/ 2004 breeding seasons, respectively (Hofmeyr *et al*. 2006).

The distribution and availability of marine resources are generally related to the spatial heterogeneity of physical and oceanographic features (Mann & Lazier 1999; Beauplet *et al*. 2004). This heterogeneity is believed to affect different levels of the trophic system, from phytoplankton to marine top-predator populations (Croxall 1992). The large temporal and spatial variability in marine productivity encountered by marine predators may impose negative effects on their breeding success (Lea *et al*. 2006). The spatial and temporal patterns in behaviour of high-level marine predators can, therefore, provide valuable insights into the spatial distribution of marine resources (McConnell *et al*. 1992; Pakhomov & McQuaid 1996; Guinet *et al*. 1997; Georges *et al*. 2000; Beauplet *et al*. 2004).

In 1989 a sampling programme of fur seal scats (faeces) was initiated in order to address our lack of knowledge of the diets of both species of fur seal resident on Marion Island (Klages & Bester 1998). Specific aims of this investigation were to determine to what extent their fish diets differ and whether temporal changes in the prey species composition are evident. It was also of interest to what degree fur seal fish diets overlap with those of king penguins (*Aptenodytes patagonicus*) on Marion Island, as they were perceived as potential competitors for food (Klages & Bester 1998).

Diets of marine mammals are inferred from direct observations of feeding (Fea & Harcourt 1997) and also from the identification of hard parts recovered from complete stomachs of culled seals (Murie & Lavigne 1986); from the partial stomach contents obtained from live seals using stomach-flushing techniques (Croxall 1993; Ferreira & Bester 1999); from scats (Klages & Bester 1998; Trites & Joy 2005); and from natural regurgitations (Kirkman *et al.* 2000). Each of these methods has shortcomings. More recently, however, greater emphasis has been placed on developing non-invasive and non-destructive methods to study pinniped diets (Pierce & Boyle 1991; Iverson *et al*. 2004), one of which is scat analysis (Klages & Bester 1998).

Scat analysis provides a large amount of information despite the expenditure of a fraction of the effort required by other methods, and with little disturbance to the animals (Carey 1992; Reid 1996; North 1996). It is now the most widely used method for inferring the diets of pinnipeds (Carey 1992; Granedeiro & Silva 2000; Arim & Naya 2003). This method assumes that solid remains pass into faeces in the same proportions as they were consumed, and therefore that their relative occurrence in the diet is not seriously biased (Reid 1996; Tollit *et al.* 1997). Nevertheless, the analysis of scats has potential biases, mainly related to the total or partial digestion of food (e.g. da Silva & Neilson 1985; Fea & Harcourt 1997; Tollit *et al.* 1997), and these need to be dealt with.

For most species of pinnipeds, fish and squid are a principal food resource (Riedman 1990). A number of hard parts resist digestion and are used to identify prey species. Fish prey is usually identified from otoliths (Fig. 1.1), and cephalopod prey from beaks (Prime & Hammond 1987; Murie & Lavigne 1991; Cottrel *et al.* 1996; Tollit *et al.* 2003; Casper *et al.* 2005). Identifying these prey remains is relatively easy (Iverson *et al.* 2004). In addition to identification of prey species, otolith measurements can be used to estimate the size and/or mass of prey by means of specific regressions (Harvey *et al.* 2000).

Identifiable hard part remains in scats

Fish otoliths

A number of problems are associated with inferring information from otoliths. Otoliths are exposed to varying degrees of chemical and mechanical abrasion in the digestive tract of predators before they are excreted (Granadeiro & Silva 2000). Small otoliths are more likely to be totally dissolved and thus some prey species may not be detected (da Silva & Neilson 1985; Jobling & Breiby 1986; Pierce & Boyle 1991). Seals tearing up large prey during consumption, and several seals feeding on the same prey item, may also affect the recovery of prey hard parts (Cottrell *et al.* 1996). In addition, fish without otoliths (e.g. lumpsucker *Cyclopterus lumpus*) or with fragile otoliths (e.g. clupeids and salmonids) and fish with cartilaginous skeletons (e.g.

lampreys, rays and dog fish) will be underrepresented or go undetected (Jobling & Breiby 1986; Murie & Lavigne 1986; Jobling 1987; Dellinger & Trillmich 1988; Carey 1992). However, feeding experiments with captive animals have been used to derive correction factors to minimize errors resulting from the digestion or partial digestion of otoliths (Prime & Hammond 1990; Hammond *et al.* 1994; Tollit *et al.* 1997).

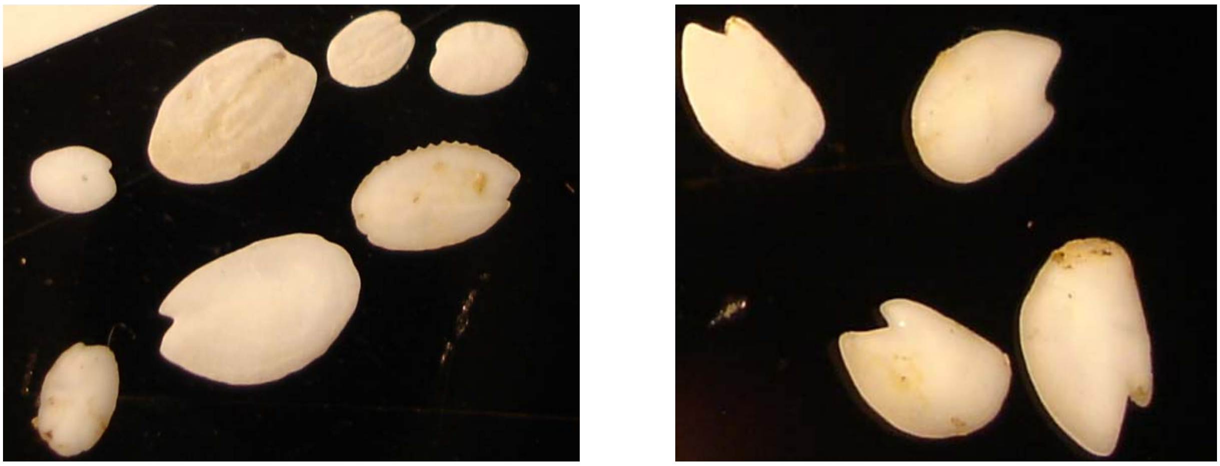
Cephalopod beaks

The indigestible beaks of cephalopods allow retrieval of a large variety of cephalopod taxa from stomach contents or scats of predators. Cephalopod beaks, particularly lower beaks, enable identification of the composition of cephalopod species in the diet of predators, providing indications as to cephalopod diversity and abundance within the foraging range of predators (Klages 1996; de Bruyn *et al*. 2003). Like the otoliths, the cephalopod portion of diet is often inaccurately represented in scats. Larger squid beaks, especially those larger than 10mm have lower recovery rates, because they are often regurgitated or retained in the gut for longer (Reid 1996; Klages & Bester 1998; Fea & Harcourt 1997; Kirkman *et al*. 2000; Casper *et al*. 2005) thereby facilitating fragmentation and rendering them unidentifiable (Staniland 2002; de Bruyn *et al.* 2003). Cephalopod remains in the scats of Subantarctic fur seals at Marion Island has been reported to be of such a small size or so damaged that positive species identification was virtually impossible (Klages & Bester 1998).

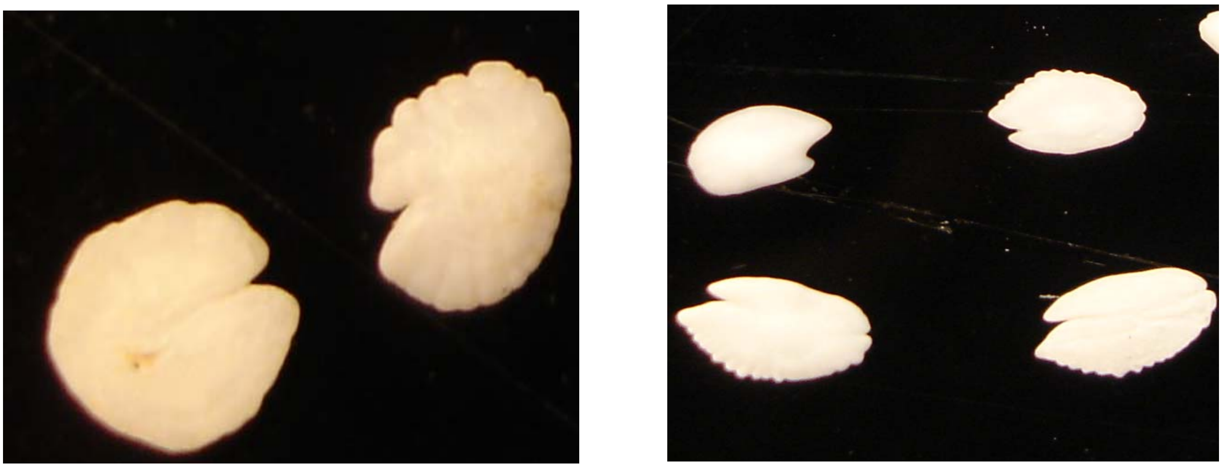
Other prey items

Other prey remains that that can be extracted from scats include crustacean carapaces (Pierce & Boyle 1991; Staniland 2002); krill (Daneri *et al.* 2005) and bird feathers (Mecenero *et al*. 2006a), are used to identify and to quantify the prey types ingested (Staniland 2002). However, the presence of other prey taxa was negligible in the seal diet (Daneri *et al*. 2005; Mecenero *et al*. 2006a). Adams & Klages (1987) indicated that crustaceans contribute less than 1% of the diet of another top predator, the king penguin, at Marion Island. In addition, the frequency and extent of bird predation, based on the incidence of feathers in the scats, is very small (Goldsworthy *et al*. 2001, Mecenero *et al*. 2006a), contributing less than 0.01% of the fur seal diet (Mecenero *et* *al*. 2006a). Furthermore, Klages & Bester (1998) reported that remains of other prey were not found in the diet of the Subantarctic fur seals at Marion Island. As a result, the present study only focus on the primary prey items of the Subantarctic fur seals, i.e. cephalopod and fish.

A number of diet-related studies of the southern fur seal species have been conducted. Most of these have concentrated on diet composition (e.g. Juan Fernandez fur seal *A. philippii* - Ochoa-Acuna & Francis 1995; *A. tropicalis* - Klages & Bester 1998; New Zealand fur seal *A. forsteri* - Fea *et al*. 1999; South American fur seal *A. australis* - Naya *et al*. 2002; Australian fur seal *A. pusillus doriferus* - Hume *et al*. 2004; Antarctic fur seal *A. gazella* – Casaux *et al*. 2003, 2004; Makhado *et al*. 2008). The Subantarctic fur seal diet in subtropical waters is essentially unknown. However, previous studies on various fur seal species exploiting subantarctic waters showed that fish constituted the main components of their diet (Ochoa-Acuna & Francis 1995; Klages & Bester 1998; Robinson *et al*. 2002). The diet of the Subantarctic fur seal at the Tristan da Cunha group of islands is largely unknown, only the cephalopod component having been described (Bester & Laycock 1985). At Amsterdam Island (37° 50'S, 77° 35'E) this species feeds on seasonally abundant Rockhopper penguins (*Eudyptes chrysochome*), squid and fish (Tollu 1974), while at Gough Island, stomach samples from Subantarctic fur seals suggested that they also prey on cephalopods (Bester & Laycock 1985). Condy (1981) suggested that cephalopods constituted about 50% of the Subantarctic fur seals' diet composition in addition to fish and perhaps small amounts of crustaceans at Marion Island**.** However, a later study at Marion Island showed that both Antarctic fur seals and Subantarctic fur seals fed predominantly on mesopelagic fish of the family Myctophidae (lanternfish) where a single scat comprised up to six different myctophid species, while squid beaks appeared in small numbers (Klages & Bester 1998; Makhado *et al*. 2008). In addition, Makhado (2002) found that pelagic myctophids (*Electrona*, *Gymnoscopelus* and *Protomyctophum* species) dominated the diet of Subantarctic fur seals at Marion Island. Green *et al*. (1990) also showed the myctophid *Electrona* species and *Gymnoscopelus* species to be the most important components in the diet of both Antarctic and Subantarctic fur seals at Heard Island. Lower cephalopod intake by fur seals at Marion Island clearly indicated that there is a temporal variation in prey species abundance and distribution. Klages & Bester (1998) also showed seasonal fluctuations in the scat composition, where *Electrona carlsbergi, E. subaspera, Metelectrona ventralis* and *G. fraseri* increased in winter in the diet of both Subantarctic fur seals and Antarctic fur seals, including *G. nicholsi* in the latter species (Makhado *et al.* 2008).



Gymnoscopelus piabilis ***G. fraseri***



Metelectrona ventralis ***Gymnoscopelus nicholsi***

Figure 1.1 Fish otoliths from four different myctophid species retrieved from the scats of Subantarctic fur seals at Marion Island

Study objectives

1.1 Aims:

The specific aims of the present study are to characterize the prey species composition of Subantarctic fur seals at Marion Island from scats and to investigate temporal variation of the presence of prey species in their diet at seasonal, annual and periodic (i.e. 1989-1994; 1995-2000; 2001-2006) scales, and to relate possible temporal variation in the presence of these species to environmental conditions.

1.2 Research Questions:

1. What were the main prey species of Subantarctic fur seals at Marion Island in the period 2001 - 2006?

2. How did the prey species in the diet of Subantarctic fur seals vary seasonally?

3. How did the prey composition during the study period compare with that obtained in previous study periods (1989 – 1994 and 1995 – 2000)?

4. How does the diet of Subantarctic fur seals at Marion Island compare with that of conspecific populations elsewhere in the Subantarctic?

5. Can changes/differences in environmental conditions explain temporal/spatial variation in the diet of Subantarctic fur seals?

Chapter 2

Study area

Marion Island (46˚ 54’S, 37˚ 45’E), one of two islands constituting the Prince Edward Archipelago, is located in the Southern Indian Ocean, approximately 2180 km southeast of Port Elizabeth, South Africa (Fig. 2.2) (Jonker 1997). It is situated 2200 km north of Antarctica, and the closest landmass is the Crozet Island Group, about 950 km to the east (Condy 1977; Wilkinson 1992).

Marion Island is about 290 km^2 in area, has a circumference of approximately 90 km, and is roughly oval in shape. It measures 24 km from east to west and 17 km from north to south (Condy 1977). Approximately 138 km^2 of Marion Island’s area has an altitude of less than 200 m, with the highest peak (formerly State President Swart Peak, now Mascarin Peak) being 1230 m above sea level (Condy 1977). The coastline is irregular and rough in nature. The western coast terminates in vertical cliffs up to 15m high (Condy 1977). The eastern coast is flatter and more irregular in appearance (Condy 1978). Most of the beaches on the exposed south and west coasts, which face the prevailing wind and ocean swell, are comprised of massive, and often jagged, rocks piled haphazardly on top of each other. The surface topography of these beaches is very rough and irregular. On the leeward east and north coast, beaches are made up of small rounded rocks, stones and pebbles, and in one instance, sand.

