Foraging ecology of the gentoo penguin, *Pygoscelis papua*, at Marion Island

By

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General Abstract

The distribution and subsequent availability of marine predators' prey is highly variable and is linked to fluctuating oceanographic parameters. It is well documented that annual breeding success of seabirds is related to the temporal availability of prey. Knowledge of a seabird's diet and at sea distribution is therefore critical in deducing the effect of a fluctuating environment on a seabirds' population and, furthermore, to understand seabirds role in the environment.

The gentoo penguin population at sub-Antarctic Marion Island experienced a decline of 52% between 1994 and 2012. It has been speculated that long term changes in the local marine environment, due to a southward shift of the sub-Antarctic Front (SAF), and subsequent changes in prey availability is the ultimate causal factor. Therefore, this thesis investigates the temporal variation in the diet these birds over three years, through the use of stomach content samples. It then investigates whether the composition of the diet has changed over the long term (approximately 18 years). Additionally, the at sea distribution of these birds was investigated using temperature-depth recorders (TDRs) and global positioning system (GPS) devices. This study represents the first to investigate variation in the diet over three years and over the long term. It is also the first study to track these birds fine scale movement.

Over three years, the diet exhibited a high degree of variability. The birds primarily foraged on the fish, *Lepidonotothen larseni* and the crustaceans, *Nauticaris marionis* and *Euphausia vallentini*y. Over three years, *L. larseni* became increasingly more important during the breeding season. This was attributed to an increase in availability of these fish during this time, as this time corresponded to the transition of these fish from the larval pelagic phase to the benthic adult phase. Furthermore, the proportions of *N. marionis* and *E. vallentini* in the diet varied significantly among years. This variation is possibly a result of the highly variable latitudinal position of the SAF. The diet changed over the long term. There was significantly less *N. marionis* and more *E. vallentini* in the diet during more recent years. The long term southward shift of the SAF is considered to be a leading cause of these significant changes in the diet.

The shallow inter-island shelf between Marion and Prince Edward Island was an important foraging area possibly due to predictable prey resources. In addition, these birds exhibited an important and possibly unique foraging strategy. They performed short self-maintenance trips where after they return to land to roost for the night. The following day these trips were followed by a longer foraging trip that was followed by chick provisioning. This strategy is unique among seabirds longer trips are associated with self-maintenance and not chick provisioning.

This study has provided important knowledge of the foraging ecology of the gentoo penguin at sub-Antarctic Marion Island. It highlights the necessity for continuation of diet and tracking studies of these birds if we are to fully understand the ultimate factors that are causing the decline in their breeding success and population numbers.

Gentoo penguin, Marion Island, foraging, diet, GPS, TDR, self-maintenance, chick provisioning

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Declaration

I, Tegan Carpenter-Kling, 214236447, hereby declare that the thesis for Master of Science to be awarded is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

Tegan Carpenter-Kling

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Chapter 1

General introduction

1.1. Foraging theory

Animals forage to meet the energy requirements needed to maintain vital functions and support physiological and physical activities (Spitz et al. 2012). Optimal foraging theory predicts that the foraging behaviour of a species is a product of natural selection that has evolved to promote fitness (Emlen 1966; MacArthur & Pianka 1966). All animals forage selectively and make decisions, such as, how far to travel and what to eat (Stephan & Krebs 1986). Optimal foraging theory predicts that these decisions shape the foraging behaviour of animals and are made to maximize energy gain per unit time. Therefore, animals should show preference for prey items that are most energetically profitable and only consume less profitable items in situations where more profitable prey are not available (Stephan & Krebs 1986). In essence, during periods when prey is scarce, animals should be less selective in their diet compared to