Climate and Oceanography

Marion Island has an oceanic climate with the following main features, amongst others: predominantly strong westerly winds, with the highest velocities during the day and gales more frequently in the winter; a relatively low mean temperature of 6.4˚C, showing little annual and diurnal variation; and abundant precipitation in the form of rain, snow and graupel (“ice rain”) with a mean annual precipitation of 2000 mm (le Roux & McGeoch 2008).

The Prince Edward Islands are sandwiched between two major oceanic fronts (Fig. 2.4), i.e. the Subantarctic Front (SAF) and the Antarctic Polar Front (APF) (Froneman *et al.* 1999). The SAF forms the northern boundary while the APF forms the southern boundary of the Polar Frontal Zone (PFZ). The positions of these two fronts exhibit a high degree of latitudinal variability (Lutjeharms & Valentine 1984). The movements in the positions of these fronts are believed to influence the composition of zooplankton communities interacting with the island system (Pakhomov *et al.* 2000), and has implications for the food availability to the top predators (Froneman *et al.* 1999). Gentry & Kooyman (1986) pointed out, the predictability of a seal's environment increases as one moves from the equator (the least predictable environment) to the Polar Regions, where prey availability are most abundant and predictable from year to year. Nevertheless, the food resources of many pinnipeds, particularly otariids that live in the temperate and tropical climates, vary more from year to year (Riedman (1990). This variability is caused mainly by the ENSO-El Nińo Southern Oscillation-events, which occur every two to ten years and influence the abundance of food resources in an unpredictable way (Riedman 1990).

Materials and methods

Scat collection and processing

Animals of different age and sex classes haul out in different months of the year, so it can be presumed as to which portion of the Subantarctic fur seal population contributes more in scat deposition in particular months or seasons. Both adult male and adult female numbers ashore increase from November and reach a peak in mid December (Kerley 1983). Lactating females suckle their pups throughout the winter (Kerley 1983). Their numbers ashore decline towards the end of October, while adult males are rarely seen during winter. As the number of adult males increases in the breeding colony sites from November until early January, the number of subadult and under-yearlings decreases (Kerley 1983). The number of subadults increases from February to a maximum in early March, then decreases from April throughout the winter (Kerley 1983).

Scats of the Subantarctic fur seals were collected on a monthly basis at the Cape Davis (46˚ 49.4’S, 37˚ 50.4’E) breeding colony (Fig. 2.3). Only whole fresh scats were collected. Each scat was kept separate in a plastic bag. In the laboratory, scats were dried in a drying room for several days. Each scat was crumbled, and then rinsed through a 0.5 mm stainless steel sieve under running warm water. Undigested prey items such as fish otoliths, crustacean hard parts and bird feathers were removed and stored dry, while cephalopod beaks were stored in 70% alcohol with a few drops of glycerol until analysis.

Sea Surface Temperatures (SSTs) data were obtained from the South African Weather Services. SSTs were recorded on daily basis at the Meteorological station on Marion Island.

Identification and Analysis

Otoliths

Fish otoliths differ markedly in gross morphology and robustness, i.e. unit otolith mass per unit otolith length, both within and between species (Harkonen 1986; Tollit *et al*. 1997; Christiansen *et al*. 2005). Otoliths are predominantly composed of calcium carbonate in the form of aragonite (>90%) and a minor proportion of trace elements embedded in a proteinaceous matrix (Christiansen *et al*. 2005).

The otoliths were identified to the lowest taxonomic grouping possible by comparison with reference specimens held in the collections of the Branch Marine and Coastal Management, DEAT in Cape Town, and with illustrations in the pertinent literature (Hecht 1987; Williams & McEldowney 1990; Smale *et al*. 1995). Biases associated with consumption and size of prey consumed was corrected by applying correction factors derived from captive studies (Dellinger & Trillmich 1988; Reid 1996). Otoliths were assigned to three categories in increasing order of erosion and correction factors were applied to compensate for erosion (20% for the most eroded and 10% for the less eroded) after Reid (1995). Otoliths that were considerably eroded and could not be identified were recorded as “unidentifiable”.

Otolith length (OL) (Fig. 2.1) of pristine specimens was measured under a dissecting microscope fitted with a graticule. OL was used to determine fish mass weight (g) and standard length (SL) in millimeters (mm) using morphometric relationships presented in Hecht (1987), Williams & McEldowney (1990) and Smale *et al.* (1995). For species without published morphometric relationships, morphometric relationships of closely related species were applied.

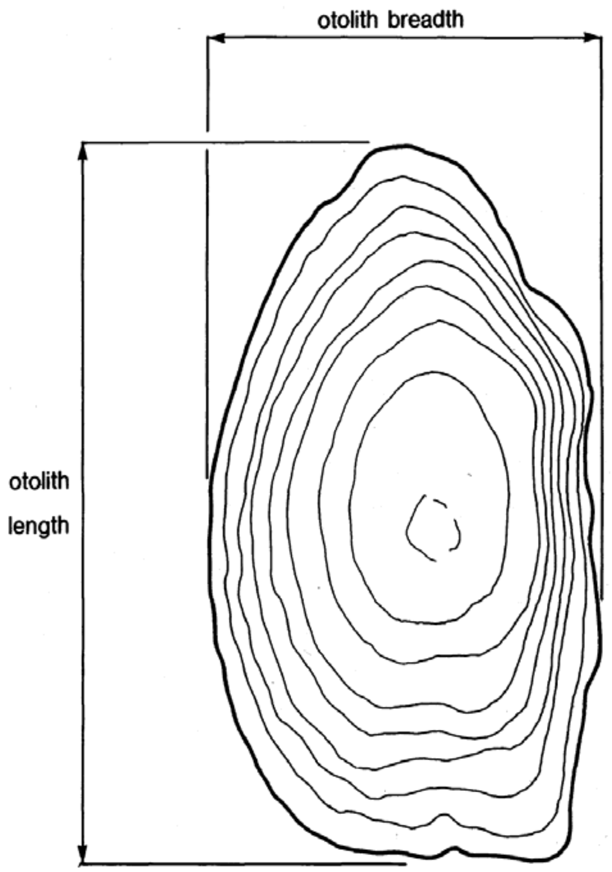


Figure 2.1 An illustration of a fish otolith, showing standard length and width measurements (taken from Croxall 1993)

Cephalopod beaks

Numbers of upper beaks were counted to estimate the total abundance of cephalopods.

Statistical Analysis

Delineation of seasons

This study's main focus is on temporal variation. So in order to determine seasonal variation, a year was divided into three seasons of equal duration i.e. early summer (October to January), late summer (February to May) and winter (June to September) (Table 2.1). The three seasons coincide with the breeding season haulout and pupping season of the fur seals (early summer), the post-breeding season moulting and lactation period (late summer), and late lactation when primarily lactating females are ashore in winter (Kerley 1983; Bester & Bartlett 1990). Delineation of seasons is also required as scat collection was irregular with no scats being collected during some months in some years.

Because the numerical data was not normally distributed, various transformations were performed to obtain a normal distribution. The basic Analysis of Variance (ANOVA) was performed where Least Square Means were used to investigate the effect of species; species on different seasons; species on different years; and species on different seasons of different years. These were carried out for relative numerical abundance (%NA = proportion of the total prey items made up by each prey taxon) and relative percentage mass (%M = reconstituted body size calculated as the proportion of each prey taxon's relative mass). Post-hoc tests were conducted for pairwise comparisons, and the effect of size was determined to find out whether the variability found on different variables were both statistically significant and practically significant. Scheffe's Test was performed to determine whether there was any significant difference between mean mass and mean length of the fish prey items. Frequency of occurrence (FO) of main prey species were calculated as the number of scats containing that species divided by the total number of scats and expressed as a percentage frequency of occurrence (%FO). Significance level was set at 99% confidence interval.

The data from the present study period was compared with the data from the previous studies conducted on Marion Island. I therefore divided the data into three study periods: Period 1 or P1 (April 1989 – March 1995, Period 2 or P2 (April 1995 – March 2000), and the present study Period 3 or P3 (April 2000 –March 2006).

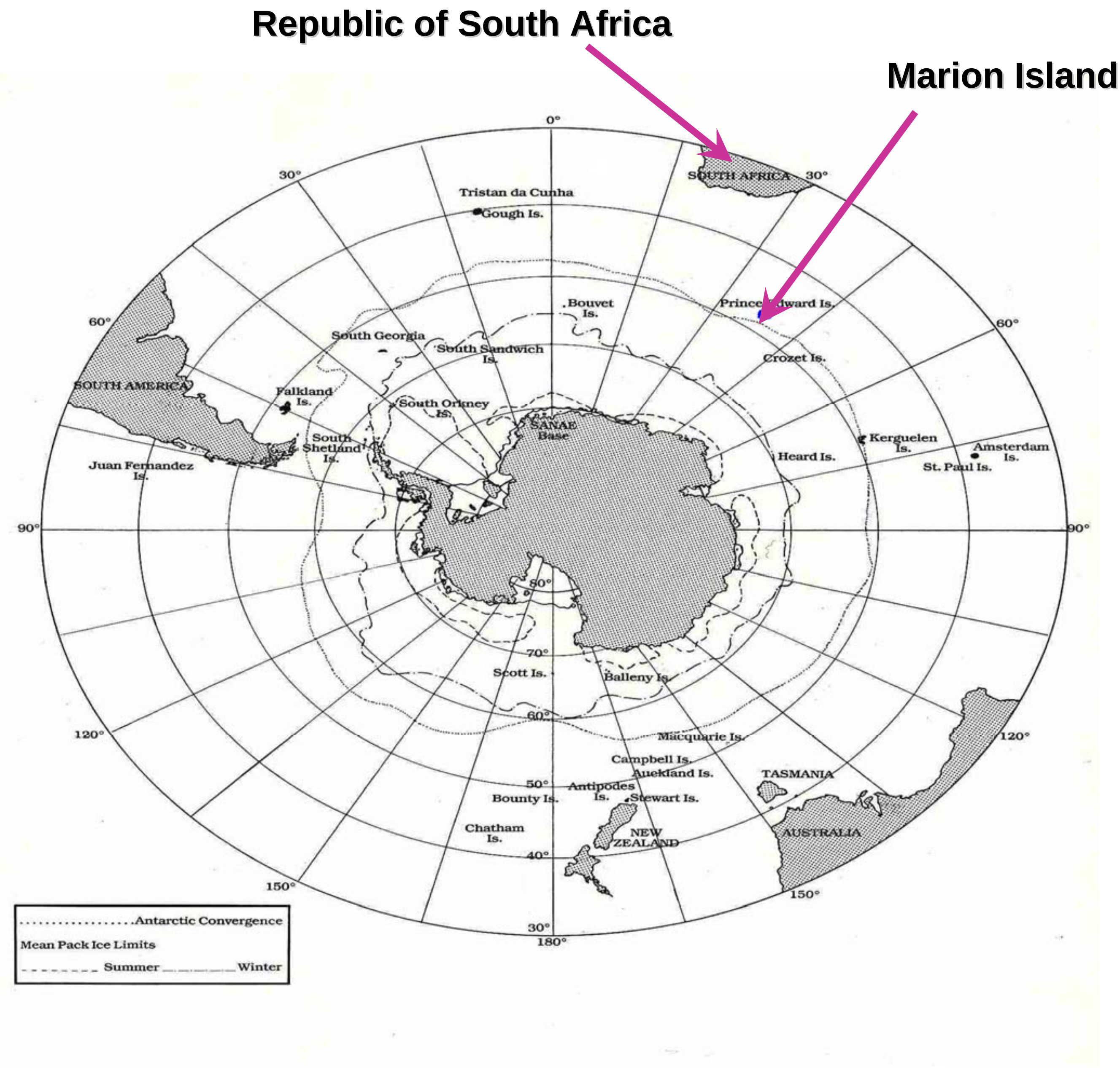


Figure 2.2 Map showing the Continent of Antarctica, and positions of Marion Island (in the Prince Edward Islands group) in the Southern Ocean

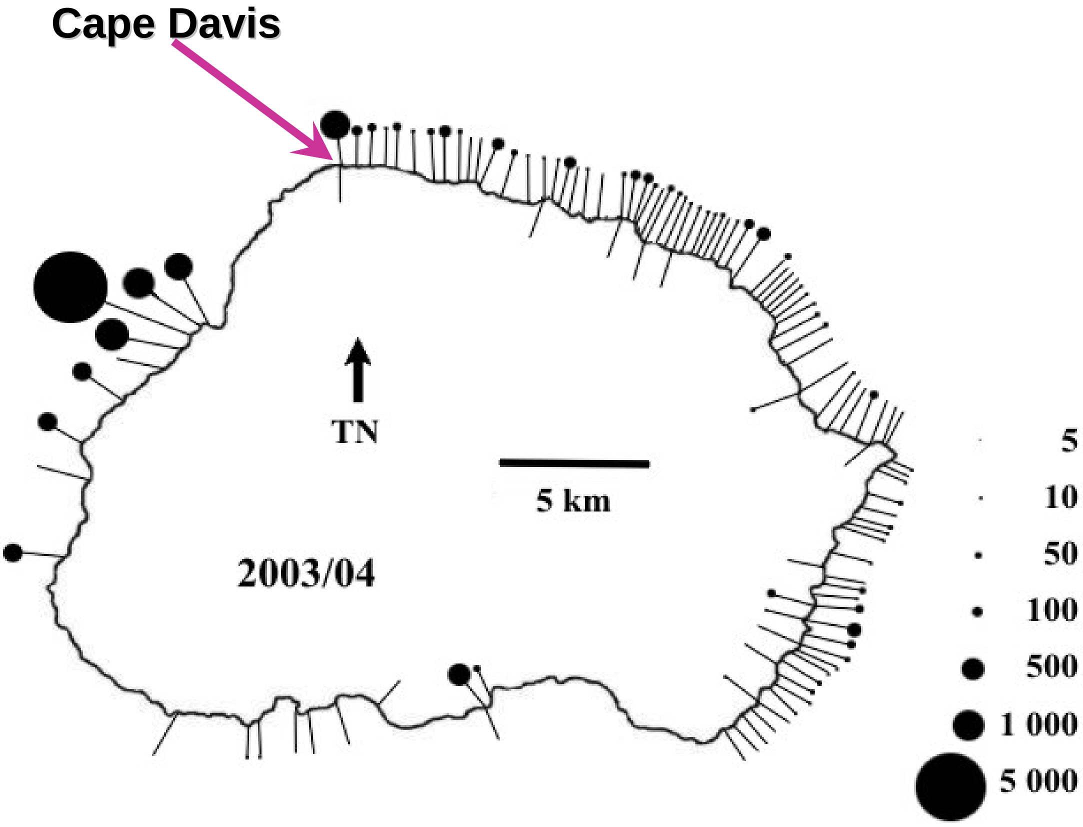


Figure 2.3. A map taken from Hofmeyr *et al.* (1997), showing the coastline of Marion Island: Circles on the outside of the coastline indicate population sizes of the Subantarctic fur seals on different beaches, including the study area in the present study (indicated by the arrow). The circles on the inside of the coastline show population sizes of the sympatric Antarctic fur seal.

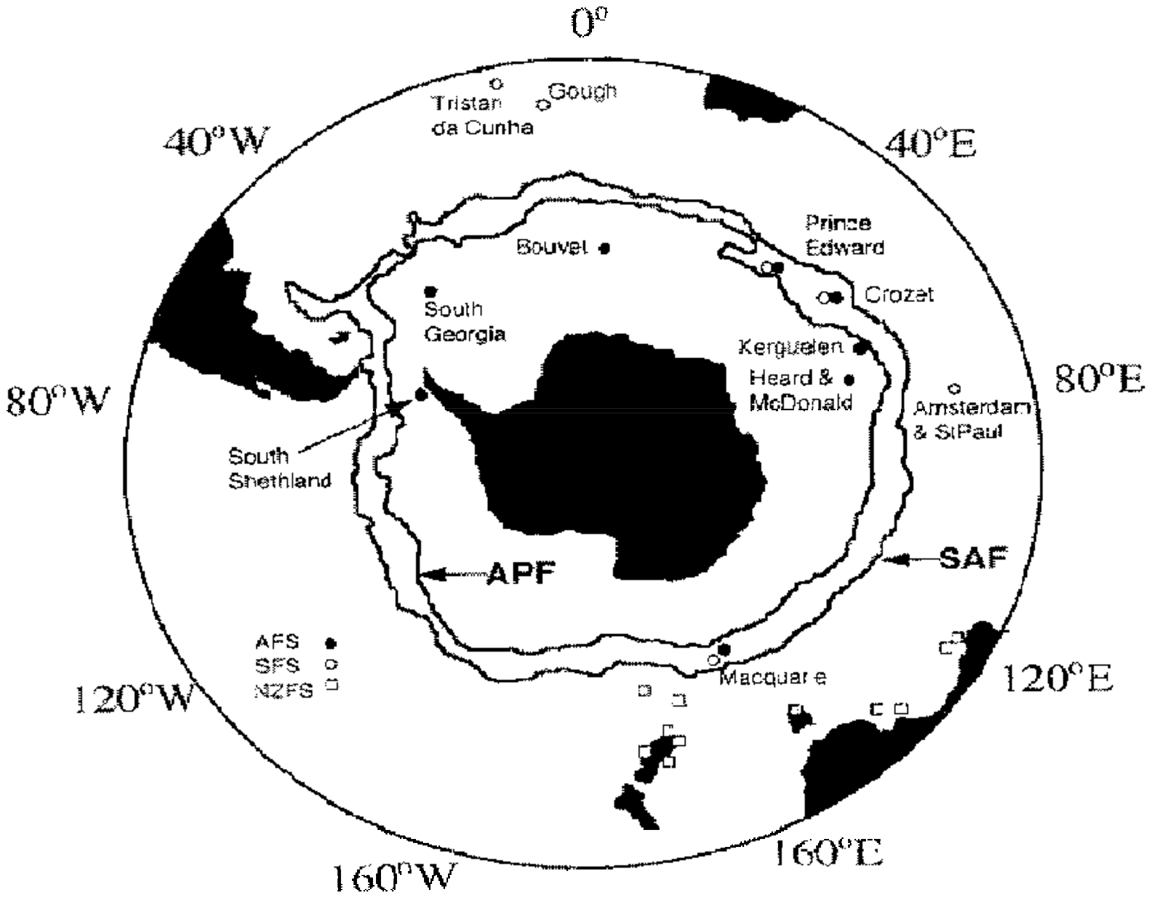


Figure 2.4 Distribution of breeding colonies of the Subantarctic fur seal (*A. tropicalis*) and Antarctic fur seal (*A. gazella*) in relation to fronts. APF = Antarctic Polar front; SAF = Sub-Antarctic Polar Front (Figure taken from Goldsworthy 1989).

Table 2.1 Seasonal delineation based on annual haulout cycles of Subantarctic fur seals at Marion Island

Early summer	**Late summer**	**Winter**
Breeding	Moulting	Late lactation
October - January	February – May	June - September

Chapter 3

Diet composition of Subantarctic fur seals at Marion Island

Introduction

Competition for resources shapes the diversity of species sizes, behaviours, ranges and prey preferences (Page *et al.* 2005). However, a more common response to interspecific competition is that individuals of one species modify the way they use resources or habitat; in this way competition is less intense and, on an evolutionary time scale, even closely related species can coexist (Page *et al.* 2005).

The quality and number of remnant hard parts of prey in faeces can be affected by several factors: (i) seals may vomit, losing part of the accumulated remains; (ii) differential digestion of hard parts in the stomach (related to otolith size and density, diet composition, resistance of fish skulls to digestion) may remove items and / or give a false view of dominance of some prey types; (iii) small prey remains (such as otoliths) may be entirely digested and thereby under-represented in fur seal prey remains (such as cephalopod beaks) which are thought to cluster at the base of the stomach and may be retained longer than otoliths (Gales & Cheal 1992; Page *et al.* 2005), and (iv) rate of passage of digesta and foraging trip duration may affect what remains in the faeces (Robinson *et al.* 2002). These factors contribute to the inherent variability in determining diet from faecal samples. However, with proper caution, scat analysis can provide qualitative and some quantitative information (North *et al.* 1983; Robinson *et al.* 2002).

The diet of the Antarctic fur seal has been investigated at a number of major breeding localities. Most of the studies, which have been based on scat analysis, reported that krill and fish constituted the bulk of the diet of fur seals though the relative proportions of the different prey taxa varied according to sex, age, localities and seasons (Daneri & Carlini 1999; Casaux *et al.* 2003; Daneri *et al.* 2005; Makhado *et al.* 2008). Also, movements of the Antarctic Polar Front (APF) can potentially affect the abundance of prey within the foraging range of Antarctic fur seals (Lea *et al*. 2006). Much less detail is known about the diet of the Subantarctic fur seal.

The present study aims to determine the relative diet composition of the Subantarctic fur seal at Marion Island through assessment of the relative importance of each prey taxa using two standardized measures: (1) Percentage numerical abundance %NA (proportion of the total prey items made up by each prey taxa) and (2) percentage frequency of occurrence %FO (proportion of samples containing a given prey taxa) following Klages & Bester (1998), Page *et al*. (2005) and Makhado *et al.* (2008). The study of this marine mammal's diet might also give us some insight into the distribution and availability of their prey species.

Results

A total of 806 scats were collected from April 2000 to December 2005 (Table 3.1) and a total of 24 199 otoliths were extracted. Only 71 cephalopod beaks were extracted from 39 of the total number of scats.

The diet of the Subantarctic fur seals was diverse during the present study period, with mesopelagic fish species constituting the bulk of the diet (Fig. 3.2). These mesopelagic prey species were dominated by the genus *Gymnoscopelus*, i.e. *G. bolini*, *G. piabilis*, *G. fraseri*, *G. nicholsi* and *Gymnoscopelus sp* (i.e. unidentified to species level) (Table 3.2 and fig 3.1). The other well represented genus in the diet of the Subantarctic fur seals was *Protomyctophum*, which comprised *P. tenisoni*, *P. choriodon* and *P. bolini*. Genus *Electrona* comprised *E. carlsbergi*, *E. subaspera, E. antarctica* and *E. cryomargaritus*. Other species were *Krefftichthys anderssoni*, *Metelectrona ventralis*, and the following are not myctophids species *Bathylagus antarctica*, *Lampichthys procerus, Icichthys australis*, *Paralepis atlantica*, *Maurolicus muelleri, Scopelosaurus ahlstromi*, and all non-myctophids were less represented in the diet of the Subantarctic fur seals (Table 3.2), and four unknown species that I could not identify. Penguins were scarcely represented by feathers.

All the aforementioned species were grouped into twelve prey species groups (Table 3.3). Out of these, five prey groups were identified as the primary prey of the Subantarctic fur seals, i.e. *P. tenisoni* and the four *Gymnoscopelus* species (Fig. 3.1). All species which were represented by less than 200 otoliths over the entire study period were grouped as the "others" prey group. Cephalopod remains occurred in low number in the scats of the Subantarctic fur seals throughout the study period (n = 71). These were not analysed further. Remains from other prey taxa e.g. crustacean hard parts were not present in the collected scats. However, few penguin feathers appeared in the scats of Subantarctic fur seals, these were not analysed further due to the small sample.

In order to have an idea of how the diet of the Subantarctic fur seals changes on a long-term basis, data from the present study was compared with data from the previous diet studies at Marion Island (Fig 3.2 and Table 3.3)

Slight variability was noticed among the minor prey species, where Subantarctic fur seals in one study period opportunistically took one prey species and in the next study period took a different prey species (Fig 3.2). These changes gave the impression that the importance of some species in period 2 (April 1995 – March 2000) changed significantly during period 3 (April 2000 – March 2006). *G. piabilis* was the most important species in %NA during period 2 followed by *G. fraseri*. Contrary to this, *G. bolini* assumed the role of *G. piabilis* during period 3 (Fig 3.2).

In contrast, *P. tenisoni* was an important prey species during the first (1989 – 1995) and last study periods (2000 – 2006), but of minor importance during the second study period (1995 – 2000). *G. bolini* had increased drastically in %NA from the second study period to third study period. *G. fraseri* was found to be an important prey species in all three study periods. The percentage frequency of occurrence (%FO) of *G. piabilis* in scats was reduced significantly during period 3, while *G. bolini* was concomitantly more frequently found in the scats (Fig 3.1). The %FO of *G. fraseri* declined slightly during period 3.

Table 3.1 Monthly numbers of scats with hard part remains collected from the Subantarctic fur seals on Marion Island from April 2000 - March 2006

Months	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**Totals**
January		8	10	1	12	24	22	77
February		27	9	3	10	27	26	102
March			9	5	20	41	30	105
April		2	16	38	21	25		102
May			6	14	25	15		60
June	3			10	16	8		37
July	6	5	3	4	12			30
August	3		1	5	11			20
September				12	27	2		41
October	14				18	22		54
November				10	24	16		50
December	11	7	22	20	42	26		128
Sum	**37**	**49**	**76**	**122**	**238**	**206**	**78**	**806**

Table 3.2 Species identified from the scats of the Subantarctic fur seals at Marion Island from April 2000 – March 2006

Species name	**Number**
Bathylagus antarcticus	3
Bathylagus sp.	14
Gymnoscopelus bolini	4079
Gymnoscopelus fraseri	3755
Gymnoscopelus nicholsi	2038
Gymnoscopelus braueri	7
Gymnoscopelus piabilis	1392
Gymnoscopelus sp.	3371
Electrona carlsbergi	1033
Electrona subaspera	519
Electrona antarctica	3371
Electrona sp.	466
E. cryomargaritus	6
Krefftichthys anderssoni	466
Lampichthys procerus	48
Metelectrona ventralis	881
Maurolicus muelleri	4
Protomyctophum tension	2440
Protomyctophum bolini	40
Protomyctophum choriodon	210
Protomyctophum sp	17
Paralepis atlantica	6
Scopelosaurus ahlstromi	11
Unknown 1	2
Unknown 2	11
Unknown 3	7
Unknown 4	2
TOTAL	24199

Table 3.3 Relative mean percentage numerical abundance (%NA), relative percentage mass (%M) and relative mean mass respectively, of the fish prey species taken by the Subantarctic fur seals at Marion Island from April 2000 - March 2006

Species name	%NA	% Mass	Mean mass	Sample size
E. carlsbergi	5.440	2.940	5.60	1033
E. subaspera	2.809	2.697	11.86	519
G. bolini	23.093	40.423	71.65	4079
G. fraseri	17.462	12.179	5.14	3755
G. nicholsi	11.859	16.273	31.02	2038
G. piabilis	8.717	18.067	83.31	1392
Gymnoscopelus sp.	14.69	0	0	3371
K. anderssoni	1.808	0.191	0.36	466
M. ventralis	4.393	2.173	8.13	881
P. choriodon	1.122	0.813	3.81	210
P. tenisoni	6.442	2.440	0.64	2440
Others	2.157	1.181	38.11	8094

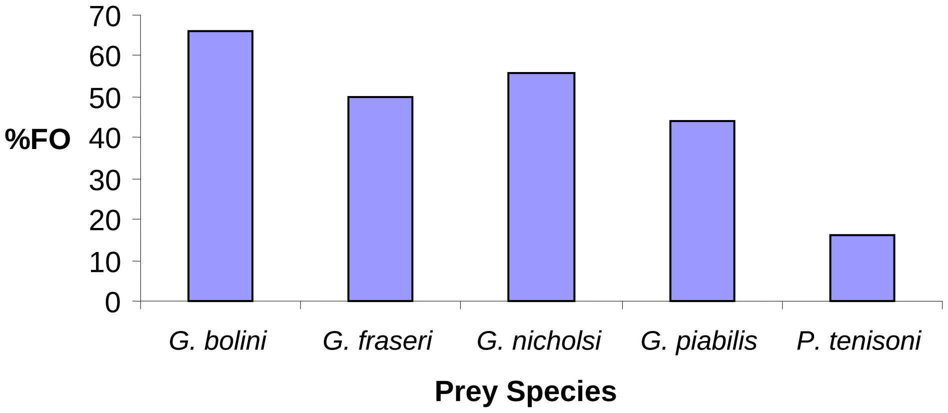


Figure 3.1 Relative means percentage frequency of occurrence (%FO) of the main prey species taken by the Subantarctic fur seals at Marion Island from April 2000 - March 2006

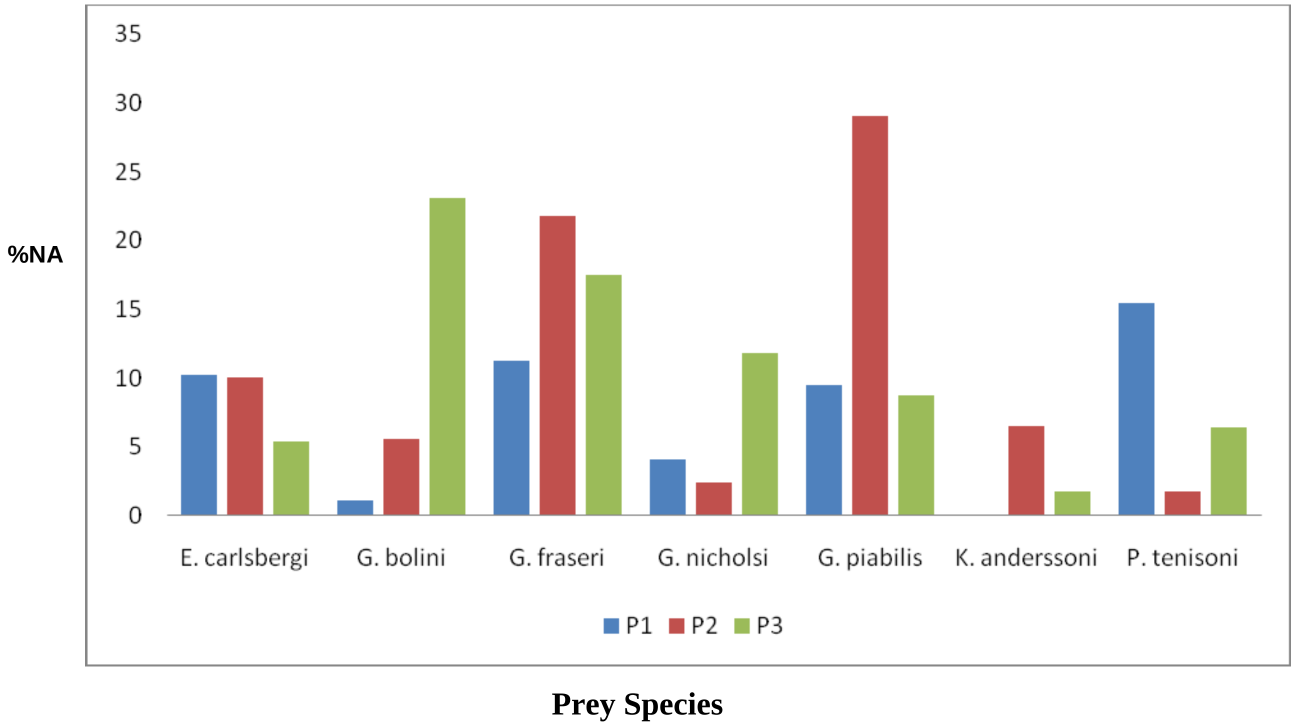


Figure 3.2 Relative percentage numerical abundance (%NA) of the main prey species over all three study periods, Period 1 (P1: April 1989 – March 1995) period 2 (P2: April 1995 – March 2000) and period 3 (P3: April 2000 – March 2006).

Table 3.4 Monthly numbers of scats with hard part remains collected from Subantarctic fur seals on Marion Island from April 1989 – March 1995 (adapted from Klages & Bester 1998)

Months	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**Totals**
January		17			5	9		31
February		8	3	11	5			27
March		11	3		5			19
April		10	5	5				20
May		3		5	15			23
June		3		5	10			18
July		3		6	8			17
August	7	3		4	5			19
September	8	3						11
October	5	3	3					11
November	4	3	5	9				21
December	20	3	5					28
Sums	**44**	**70**	**24**	**45**	**53**	**9**	**0**	**245**

Table 3.5 Monthly numbers of scats with hard part remains collected from Subantarctic fur seals on Marion Island from April 1995 – March 2000 (adapted from Makhado 2002)

Months	**1996**	**1997**	**1998**	**1999**	**2000**	**Totals**
January				2	9	11
February		8		1	6	15
March		6		11	4	21
April			15	8	14	37
May			27	3		30
June	11					11
July	8		6			14
August			4			4
September	9		9	13		31
October	5		7	1		13
November	6			7		13
December	7			6		13
Sum	**46**	**14**	**68**	**52**	**33**	**213**

Discussion

The competition between species is extremely difficult to assess, however, we can often determine overlap in resource use between species (Barlow *et al.* 2002). For example, Page *et al.* (2005) reported that adult male, female and juvenile New Zealand and Australian fur seals *Arctocephalus forsteri* and *A. pusillus doriferus* frequently return to colonies, creating the potential for intra- and inter-specific foraging competition in nearby waters. Furthermore, it is suggested that the fur seals in that study exploit different prey resources, thereby reducing competition and facilitating coexistence (Page *et al.* 2005), with the adult female diet reflecting that of a generalist predator, dictated by prey abundance and their pups' fasting ability (Page *et al.* 2005). In contrast, adult male New Zealand and Australian fur seals consumed proportionally more energy-rich prey such as large fish or birds, possibly because they could efficiently access and/or handle such prey (Page *et al*. 2005). Juvenile fur seals mainly consumed small fish that occur in pelagic waters, south of the shelf break, suggesting juveniles cannot competently exploit prey where adult fur seals forage (Page *et al*. 2005). Unfortunately, the situation with regards to possible resource partitioning amongst age and sex classes of sympatrically breeding Subantarctic fur seals and Antarctic fur seals at both Marion and Macquarie islands is unknown, but overall the diet of the adult female component of the two species is similar at, and between, these sites (Klages & Bester 1998; Robinson *et al.* 2002).

The diet of the Subantarctic fur seals at Marion Island, in the current study, is dominated by myctophid fish species of the genus *Gymnoscopelus* and one *Protomyctophum* species. This is not surprising, as myctophids have been reported to be the dominant fish family in the Southern Ocean, in terms of diversity, biomass and abundance (Pusch *et al*. 2004). Thirty–three myctophid species are known from the Southern Ocean, of which eleven have a circumpolar distribution (Pusch *et al*. 2004). Similarly, the main prey items in the diet of Dall's porpoise were myctophids (Ohizumi *et al.* 2003). Robinson *et al.* (2002) also reported that the myctophid, *Electrona subaspera*, was the most important prey item in all months of their study on both *A. tropicalis* and *A. gazella* at Macquarie Island.

Myctophid fish are generally regarded as mesopelagic, occurring between depths of 50 – 2,500 m (Hulley 1981). This makes them accessible to fur seals the diving depth of which is between the sea surface and 50 m (Hulley 1981). *Krefftichthys anderssoni,* for one, forms a large proportion of the catch of krill nets trawled between 50 – 150 m south of the Antarctic Polar Front (APF) (Hulley 1981; Adams & Klages 1987). Moreover, Dalls's porpoises may also prefer myctophids owing to their high energy density (Ohizumi *et al*. 2003) as was also suggested by Mecenero *et al*. (2006a) who considered that it is possible that fur seals target more energy-rich prey when available**.** It is anticipated that selecting myctophids is advantageous in terms of efficient foraging and high energy gains (Ohizumi *et al.* 2003). Cape fur seals *A. p. pusillus* also mainly consume small prey that exhibit shoaling behaviour and are found in surface waters (Mecenero *et al*. 2006a). Abundant shoaling fish maximize energy gain for seals, because they are more frequently encountered, have higher capture rates than dispersed species, can be ingested whole, which results in a reduced handling time, and have high energy levels during certain times of the year (Mecenero *et al*. 2006a).

Trawl surveys in the vicinity of Macquarie Island where both *A. tropicalis* and *A. gazella* forage confirm that myctophids dominate the pelagic fish fauna (Williams 1988). At night these fish migrate upwards to between 200m depth and the sea surface (Hulley 1981), and behaviour studies indicated their presence in the top 20m (Robinson *et al*. 2002). The pattern of fish consumption might reflect the fish availability within the seals' foraging areas at the different localities (Casaux *et al.* 2003).

It had been suggested that Subantarctic fur seals consume a wider range of prey species than other otariids (Ochoa–Acuna & Francis 1995; Robinson *et al.* 2002; Beauplet *et al*. 2004), and for this reason Subantarctic fur seals are classified as generalist feeders (Lipinski & Woyciechowski 1981). However, this does not necessarily suggest that top predators do not actively select prey, as it had been suggested by Ohizumi *et al*. (2003). We hypothesize that Subantarctic fur seals from Marion Island primarily select myctophids fish species. This is also supported by a large number of Gymnoscopelus spp which were not identified to species level because some of them were broken or eroded in such a way that it was bit tricky to place them in any species taxon.

Prey species diversity in the diet of the Subantarctic fur seal in the present study confirms that seals normally feed on dense schooling, vertically migrating pelagic prey such as myctophids (Klages & Bester 1998; Robinson *et al*. 2002). Indices used (i.e. percentage numerical abundance (%NA) and percentage frequency of occurrence (%FO) to examine the diet of the Subantarctic fur seals in the present study suggested that this species chose its prey depending on availability of prey species. For example, if we are to compare %NA and mean mass of *G. fraseri* and *G. piabilis*, the former has a %NA of 17.46 and mean mass of 5.14g while %NA of the latter is just 8.72 but its mean mass is 83.31g. This seems to suggest that when species are present and abundant in the foraging area (in this case *G. fraseri*), the seals forage intensively on them rather than on more predicted resources (Casaux *et al*. 1997), in this case *G. piabilis* which contributed considerably more in terms of mean mass.

The diet of the Subantarctic fur seals at Marion Island was formerly (April 1989 – March 1995) dominated by *P. tenisoni* (Fig 3.2). However, the abundance of *G. piabilis* increased considerably in the fur seals' diet during the second study period (April 1995 – March 2000) (Fig 3.2). These might imply that the availability of *G. piabilis* was increasing in the foraging grounds of the Subantarctic fur seals around Marion Island, perhaps due to poor recruitment of *P. tensioni* or overutilization by top predators. Similarly, *G. bolini* became the dominant prey species in P3 despite a poor showing in P1 and P2 (Fig 3.2). Poor recruitment effort may be linked to changes in environmental conditions around the Southern Ocean. However, there appears to be no information on how changes in environmental conditions impact the behaviour or recruitment of the above mentioned prey species.

The abundance of the various prey species in the diet of the Subantarctic fur seals suggests that prey were not evenly distributed in the foraging zone around the Prince Edward Islands. Similarly, Lake *et al.* (2003) indicated that the variety in the diet composition of Weddell seals demonstrated both flexibility in their foraging response and the range of different prey species available to the Weddell seals over the Antarctic continental shelf. The prey species that were of minor importance during the present study (e.g. cephalopods) are probably less numerous in foraging grounds as compared to the main prey species. Cephalopods might even be taken opportunistically (Kirkman *et al.* 2000), when fur seals prey on krill and associated myctophid fish (Daneri *et al.* 2005). As cephalopod beaks are likely to accumulate in the stomachs of marine predators (Reid 1996; Klages and Bester 1998) or to have been ejected by vomiting (Kirkman *et al.* 2000), they may not appear in scats on a regular basis. However, cephalopod remains are frequently present in scats of fur seals at other sites (e.g. Green *et al.* 1989) and therefore it follows that they are probably of little importance in the diet of Subantarctic fur seals at Marion Island (Klages & Bester 1998; this study).

Although the diet of conspecifics at Gough Island appeared to be dominated by cephalopods (Bester & Laycock 1987), the study was based on complete stomach samples and therefore biased due to the selective retention of cephalopod beaks (Klages & Bester 1998). However, the diet composition of the Antarctic fur seals and the Subantarctic fur seals at Macquarie Island and the Prince Edward Islands were not significantly different in sympatry (Robinson *et al.* 2002, Makhado 2002). At Macquarie Island, the diet of the two fur seal species was virtually the same (Robinson *et al.* 2002) as it was at Marion Island in former years (Klages & Bester 1998). No inter-specific differences in diet were found, with *E. subaspera* dominating in both %NA and %FO, while the *G. nicholsi–G. piabilis* component was the next most important taxon, but substantially lower in abundance and frequency (Robinson *et al.* 2002). All other fish species were rare, as were cephalopods and crustaceans.

The results of the present study are therefore in accord with that of Robinson *et al.* (2002) who speculated that differences in diet between and within seal species are more influenced by the biogeography of fish species than by phylogenetic patterns. Most probably, however, is that local variations in diet composition are due to variations in prey distribution and abundance (Hume *et al.* 2004). Because the diet of top predators apparently reflect the distribution and abundance of prey (Hammond *et al.* 1994), and therefore prey abundances and distributions vary spatially and temporally (Reid & Arnould 1996; Daneri & Carlini 1999; Naya *et al.* 2002; Mecenero *et al.* 2006a), it is expected that they also vary seasonally and monthly (Mecenero *et al.* 2006a; this study, next chapter).

The importance of fish in diets of seabirds and seals at Macquarie Island was in contrast to many locations south of the APF, particularly in the South Atlantic Ocean, where the diets of most seals and seabirds are mainly pelagic crustaceans (Goldsworthy *et al.* 2001), but similar to those at the Prince Edward Islands, also located north of the APF, where consumption by the two species of fur seals (Klages & Bester 1998, Makhado *et al.* 2008; this study) and four species of penguin (Adams *et al.* 1993) was mostly of pelagic fishes (Klages & Bester 1998; Goldsworthy *et al.* 2001).

It can be concluded that the diet composition did not change significantly since the diet monitoring programme started in 1989. The diet was dominated by myctophids from three genera, *Gymnoscopelus*, *Electrona* and *Protomyctophum* throughout. Slight variability was noticed among the minor prey species, where the Subantarctic fur seals during one study period predominantly took one prey species and during the other study period took a different prey species. This might be due to variable encounter rates on the foraging grounds of the Subantarctic fur seals around Marion Island. All non-myctophids species are considered as the minor prey species and no crustaceans were found during the present study period, as was the case during the first period of monitoring (i.e. April 1989 to March 1995) (Klages & Bester 1998, present study, 2000 - 2006).

There is, however, a huge difference between the number of scats collected during the present study period and the previous two study periods (Tables 3.1; 3.4 and 3.5). This could have also influenced the importance of species in the diet of Subantarctic fur seals at Marion Island. On the other hand, there is evidence of a long-term southward shift in the position of the SAF around Marion Island (Pakhomov & MacQuaid 2001). For example, the SAF shifted 50km northwards between 5 April and 17 April 1998 and 20km southwards between 17 April and 8 May in the same year (Pakhomov *et al.* 2000). This, coupled with the effects of the El Niño during 1997/98 (Lea *et al*. 2006), give a possible explanation for inter-annual variation in the diet of the Subantarctic fur seals.

Chapter 4

Seasonal variation in the diet of Subantarctic fur seals at Marion Island

Introduction

Fur seals of different age and sex classes haul out in different months of the year (Kerley 1983). The inclusion of detailed information about different phases of the annual cycle and about the different activities during those phases allows the seasonal changes in food consumption to be resolved (Boyd 2002). Therefore, the distribution and availability of marine resources are directly affected by seasonal spatial changes in physical and oceanographic features (Beauplet *et al*. 2004). These are thus likely to influence maternal foraging provisioning patterns, efficiency, and subsequently pup growth rate of central place foragers such as otariid seals (Beauplet *et al*. 2004).

The lowest intensity of population food demand tends to occur in the early summer (November – January) when breeding take place and numerous adult seals were ashore (Boyd 2002). Increasing demand through the breeding season in fur seals is due to increase in number of males that return to sea to feed after the breeding season and because of gradually increasing demand from pups for food (Boyd 2002). The successive decline in food expenditure by fur seals is caused by a combination of mortality (mainly of juveniles), reduced demand from males after improving from fasting during the breeding season, and reduced demand of mothers when pups wean (in Antarctic fur seals) and their diet requirements are met by direct foraging (Boyd 2002 (Boyd *et al.* 1998, Boyd 2002). Furthermore, the diet composition of myctophids, also vary by locality and probably by season as well (Pusch *et al*. 2004; Page *et al*. 2005). We therefore expect that seasonal distribution of these myctophids (a major fish prey of Subantarctic fur seals) around the Subantactic region is to be the cause for the seasonal variation in the food composition of the Subantarctic fur seals.

In this chapter a year was divided into three seasons i.e., early summer (October to January), late summer (February to May), and winter (June to September) following (Klages & Bester 1998) and the data analysed separately for each season. By comparing the food composition amongst seasons, I attempt to investigate any seasonal variation in the diet of Subantarctic fur seals at Marion Island.

Results

Seasonal variation in diet over the study period 3 (April 2000 – March 2006)

Seasonal variation in diet was detected between early summer and late summer in the present study. In early summer there was no difference in %NA amongst the two most important prey species in the scats i.e. *Gymnoscopelus fraseri* and *G. bolini* (Fig 4.1) but *G. fraseri* was significantly low compared to *G. bolini* during late summer. *P. tenisoni* was completely replaced by *Electrona carlsbergi* during winter, where %NA of the later was identical to %NA of the most important prey groups (Table 4.1).

In terms of %M, no significant difference among the main prey species groups in all seasons existed. Similarly, in terms of mean fish mass, there was no significant difference between the three seasons (P = 0.5555) at the 1% significance level. Although variable in size, *G. fraseri* and *P. tenisoni* are small myctophid fish species which contributed low in terms of %M (Table 4.3), although they were frequently taken in some seasons (e.g. during early summer).

Among the five main prey species that make up the major components of the Subantarctic fur seal diet, four of these resort under the genus *Gymnoscopelus* and one a *Protomyctophum* species. In all three seasons, *G. bolini* was the most important in terms of %NA (Table 4.1), followed by *G. fraseri* which occurred significantly less as compared to *G. bolini*. The remaining *Gymnoscopelus* species was significantly less abundant than *G. fraseri*, and there were no seasonally significant differences amongst *G. nicholsi*, *G. piabilis* and *P. tenisoni*.

The remaining species groups contributed significantly less to the diet of the Subantarctic fur seals over the study period (2000 – 2006) on a seasonal basis in terms of %NA. In terms of %M, *G. fraseri*, was significantly lower during both winter and late summer (L. summer) seasons as compared to *G. bolini* and *G. piabilis*. *G. nicholsi* was higher than *G. fraseri* with differences close to significance (P = 0.003) during both winter and L. summer from 2000 (Table 4.3). Species that replaced some of the key prey species start to increase during late summer, while some of the main prey species show an opposite trend (Table 4.1). *G. bolini* and *G. fraseri* also show different pattern (Fig. 4.1) as, in terms of numbers, the Subantarctic fur seals took more *G. bolini* in early summer and less *G. fraseri*. During winter, there were less *G. bolini* and more *G. fraseri* (Fig. 4.1).

In terms of %FO, three of the main prey species (i.e. *G. bolini*, *G. piabilis* and *G. nicholsi*) were found in most of the scats during late summer and in fewer scats during early summer. Contrary to this, *G. fraseri* and *P. tenisoni* were found in fewer scats in late summer than in early summer (Table 4.2). In the overall seasonal variation context, the Subantarctic fur seals were taking larger fish in early summer and quite small fish in winter although this difference was not statistically significant (Table 4.3). *G. piabilis* taken in winter were much heavier than the ones taken during early summer, and *G. bolini* showed an opposite trend (Fig. 4.2).

Seasonal variation between years (from 2000 – 2006)

The main prey species in most of the seasons contributed the same to the diet of the Subantarctic fur seals in terms of both %NA (Appendix 1) and %M. Some of these main prey species were replaced by other species in a few of the seasons as it was the case in the overall seasonal and inter-annual variations mentioned earlier (Appendix 1).

Early summer

In terms of %NA, *G. fraseri*, *G. piabilis* and *G. nicholsi* were replaced by *Krefftihcthys anderssoni* in early summer 2000 (Appendix 1). There was no significant difference between *G. bolini*, *P. tenisoni* and *K. anderssoni* amongst all the years, but there was a significant difference between *G. bolini* and *G. piabilis*. Though there was significant difference between *G. bolini* and *G. piabilis* in terms of % NA, in terms of %M, in early summer of 2000, *G. piabilis* was significantly higher compared to *G. bolini*. There was no difference amongst *G. bolini*, *G. nicholsi* and *G. fraseri* in %M. In 2001, *P. choriodon* was more abundant, contributing almost the same as the main prey groups. In 2002, 2003 and 2004 *G. fraseri* was significantly higher in terms of %NA. But in terms of %M there was no significant difference between *G. fraseri* and other main prey species, probably due to their small body size. In 2004, there was significant difference between *G. fraseri* and *P. tenisoni* in terms of both %NA and %M. In 2005, *G. nicholsi* was significantly higher in terms of both the %NA and %M as compared to *G. piabilis* (Appendix 1).

Late summer

There was considerable variation during late summer seasons over different years, where in the year 2000 *P. tenisoni* was replaced by *E. carlsbergi* with %NA similar to *G. bolini* and *K. anderssoni* (Appendix 1). In terms of %M, *E. subaspera* contributed the same as each of the following key prey species in the diet of the Subantarctic fur seals: *G. bolini*, *G. piabilis*, *G. nicholsi* and *E. carlsbergi*. This was also the case during late summer seasons of years 2001 and 2002 where *M. ventralis* contributed the same as the key prey species in terms of %NA. During these years (2001 and 2002) *G. fraseri* was present in significantly lower numbers. In terms of %M, there was significant difference between *P. tenisoni* and *G. piabilis*. During 2002, there were differences between *G. bolini* and *M. ventralis*, *G. piabilis* and *G. fraseri*, in terms of %NA. Marked change was noticed during late summer of 2003 where *E. carlsbergi* was significantly more abundant than *G. piabilis*. During 2004, there was significant differences between *E. carlsbergi* and *G. piabilis*, *G. fraseri* and *G. piabilis*, *G. nicholsi* and *G. piabilis*, *M. ventralis* and *G. bolini,* and between *G. nicholsi* and *M. ventralis* respectively. In terms of %M, there was no difference amongst *G. bolini*, *G. nicholsi*, *G. piabilis*, *M. ventralis*, *E. carlsbergi* and *G. fraseri*. The only difference was between *G. bolini* and *E. carlsbergi* (Appendix 1).

Winter

During the winter season of the year 2000, *G. bolini* contributed significantly less in terms of both %NA and %M while *G. piabilis* was high in terms of %NA, followed by *G. fraseri*, *K. anderssoni* and *G. nicholsi* (Appendix 1) although statistically there was no significant difference amongst these species. In winter season during 2001, *P. tenisoni*, *P. choriodon* and the "others" prey groups were completely absent. There was no significant difference between "other" prey groups in terms of both %NA and %M. During winter season of 2002, *G. piabilis* had high %NA followed by the "others"prey group, then *G. bolini, Gymnoscopelus* sp. and *G. fraseri,* respectively. During 2003, *E. carlsbergi* was significantly higher in %N than *G. piabilis* as were *E. subaspera* and *M. ventralis*. During 2004 winter months, *P. tenisoni* was completely replaced by *E. carlsbergi* and *E. subaspera*. There were no significant difference between *E. subaspera, M. ventralis* and the main prey species as far as %NA is concerned. In terms of %M there was a significant difference between *G. bolini* and *E. carlsbergi* (Appendix 1).

Some seasonal variations in mean sea surface temperature occurred between 1989 and the end of this study period (Table 4.4). There were more temperature fluctuations during early summer and winter seasons compared to late summer, which seemed to be linked to the variation in the diet of the Subantarctic fur seals (Table 4.5).

Table 4.1 Seasonal relative percentage numerical abundance (% NA) over the entire study period (April 2000 – March 2006) for prey species taken by Subantarctic fur seals at Marion Island

Species name	**E. summer**	**L. summer**	**Winter**
E. carlsbergi	1.26	6.39	12.81
E. subaspera	0.94	3.24	6.06
G. bolini	25.91	22.83	17.07
G. fraseri	27.21	9.50	16.58
G. nicholsi	7.43	16.00	10.80
G. piabilis	6.30	9.74	11.65
Gymnoscopelus sp.	12.42	15.77	17.14
K. anderssoni	2.26	1.43	1.79
M. ventralis	0.24	8.23	3.53
P. choriodon	1.29	1.33	0.11
P. tenisoni	12.99	3.16	0
Others	6.17	11.19	8.01

Table 4.2 Mean percentage frequency of occurrence (% FO) followed by standard deviations (SD) of the five most important prey species of Subantarctic fur seals in different seasons over the entire study period (April 2000 – March 2006) at Marion Island.

Species	**L. summer**	**E. summer**	**Winter**
	Mean ± SD	**Mean ± SD**	**Mean ± SD**
G. bolini	73 ± 44	61 ± 0.49	59 ± 0.49
G. fraseri	46 ± 0.50	53 ± 0.50	59 ± 0.49
G. nicholsi	63 ± 0.48	43 ± 0.50	64 ± 0.48
G. piabilis	52 ± 0.50	45 ± 0.45	53 ± 0.50
P. tenisoni	10 ± 0.30	31 ± 0.46	00 ± 00

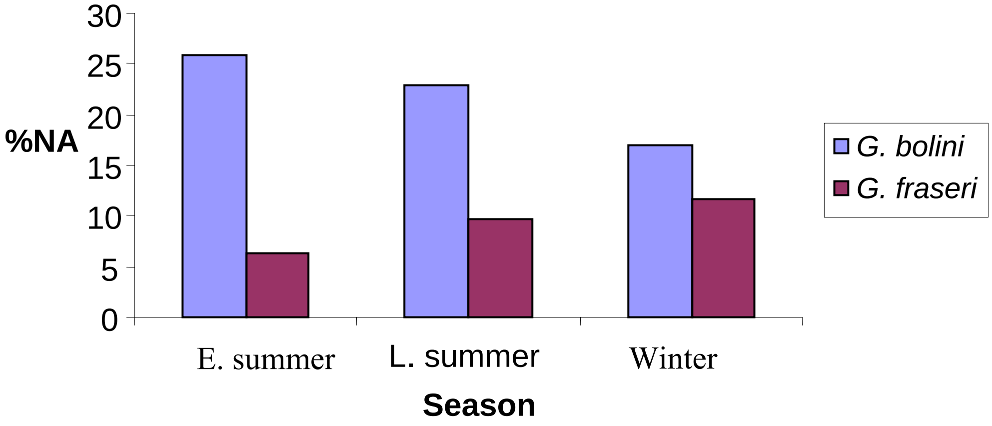


Figure 4.1 Seasonal relative percentage numerical abundance (%NA) of *G. bolini* and *G. fraseri* in the diet of the Subantarctic fur seals at Marion Island from April 2000 - March 2006

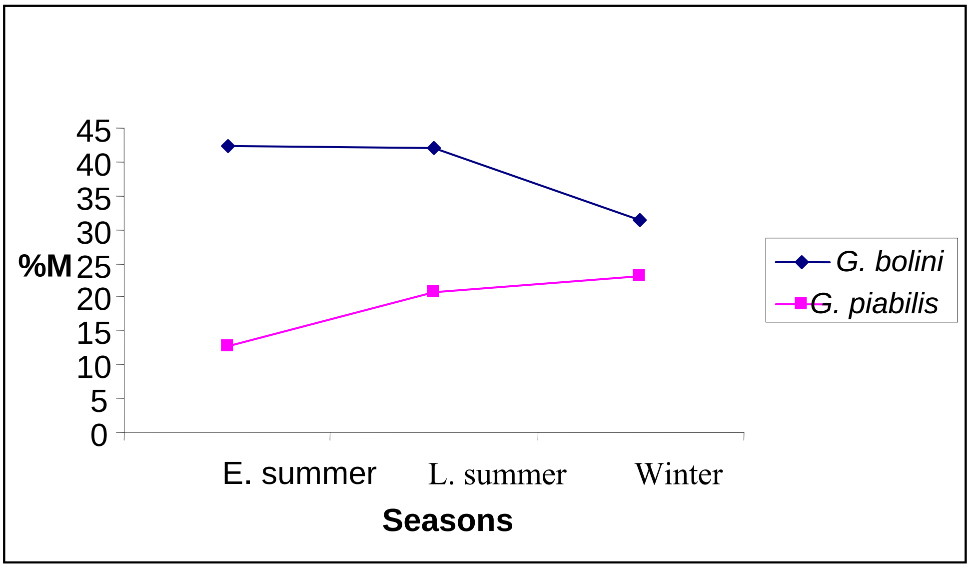


Figure 4.2 Trends in seasonal relative percentage mass (%M) of the two main prey species (i.e. *G. bolini* and *G. piabilis*) of the Subantarctic fur seals at Marion Island from April 2000 - March 2006

Table 4.3 Seasonal relative percentage mass (% M) of the twelve main prey species of the Subantarctic fur seals at Marion Island from April 2000 - March 2006

Species name	**E. summer**	**L. summer**	**Winter**
E. carlsbergi	0.56	3.55	6.95
E. subaspera	0.87	2.87	6.60
G. bolini	42.24	42.04	31.45
G. fraseri	23.31	3.63	9.36
G. nicholsi	12.07	19.70	16.92
G. piabilis	12.72	20.85	23.13
Gymnoscopelus sp.	-	-	-
K. anderssoni	0.44	0.03	0.06
M. ventralis	0.23	3.95	1.83
P. choriodon	1.12	0.80	0.11
P. tenisoni	5.07	1.07	0
'Others'	0.80	1.35	1.69

Table 4.4 Seasonal Mean Sea Surface Temperature from the start of the diet monitoring in April 1989 until the end of the present study in March 2006

Season	**Mean ± SD**	**Minimum**	**Maximum**
Winter	5.6 ± 1.81	2.8	14.9
E. summer	6.0 ± 1.47	3.0	13.8
L. summer	6.9 ± 1.06	4.0	13.8

Table 4.5 Seasonal relative percentage numerical abundance (% NA) during study period 2 (April 1995 - March 2000) and period 3 (present study, April 2000 – March 2006)

Species	**E. summer**		**L. summer**		**Winter**	
	P2	P3	P2	P3	P2	P3
E. carlsbergi	2.37	1.26	10.64	6.39	16.11	12.81
E. subaspera	1.56	0.94	3.59	3.24	5.34	6.06
G. bolini	3.78	25.91	7.41	22.83	4.07	17.07
G. fraseri	10.76	27.21	22.66	9.50	30.44	16.58
G. nicholsi	1.08	7.43	3.56	16.00	1.58	10.80
G. piabilis	38.77	6.30	25.37	9.74	26.40	11.65
Gymnoscopelus sp.	5.10	12.42	4.90	15.77	4.26	17.14
K. anderssoni	22.79	2.26	1.34	1.43	0.80	1.79
M. ventralis	0.37	0.24	10.40	8.23	13.54	3.53
P. choriodon	15.56	1.29	9.24	1.33	18.25	0.11
P. tenisoni	7.60	12.99	7.66	3.16	3.05	0
‘Others’	7.03	6.17	6.37	11.19	2.13	8.01

Appendix 1. Seasonal relative means followed by standard deviations of the twelve main prey species for the Subantarctic fur seals at Marion Island from April 2000 - March 2006 expressed in terms of percentage numerical abundance (%NA) and relative percentage mass (%M).

		Mean ± SD percentage abundance of prey group					
		(Mean ± SD percentage mass of prey group)					
Year	**Season**	***E. carlsbergi***	***E. subaspera***	***G. bolini***	***G. fraseri***	***G. nicholsi***	***G. piabilis***
2000	E. summer	1.53 ± 4.78	0.51 ± 2.07	22.01 ± 29.09	4.40 ± 11.97	5.33 ± 9.01	19.94 ± 25.97
		(0.6 ± 1.86)	(0.40 ± 1.61)	(40.68 ± 35.42)	(2.60 ± 8.40)	(6.90 ± 15.66)	(42.55 ± 35.61)
	L. summer	10.65 ± 16.17	4.60 ± 14.00	21.91 ± 20.66	9.78 ± 13.54	10.04 ± 14.06	6.04 ± 10.02
		(6.47 ± 15.44)	(7.06 ± 20.29)	(48.87 ± 36.56)	(2.92 ± 5.22)	(14.93 ± 24.58)	(15.97 ± 25.07)
	Winter	4.11 ± 10.16	2.25 ± 4.19	3.99 ± 7.97	18.50 ± 19.59	10.03 ± 10.36	35.14 ± 28.79
		(1.97 ± 5.68)	(2.07 ± 4.51)	(4.99 ± 10.05)	(7.91 ± 10.73)	(14.97 ± 16.91)	(67.70 ± 25.21)
2001	E. summer	0.94 ± 2.72	0.53 ± 2.017	18.05 ± 29.40	0.21 ± 0.66	3.34 ± 5.38	8.54 ± 14.92
		(0.22 ± 0.57)	(0.74 ± 2.56)	(32.99 ± 35.02)	(0.15 ± 0.46)	(14.51 ± 22.65)	(29.90 ± 31.37)
	L. summer	1.94 ± 3.77	2.15 ± 3.37	19.11 ± 22.90	4.39 ± 7.72	16.31 ± 20.86	9.24 ± 12.89
		(0.54 ± 1.14)	(1.35 ± 2.51)	(38.92 ± 34.06)	(2.39 ± 6.48)	(20.04 ± 26.28)	(24.60 ± 25.22)
	Winter	1.33 ± 2.09	0.00 ± 0.00	39.70 ± 35.60	1.15 ± 2.82	13.99 ± 19.50	11.36 ± 19.21
		(0.28 ± 0.54)	(0.00 ± 0.00)	(72.65 ± 34.78)	(0.14 ± 0.34)	(11.30 ± 15.39)	(15.17 ± 28.07)
2002	E. summer	0.62 ± 2.24	0.42 ± 1.89	2.81 ± 5.68	66.70 ± 32.92	6.32 ± 8.13	2.01 ± 5.97
		(0.93 ± 3.83)	(0.29 ± 1.10)	(13.36 ± 21.88)	(59.21 ± 36.22)	(9.68 ± 12.52)	(7.43 ± 18.88)
	L. summer	7.82 ± 14.89	4.87 ± 10.13	20.01 ± 19.07	11.12 ± 23.53	9.51 ± 14.57	16.69 ± 16.14
		(2.72 ± 6.91)	(4.50 ± 14.07)	(34.57 ± 28.17)	(7.25 ± 22.37)	(8.37 ± 12.88)	(37.26 ± 31.16)

	Winter	0.00 ± 0.00	4.17 ± 8.33	20.31 ± 26.70	0.00 ± 0.00	3.13 ± 6.25	29.69 ± 32.83
		(0.00 ± 0.00)	(0.53 ± 1.05)	(30.46 ± 35.17)	(0.00 ± 0.00)	(3.20 ± 6.40)	(40.42 ± 41.50)
2003	E. summer	0.34 ± 1.94	0.45 ± 2.05	26.20 ± 33.30	52.72 ± 38.72	3.32 ± 6.27	2.49 ± 7.78
		(0.10 ± 0.47)	(0.38 ± 1.42)	(42.39 ± 41.27)	(44.15 ± 42.48)	(8.36 ± 18.95)	(4.38 ± 11.75)
	L. summer	6.20 ± 15.98	2.22 ± 6.25	32.61 ± 29.55	6.26 ± 14.64	18.67 ± 25.40	4.80 ± 12.85
		(4.5 ± 16.48)	(1.75 ± 5.59)	(55.85 ± 38.16)	(1.90 ± 7.47)	(23.37 ± 31.99)	(8.85 ± 18.36)
	Winter	13.60 ± 24.33	9.88 ± 14.36	18.54 ± 23.70	14.65 ± 18.66	3.13 ± 6.25	6.41 ± 9.97
		(7.85 ± 15.37)	(10.62 ± 19.87)	(34.63 ± 38.99)	(4.62 ± 6.12)	(18.03 ± 23.74)	(13.62 ± 19.74)
2004	E. summer	0.19 ± 0.59	0.77 ± 4.15	20.06 ± 29.33	33.49 ± 35.23	6.94 ± 10.35	3.19 ± 11.73
		(0.65 ± 2.91)	(0.51 ± 2.59)	(35.50 ± 41.38)	(31.44 ± 38.37)	(12.65 ± 20.16)	(6.56 ± 17.70)
	L. summer	7.03 ± 12.75	2.83 ± 7.60	19.79 ± 22.26	12.24 ± 17.92	20.94 ± 25.28	6.97 ± 16.86
		(3.96 ± 12.56)	(2.27 ± 7.92)	(38.90 ± 34.65)	(3.45 ± 5.60)	(27.90 ± 31.57)	(13.02 ± 25.24)
	Winter	15.53 ± 21.52	5.05 ± 10.10	17.89 ± 22.76	20.41 ± 24.20	7.56 ± 8.26	7.95 ± 14.71
		(8.33 ± 15.84)	(6.23 ± 13.43)	(33.68 ± 35.69)	(14.01 ± 24.91)	(19.99 ± 23.62)	(15.93 ± 25.49)
2005	E. summer	1.65 ± 6.53	1.83 ± 1.26	42.87 ± 34.48	10.79 ± 22.22	12.14 ± 24.11	0.62 ± 1.54
		(0.63 ± 3.85)	(1.96 ± 11.64)	(61.27 ± 41.58)	(6.18 ± 17.85)	(15.56 ± 29.89)	(10.00 ± 21.30)
	L. summer	0.50 ± 0.92	3.71 ± 9.98	21.83 ± 22.32	10.36 ± 18.02	12.92 ± 18.22	16.31 ± 17.31
		(3.07 ± 13.81)	(2.67 ± 13.42)	(36.91 ± 31.95)	(3.64 ± 14.48)	(13.49 ± 22.13)	(33.79 ± 29.20)
	Winter	6.10 ± 12.74	9.89 ± 13.55	7.92 ± 12.02	10.88 ± 16.05	3.65 ± 5.20	17.09 ± 13.54
		(7.79 ± 17.15)	(8.41 ± 12.63)	(14.49 ± 23.50)	(10.88 ± 16.05)	(5.37 ± 8.16)	(45.85 ± 35.12)
	Sample size	**1033**	**519**	**4079**	**3755**	**2038**	**1392**

Appendix 1 (cont.)

		Mean ± SD percentage abundance of prey group					
		(Mean ± SD percentage mass of prey group)					
Years	**Seasons**	***Gymnoscopelus* sp.**	***K. anderssoni***	***M. ventralis***	***P. choriodon***	***P. tenisoni***	**Others**
2000	E. summer	9.59 ± 14.54	12.22 ± 16.39	0.00 ± 0.00	0.79 ± 1.89	20.84 ± 28.79	2.85 ± 5.012
		(0.00 ± 0.00)	(1.29 ± 6.09)	(0.00 ± 0.00)	(0.48 ± 1.60)	(2.08 ± 4.56)	(2.55 ± 12.97)
	L. summer	10.64 ± 14.64	14.20 ± 11.45	4.17 ± 10.24	4.67 ± 10.74	1.05 ± 2.92	2.26 ± 4.20
		(0.00 ± 0.00)	(0.24 ± 0.36)	(02.07 ± 5.76)	(1.37 ± 3.93)	(0.03 ± 0.07)	(0.31 ± 1.02)
	Winter	8.22 ± 10.47	14.13 ± 15.49	0.65 ± 1.74	0.00 ± 0.00	0.00 ± 0.00	2.98 ± 9.58
		(0.00 ± 0.00)	(0.00 ± 0.00)	(0.259 ± 0.68)	(0.00 ± 0.00)	(0.00 ± 0.00)	(0.00 ± 0.00)
2001	E. summer	6.17 ± 10.24	4.38 ± 11.41	0.00 ± 0.00	4.51 ± 12.69	51.50 ± 40.13	1.84 ± 5.01
		(0.00 ± 0.00)	(0.85 ± 1.70)	(0.00 ± 0.00)	(0.99 ± 3.10)	(19.65 ± 29.65)	(0.01 ± 0.04)
	L. summer	16.65 ± 18.18	0.39 ± 1.37	5.23 ± 13.32	4.39 ± 10.81	16.26 ± 27.07	3.95 ± 7.66
		(0.00 ± 0.00)	(0.02 ± 0.08)	(2.55 ± 7.26)	(3.92 ± 12.52)	(5.07 ± 12.54)	(0.98 ± 3.002)
	Winter	29.59 ± 36.71	0.00 ± 0.00	2.87 ± 7.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
		(0.00 ± 0.00)	(0.00 ± 0.00)	(0.46 ± 1.13)	(0.00 ± 0.00)	(0.00 ± 0.00)	(0.00 ± 0.00)
2002	E. summer	14.42 ± 21.86	0.06 ± 0.29	1.19 ± 5.69	0.40 ± 1.90	0.72 ± 1.80	4.35 ± 20.85
		(0.00 ± 0.00)	(0.10 ± 0.04)	(0.27 ± 1.30)	(0.08 ± 0.39)	(0.05 ± 0.14)	(0.00 ± 0.00)
	L. summer	14.58 ± 14.45	0.10 ± 0.45	13.32 ± 18.89	0.37 ± 2.11	0.05 ± 0.36	1.57 ± 4.31
		(0.00 ± 0.00)	(0.01 ± 0.04)	(4.97 ± 13.42)	(0.15 ± 0.79)	(0.004± 0.03)	(0.56 ± 3.99)
	Winter	16.14 ± 20.91	0.00 ± 0.00	1.56 ± 1.80	0.00 ± 0.00	0.00 ± 0.000.	25.00 ± 50.00
		(0.00 ± 0.00)	(0.00 ± 0.00)	(0.40 ± 0.55)	(0.00 ± 0.00)	(0.00 ± 0.00)	(0.00 ± 0.00)

2003	E. summer	12.31 ± 14.72	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.96 ± 12.00	0.22 ± 1.40
		(0.00 ± 0.00)	(0.00 ± 0.00)	(0.00 ± 0.00)	(0.00 ± 0.00)	(0.24 ± 1.53)	(0.00 ± 0.00)
	L. summer	21.26 ± 23.27	0.84 ± 5.85	4.22 ± 9.72	0.75 ± 5.84	0.21 ± 1.35	1.97 ± 4.86
		(0.00 ± 0.00)	(0.02 ± 0.12)	(1.78 ± 5.41)	(0.26 ± 1.95)	(0.02 ± 0.15)	(1.50 ± 7.59)
	Winter	21.94 ± 20.62	0.93 ± 2.66	6.18 ± 16.91	0.25 ± 0.80	0.00 ± 0.00	1.00 ± 3.28
		(0.00 ± 0.00)	(0.10 ± 0.72)	(3.73 ± 13.16)	(0.12 ± 0.51)	(0.00 ± 0.00)	(4.14 ± 16.07)
2004	E. summer	11.31 ± 15.66	1.33 ± 5.44	0.20 ± 1.66	2.53 ± 10.92	16.48 ± 28.29	2.31 ± 6.45
		(0.00 ± 0.00)	(0.68 ± 5.19)	(0.51 ± 4.97)	(2.61 ± 12.25)	(7.88 ± 21.16)	(1.15 ± 7.45)
	L. summer	16.52 ± 17.82	0.11 ± 0.12	9.79 ± 18.06	0.80 ± 5.23	0.96 ± 7.75	2.12 ± 4.95
		(0.00 ± 0.00)	(0.000 ± 0.000)	(6.17 ± 16.64)	(0.63 ± 5.59)	(0.23 ± 2.32)	(2.19 ± 7.77)
	Winter	14.58 ± 18.71	0.93 ± 2.66	2.12 ± 5.60	0.02 ± 0.20	0.00 ± 0.00	1.79 ± 4.73
		(0.00 ± 0.00)	(0.10 ± 0.718)	(1.12 ± 4.57)	(0.02 ± 0.15)	(0.00 ± 0.00)	(0.59 ± 3.23)
2005	E. summer	15.84 ± 19.94	0.47 ± 2.95	0.30 ± 2.73	0.17 ± 1.37	6.22 ± 21.37	0.65 ± 2.70
		(0.00 ± 0.00)	(0.01 ± 0.03)	(0.13 ± 1.20)	(0.35 ± 3.18)	(3.55 ± 16.02)	(0.39 ± 2.35)
	L. summer	10.37 ± 15.70	0.12 ± 0.48	9.34 ± 17.83	0.24 ± 1.02	6.29 ± 22.36	3.27 ± 8.35
		(0.00 ± 0.00)	(0.01 ± 0.09)	(3.27 ± 7.36)	(0.04 ± 0.22)	(2.90 ± 11.52)	(1.10 ± 4.00)
	Winter	22.80 ± 30.75	0.00 ± 0.00	9.26 ± 9.34	0.54 ± 1.69	0.00 ± 0.00	3.09 ± 5.25
		(0.00 ± 0.00)	(0.00 ± 0.00)	(4.14 ± 5.77)	(0.86 ± 2.71)	(0.00 ± 0.00)	(3.67 ± 8.63)
	Sample size	**3371**	**466**	**881**	**210**	**2440**	**8094**

Discussion

Marine mammal diets and foraging behaviour are direct results of both the spatial and temporal patterns of marine productivity (Berta & Sumich 1999). They are expected to make adjustments to deal with seasonal variability in their food supplies, including extended winter time fasting periods (Berta & Sumich 1999). Therefore**,** seasonal variations in diet are likely to be a reflection of changes in prey availability, with the female fur seals taking the most available prey in different water masses that they forage in during the pup-rearing period (Beauplet *et al.* 2004).

In the present study, lactating females of the Subantarctic fur seal frequent the island throughout a 10-11 month period (Kerley 1983, Kirkman *et al.* 2002) to suckle their pups at frequent intervals (Bester & Bartlett 1990; Kirkman *et al.* 2002). Early summer coincided with breeding of fur seals when large numbers of males haul out at Marion Island (Kerley 1983), where they are thought to fast throughout the breeding season. L. summer coincide with the moulting season. Subadults are hauled out during winter, and just before the next breeding season they go back to sea (Kerley 1983). Therefore, the sex and age of fur seals present on the study site may play a crucial role in the diet composition of fur seals based on scat collections. Diet varies with age, with juvenile diets differing from those of adult animals, for example, adult harp seals normally feed on fish and some crustaceans whereas pups feed mainly on zooplankton. Riedman (1990) suggested that one reason for this difference may be that juveniles require prey that is easier to capture (Berta & Sumich 1999). In this respect, the diet analysis in all the three seasons over the entire study period largely represents the diet of lactating female Subantarctic fur seals (Klages & Bester 1998; this study).

During the present study marked seasonal difference was recorded in the diet of Subantarctic fur seals between early summer (E. summer) and late summer (L. summer). This difference probably occurred as a result of considerable increase in abundance of *P. tenisoni* and *G. fraseri* in E. summer, and rapid decrease during L. summer, with *G. nicholsi* and *G. piabilis* showing an opposing trend. Such changes in diet are likely to be a result of prey availability within the foraging range of the fur seal females (Kirkman *et al*. 2002). At Amsterdam Island, in considerably lower latitudes (37º 55′S and 77º 30′E) than Marion Island (46º 54′S, and 37º 51′E), lactating Subantarctic fur seals generally exploited the distant Subtropical Front, but also exhibited large differences in seasonal distribution, from short trips in restricted foraging areas during summer to widely distributed foraging grounds during the winter (Beauplet *et al*. 2004). Similarly, at higher latitude (54º 30′S, 158º 57 ′E) Macquarie Island, early in lactation, i.e. from late December, lactating females made short duration nocturnal foraging trips, and foraging was limited to a small area within 20 km of the breeding site (Robinson 2002). By late summer, trips were more than 6 days long and range over 195 km from the island (Robinson 2002). This is consistent with a seasonal shift in diet and an increasing proportion of time being devoted to diving and resting of the fur seal females, at least at Amsterdam Island (Beauplet *et al*. 2004). In the South American fur seal, *Arctocephalus australis*, in autumn, both distance and time away from the breeding site increased, the dispersal of foraging effort later in the season perhaps indicating a relative increase in prey density further from the Island (Thompson *et al*. 2003). In early summer, the pups are small and may benefit from frequent, relatively small meals, while later in the season, when pups are capable of withstanding longer fasts and metabolic demands of pregnancy and lactation are higher, it may be more efficient for females to stay at sea longer and forage in far-off patches (Thompson *et al*. 2003). Similarly, early summer foraging trips of lactating females are shorter on average (mean 7.0 ± 0.4 days) than during late summer and winter (25.5 ± 2.4 days) at Marion Island (Kirkman *et al.* 2002). Although such a difference in feeding trip duration, did not translate into a significant difference between the summer and winter seasons for trip duration, maximum distance or total distance travelled in the 2000 - 2006 seasons at Marion Island, these were, however, consistently shorter and less variable in summer (de Bruyn *et al.* in press). This is likely to explain the source of seasonal variation in diet composition of the Subantarctic fur seal at Marion Island in the period 2000 – 2006 (present study).

Krefftichthys anderssoni made a remarkably highest contribution in terms of %NA in early summer 2000 when compared to all other years during the current study period (April 2000 – March 2006), while *G. piabilis* was considerably low, though in terms of percentage mass (%M) its contribution was high. Surprisingly, *P. choriodon*'s contribution to the diet was significantly highest in early summer of 2001, while in the early summers of 2002, 2003 and 2004 *G. fraseri* was the most important prey species. In the absence of data on the actual foraging areas in those seasons, the predators probably responded to a seasonally reduced relative availability of both *G. bolini* and *G. piabilis* in its foraging range, resulting in this predator switching over to the small *G. fraseri*. Similarly, in early summer of 2005, the numerical availability of *G. nicholsi* and *P. tenisoni* must have peaked.

Such seasonal fluctuation in prey availability is hardly surprising. Antarctic waters in particular have marked seasonal fluctuations in light and productivity, both factors being linked and attenuated by summer melt of snow and sea-ice (Lake *et al*. 2003). In addition, climate and oceanography cycles around the Southern Ocean have a four to five year periodicity (White & Peterson 1996; Lake *et al*. 2003). The variation in the diet in Weddell seals (Plötz *et al*. 1991) could have had both seasonal and interannual elements because seasons were sampled in different years (Lake *et al*. 2003). In lower latitudes, Beauplet *et al*. (2004) indicated that in late autumn and winter, *Electrona paucirastra* progressively replaced *Symbolophorus* species and *Myctophum phengodes* as the main prey species of the fur seals, a situation reminiscent of the present study, only with different myctophid prey species involved due to the ~ 08^{o} difference in latitude between the two study areas.

Some studies indicated that variations in the location of the foraging grounds and the change in seals diet patterns during the breeding season are consistent with fluctuations in the Subtropical front (STF) location (e.g. Beauplet *et al*. 2004). Subantarctic fur seals at Amsterdam Island undertake extremely long winter foraging trips (> 1000 km; ~30 days), which is linked to the southward migration of the STF (Georges *et al*. 2000; Beauplet *et al*. 2004). Otariids are known to have opportunistic feeding habits (Antonelis *et al*. 1984), and their seasonal variations in diet are likely to be a indication of changes in prey availability, with the seals taking advantage of the most available prey that occupy the different water masses they sequentially exploit during the pup-rearing period (Beauplet *et al*. 2004). On Marion Island the Subantarctic fur seals seem to be more dependent on the SAF, which migrates north in winter and south in summer, also resulting in longer winter foraging trips (>700 km; ~30 days) for the Marion Island fur seals (de Bruyn *et al*. 2009).

The Subantarctic fur seal during the late summer take more species of lesser importance (i.e. other than the five main prey species) such as *M. ventralis*, *E subaspera* and *E. carlsbergi*. This is the season when most of the variations were noticed. The contribution of *M. ventralis* during late summer was not statistically different from the main prey species, especially in 2001, 2002 and 2004. *E. subaspera* in 2000 late summer contributed the same as the main prey species in terms of %M. The number of *E. carlsbergi* increased gradually during late summer. In contrast, *P. tenisoni* gradually declined during late summer. This peak coincides with the breeding season, i.e. the period of greatest demand and competition for resources (from December to March) (Goldsworthy *et al*. 2001).

The decrease in the mean length of fish prey species through both early summer and late summer and an increase in availability of smaller individuals (Robinson *et al*. 2002), indicated the recruitment in the fish population. Adams & Klages (1989) suggested that the smaller size class represent juvenile fish, whereas the larger size class may be considered adult. Although the relative body sizes of each fish species taken in summer and in winter were different, statistical examinations indicated this difference to be insignificant, suggesting that the Subantarctic fur seals at Marion Island were mostly feeding on adults rather than on juvenile fish. In contrast, Beauplet *et al.* (2004) observed an increase in average otolith length of the main prey species consumed throughout the pup-rearing period, and these changes in otolith length, and thus the fishes' respective body sizes, may be due to growth of the fish during this period. Moreover, the same authors also suggested that increasing size of prey items could also be due to seasonal changes in the water masses, in accord with the fish patches being exploited by the seals during different seasons.

Foraging strategies exhibit extensive plasticity depending on the type and distribution of the food resource (Berta & Sumich 1999). Diet also is likely to vary with age, with juvenile diets differing from those of adult animals for example, adult harp seals normally feeding on fish and some crustaceans whereas pups feed mainly on zooplankton (Berta & Sumich 1999). Riedman (1990) suggested that one reason for this difference may be that juveniles require prey that is easier to capture, and also as mentioned earlier on, due to the large number of seals ashore during early summer season.

Chapter 5

Interannual variation in the diet of Subantarctic fur seals (*Arctocephalus tropicalis*) at Marion Island

Introduction

The Southern Ocean, including Marion Island, is deemed a system consisting of a series of interconnected ecosystems (Knox 1994), in which top predators can provide information about a number of layers of primary and secondary production and thus can be used for describing and monitoring spatial and temporal ecosystem dynamics (Lake *et al*. 2003) and distribution of marine resources (McConnell *et al.* 1992; Pakhomov & McQuaid 1996; Guinet *et al.* 1997; Georges *et al*. 2000; Beauplet *et al*. 2004). Myctophids have been reported to be the important food source for predators of higher trophic levels like seabirds (Guinet *et al.* 1996), fur seals (Cherel *et al.* 1997) and squid (Rodhouse *et al.* 1992; Pusch *et al*. 2004). However, there is lack of information on temporal variation in fish stocks exploited by far-ranging species to determine how prey species population decline may affect the population of top predators. In practice, predators require a certain density of food in order to be able to meet their energy demands. The amount of food they require to consume may be much less than the amount available in the local environment in order to forage effectively (Furness *et al.* 2006).

There is therefore a need for an integrated study on temporal variation that will incorporate prey species distribution and abundance in the foraging grounds of the Subantarctic fur seals around Marion Island. Scats collected over several years can be compared, although inter-annual comparison could be confounded by fine-scale temporal and spatial variation in the diet (Lake *et al*. 2003). Furthermore, although fur seals are expected to forage further away from the island in years of reduced prey availability (Lea *et al*. 2006), there may be reduced costs associated with remaining closer to the colony, even at the risk of higher levels of intraspecific competition (Lea *et al*. 2006). The aim of the present chapter is to investigate how the diet of the

Subantarctic fur seal at Marion Island might change on inter-annual scales, and to interpret such possible changes.

Results

The five main prey species contributed almost the same in the diet of the Subantarctic fur seal. Statistical examination could not detect any significant difference between the five key prey species in terms of %NA. In year 2000, one of the lesser species *Krefftichthys anderssoni* contributed a similar amount compared to the five key prey species, an exceptional difference compared to years 2001 to 2006. Nevertheless, *Gymnoscopelus bolini* remained most abundant followed by *G. piabilis* then *K. anderssoni* and *Protomyctophum tenisoni.*

Although all the key prey species were statistically identical in %NA, a slight difference was detected between *G. fraseri* and *G. piabilis* although this difference was less pronounced (P = 0.0056) at a 1% significance level. This pattern was similar for the main prey species throughout the study period, except for two years, where during 2001 *P. tenisoni* was the most important prey species replacing *G. fraseri*, and during 2003 where *G. piabilis* was significantly lower, with %NA almost similar to that of *E. carlsbergi*. In terms of %NA *K. anderssoni*'s contribution declined significantly in the subsequent years from 2001 to 2005 (Table 5.2).

In terms of relative percentage mean mass (%M), *G. piabilis* contributed more, followed by *G. bolini* with the exception of 2003 and 2004 where *G. fraseri* was the second most important prey species (Fig 5.3) . All the four main prey species with the exclusion of *P. tenisoni* contributed almost the same in terms of %M. *G. fraseri* in 2001 was significantly low compared to other main prey species. In the same year *P. tenisoni* contributed approximately the same amount as contributed by other main prey species in the diet of the Subantarctic fur seal (Table 5.3).

In all the years during the present study period (April 2000 – March 2006) *G. piabilis* seemed to be the largest prey species taken by the Subantarctic fur seals at Marion Island (Table 5.3; Fig 5.2), with the exception of 2003, where the “others” prey species group predominated. There was significant difference between year 2000 and the subsequent years to 2006 during the present study. Nevertheless, the mean mass and relative mean length of *G. piabilis* taken in all years were higher than both the mean mass and mean length of *G. bolini* (Fig 5.3 and Table 5.5) although in terms of numbers *G. bolini*'s contribution was considerably high as compared to that of *G. piabilis* (Fig. 5.2). Subantarctic fur seals seem to take *G. bolini* more often than any other species throughout the study period (Table 5.1). In addition, *G. bolini* and G. fraseri show opposite trends throughout the years, because when Subantarctic fur seals take more of *G. bolini*, less of *G. fraseri* were taken and *vice versa* (Fig 5.1).

The Chi Square test indicated that amongst the five most important species in the diet of Subantarctic fur seals, *G. bolini* significantly occurred in most of the scats at the 1% level when species were compared by %FO both seasonally and inter-annually over the entire study period (Tables 5.1 and 5.2). All the findings since the diet monitoring started in 1989 were linked with mean sea surface temperature. For example, there was an increase in SST towards the end of the second period (from 1998 to 2000) (Table 5.3). When comparing the three study periods, period 1 (April 1989 – March 1995) and period 3 (April 2000 – March 2006) were almost similar in mean sea surface temperature. But study period 2 (April 1995 – March 2000) was different from period 1 and 3 in terms of both %NA (Fig. 3.2) and SST (Table 5.3).

Table 5.1 Relative means percentage frequency of occurrence (%FO) of the five most important prey species in different years taken by the Subantarctic fur seals at Marion Island from April 2000 - March 2006 (a year starts in April and ends in March of the following year).

Species	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**
	Mean ± SD	**Mean ± SD**	**Mean ± SD**	**Mean ± SD**	**Mean ± SD**	**Mean ± SD**
G. bolini	65 ± 0.48	70 ± 0.46	66 ± 0.48	71 ± 0.46	61 ± 0.49	71 ± 0.45
G. fraseri	43 ± 0.50	35 ± 0.48	53 ± 0.50	52 ± 0.50	61 ± 0.49	38 ± 0.49
G. nicholsi	57 ± 0.50	62 ± 0.49	56 ± 0.50	54 ± 0.50	62 ± 0.49	44 ± 0.50
G. piabilis	66 ± 0.48	65 ± 0.48	60 ± 0.49	32 ± 0.47	31 ± 0.47	47 ± 0.50
P. tenisoni	30 ± 0.46	46 ± 0.50	0.07 ± 0.25	03 ± 0.16	18 ± 0.39	12 ± 0.33

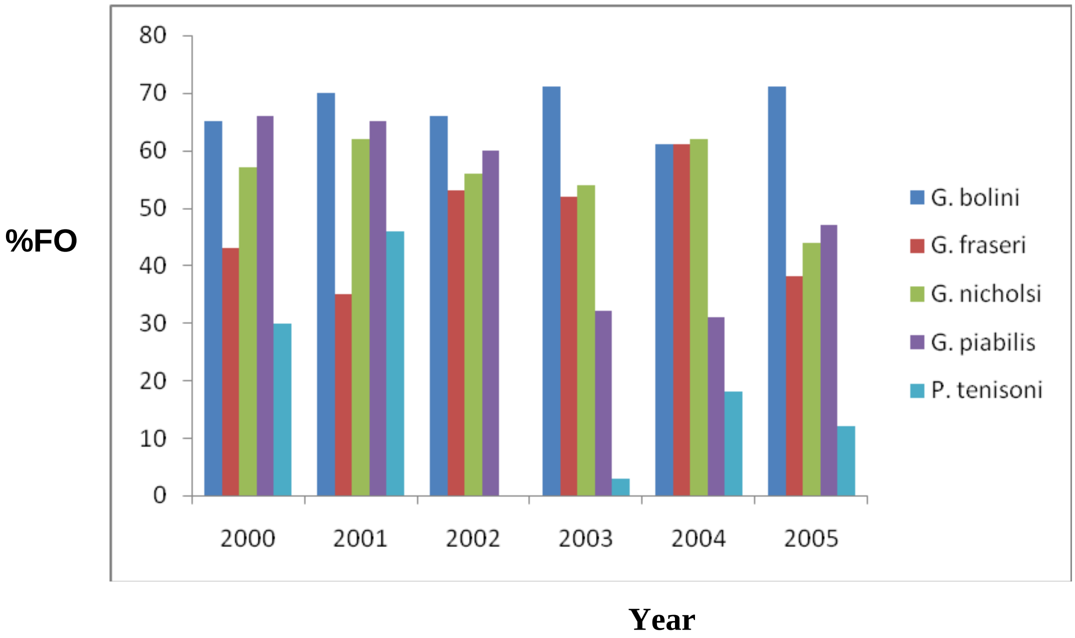


Figure 5.1 Inter-annual relative means percentage frequency of occurrence (%FO) of the five key prey species taken by the Subantarctic fur seals at Marion Island from April 2000 – March 2006 (a year starts in April and ends in March of the following year).

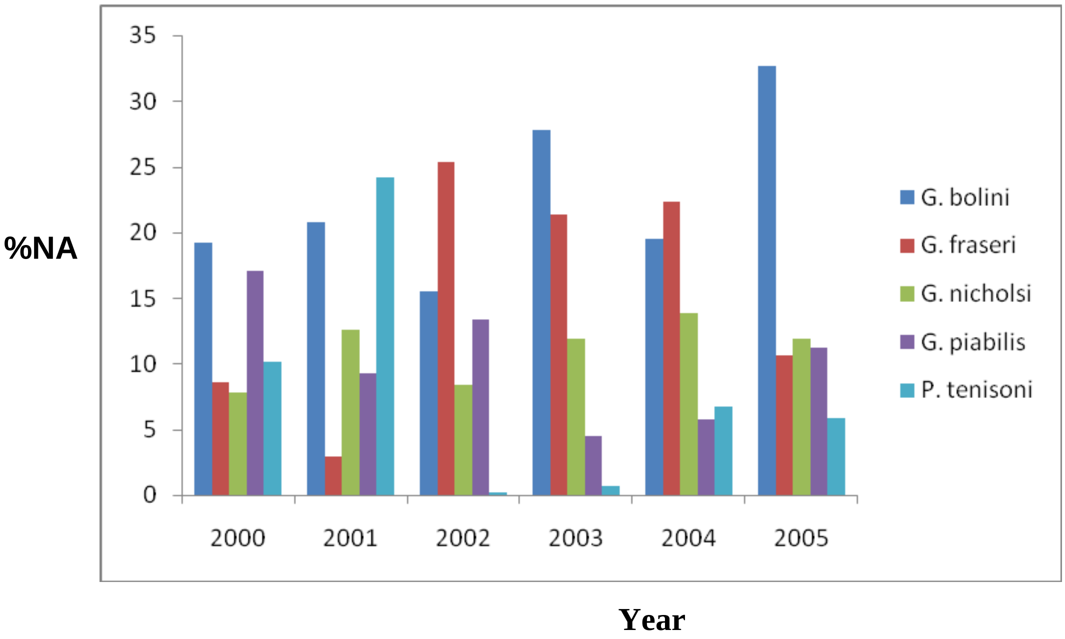


Figure 5.2 Inter-annual relative means percentage numerical abundance (%NA) of the five key prey species taken by the Subantarctic fur seals at Marion Island from April 2000 – March 2006 (a year starts in April and ends in March of the following year)

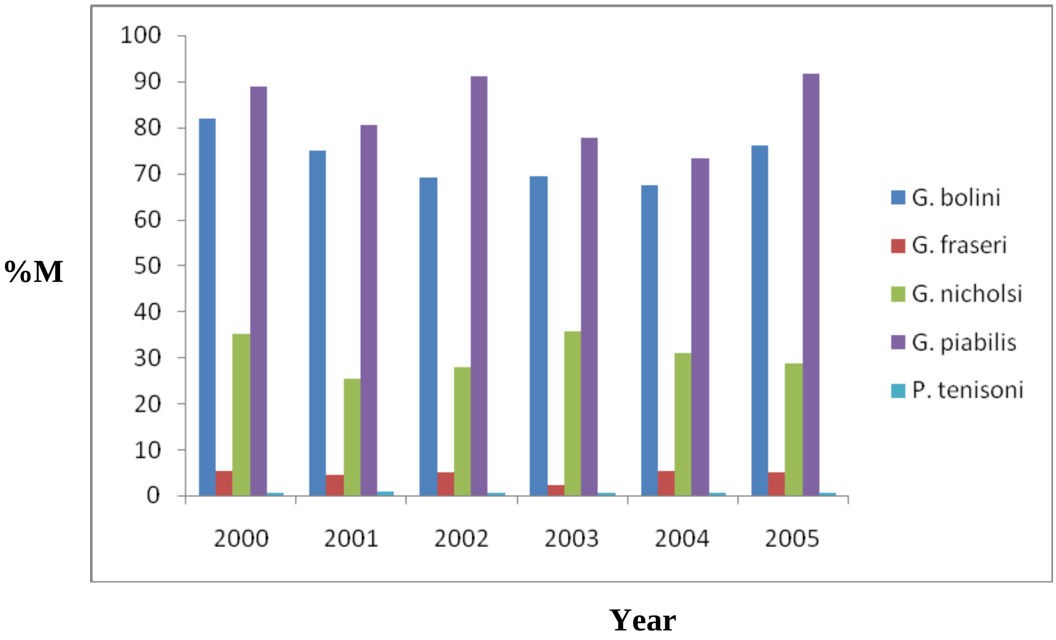


Figure 5.3 Inter-annual variation in relative mean mass of the fish prey species taken by Subantarctic fur seals at Marion Island from April 2000 - March 2006 (a year starts in April and ends in March of the following year)

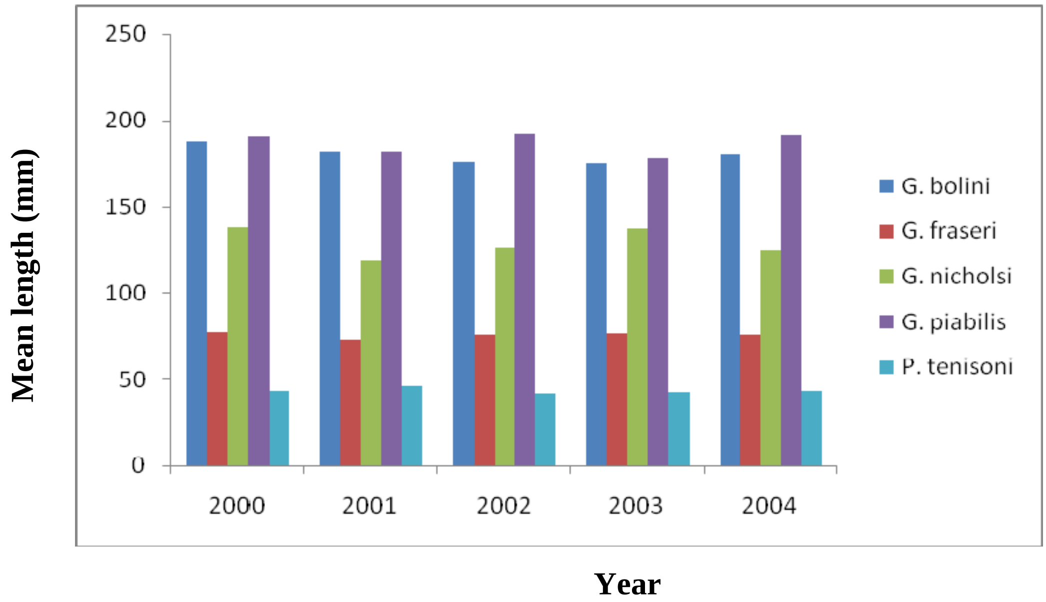


Figure 5.4 Inter-annual variation in mean length of the five key prey species taken by Subantarctic fur seals at Marion Island from April 2001 - March 2006 (a year starts in April and ends in March of the following year).

Table 5.2 Inter-annual relative percentage of occurrence (%FO) of the main prey species of Subantarctic fur seal at Marion during study period 2 (April 1995 – March 2000) and present study (April 2000 – March 2006), (a year starts in April and ends in March of the following year).

Species	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**
G. bolini	15	32	31	15	65	70	66	71	61	71
G. fraseri	69	66	48	47	43	35	53	52	61	38
G. nicholsi	10	22	15	18	57	62	56	54	62	44
G. piabilis	66	73	69	68	66	65	60	32	31	47
P. tenisoni	0.03	0	0	0.1	30	46	0.07	03	18	12

Table 5.3 Inter-annual Mean Sea Surface Temperature (SST) at Marion Island since the diet monitoring studies started (from 1989 – 2005).

Year	**Mean**	**SD**	**Minimum**	**Maximum**
1989	5.4	1.15	3.6	8.1
1990	5.8	0.89	4.3	7.4
1991	5.8	1.01	4.2	8.5
1992	5.4	1.08	2.8	7.2
1993	5.5	0.91	3.7	6.9
1994	5.5	1.13	3.0	8.1
1995	6.0	1.06	4.0	7.9
1996	6.1	1.10	4.2	8.7
1997	6.6	1.13	4.8	9.6
1998	8.4	1.93	4.9	13.8
1999	7.7	0.96	5.3	12.8
2000	8.6	2.55	5.2	14.9
2001	6.3	1.11	4.3	8.5
2002	5.4	0.89	3.7	8.0
2003	5.5	1.10	3.7	7.4
2004	5.91	0.58	4.0	7.1
2005	5.3	0.94	2.8	7.2

Discussion

Inter-annual variation in pinniped diets is generally assumed to reflect changes in prey abundance and encounter rates (Bowen *et al.* 2006). Although there were some inter-annual variations among the main prey species during this study period, in most instances there were no statistical differences amongst their relative abundances. The year 2000 seemed to be very different from all other years, perhaps due to the contribution of *Krefftithys anderssoni* and *Gymnoscopelus piabilis*. The two species during that year were more important than in any other years, with *K. anderssoni*'s contribution in the subsequent years negligible. Furthermore *P. tenisoni* was most important during 2000 and 2001, where its %NA in 2001 was the highest compared to any other species.

During this study, Subantarctic fur seals preferred *G. bolini* over any other prey species. This coincided with lowest abundance in *G. fraseri* and reduction in *G. piabilis*, which suggests that *G. fraseri*'s recruitment was not effective or else it was over utilized by Subantantarctic fur seals and other marine predators during that year or in the preceding years. However, it must be taken into consideration that the sample size during the present study period was considerably higher (806 scats, Table 3.1) compared to the previous study periods (P1 = 245 scats and P2 = 213 scats) (Tables 3.5 and 3.6). Although *G. piabilis* in terms of body size (relative mean mass and mean length) was larger than that of all the main prey species, followed by *G. bolini*, it occurred in fewer scats and in fewer numbers. The presumed increased effort to catch this prey species (due to its distribution which might make it difficult for Subantarctic fur seal to access, low density of this species in the foraging grounds of Subantactic fur seal, or higher swimming speed of this prey species) might be responsible for the lower %FO of this prey species. Unfortunately, no information is available on the distribution pattern of *G. piabilis*. Interestingly, when Subantarctic fur seals take more of *G. bolini*, *G. fraseri* was low in terms of %NA and vice versa. This implies that when there is less of the larger *G. bolini* in the Subantarctic fur seal's foraging grounds, the predator shifts to smaller, probably schooling *G. fraseri* in order to meet its dietary needs. The same pattern was also noticed between *G. bolini* and *G. piabilis*. This suggests that Subantarctic fur seals indeed select its prey.

In addition, Mecenero *et al.* (2006b) found that the annual consumption estimates for the Cape fur seal diet varied greatly and this is expected to reflect life-history patterns of some of the prey, or changes in prey distribution and abundance in response to fluctuating environmental conditions of the Benguela ecosystem. Other environmental factors that also influence distribution of fish prey species of Subantarctic fur seals at Marion Island include, for example, the effects of El Niño during 1997 and 1998 which were responsible for the rise in temperature during the second study period (between 1995 and 2000) around Marion Island (Table 5.3). Consequently, changes in this environmental variable seemed to have influenced prey availability and distribution. This is in accord with the rise in temperature from 5.5ºC in 1994 to 8.6ºC in 2000.

Chapter 6

Conclusions

In the present study two standardized measures, i.e. percentage numerical abundance (%NA) and percentage frequency of occurrence (%FO) were used to determine the relative diet composition and temporal variation in the diet of the Subantarctic fur seal at Marion Island. However, it must be borne in mind that the sample size was not large enough (only 804 scats were collected over a five year period from April 2000 to March 2006) for reliable diet analysis and to readily detect possible interannual and seasonal variation in the diet, inadequate sample size influencing the statistical power of comparisons (Trites & Joy 2005).

The diet of the Subantarctic fur seal was diverse during the present study period (April 2000 – March 2006), with mesopelagic fish species constituting the bulk of the diet. These mesopelagic fish prey species were dominated by the genus *Gymnoscopelus*, i.e. *G. bolini*, *G. piabilis*, *G. fraseri* and *G. nicholsi*. The other well represented genus in the diet of the Subantarctic fur seal was *Protomyctophum*, which comprised *P. tenisoni*, *P. choriodon* and *P. bolini*. Out of these, five prey groups were identified as the primary prey of the Subantarctic fur seals, i.e. *P. tenisoni* and the four *Gymnoscopelus* species. Cephalopod remains occurred in low number in the scats of the fur seals throughout the study period. Furthermore, remains from other prey taxa e.g. crustacean hard parts were not present in the collected scats.

During the present study distinct seasonal variations were recorded in the diet of the Subantarctic fur seals between early summer (E. summer) and late summer (L. summer). This variation probably occurred as a result of huge increase in abundance of *P. tenisoni* and *G. fraseri* in E. summer, and rapid decrease during L. summer, with *G. nicholsi* and *G. piabilis* showing an opposite trend.

There were some inter-annual variation in terms of relative %NA during 2000. The five main prey species contributed almost the same in the diet of the Subantarctic fur seal. Statistical analysis could not detect significant difference amongst the contributions (%NA) of the five main prey species, except that Subantarctic fur seals took a similar amount of *Krefftichthys anderssoni* to each of the five main prey species, which made the year 2000 to be remarkably different from other years (2001 – 2006). Subantarctic fur seals seem to take *G. bolini* more often than any other species throughout the study period.

The current study attempted to compare different study periods at Marion Island since the diet monitoring started in 1989. Apparently the diet composition did not change significantly throughout the three study periods. The importance of the main prey species at Marion Island were similar for period 1 (1989-1995) and during the present study (2000-2006). Nevertheless, during period 2 (1995-2000) the importance of the main prey species appeared to have changed. One possible factor which could have influenced this variability is fluctuations in the positions of the Subantarctic Front (SAF) and Antarctic Polar Front (APF) which are thought to have critical implications for the island systems with which they come into contact, as this in turn influence the surrounding sea surface temperature (SST). SST is highly correlated with other physical variables such as air temperature and sea ice extent, hence it is considered to be a good indicator of the connectivity of environmental variability (Forcada *et al.* 2005). However, in the present study we did not explore the variability of diet composition simultaneously with environmental factors which are thought to influence the distribution of prey species. Moreover, the foraging grounds of the Subantarctic fur seals at Marion Island are not fully known as yet. So future research should consider describing the at-sea distribution and foraging effort of lactating Subantarctic fur seals from Marion Island on a long-term basis, taking cognisance of changing oceanography and prey availability within their foraging areas which are likely to be situated between the APF and the SAF.

The possibility of using marine top predators as oceanographic indicators in the Subantactic region needs to be extensively investigated. One cannot ignore the use of molecular scatology in diet studies, as this can provide new insight into the diet of top predators at Marion Island. Furthermore, employing genetic methods has obvious benefits in cases where soft-bodied prey or prey with fragile bones is suspected to be an important part of the diet (Deagle *et al.* 2005).

The present study mainly represents the diet of lactating female fur seals that nurse their pups for about 300 days. However, diet is also known to vary with age amongst pinniped species. This could imply that the diets of newly weaned or juvenile seals generally differ from those of adults of the same species (Riedman 1990). Therefore, future diet investigations at Marion Island should attempt to compare the diet of different age and sex classes of Subantarctic fur seals.

This study reports that mesopelagic fishes form the major components of the diet of Subantactic fur seals at Marion Island. However, details of the interaction between mesopelagic fishes and their predators are still not well-known (Ohizumi *et al.* 2003; this study). I therefore suggest that a multidisciplinary study examining the myctophids predator-prey relationship at Marion Island is needed to determine whether the foraging behaviour and consequent energy acquisition of Subantarctic fur seals, in particular lactating females, is responsive to changes in environmental conditions.

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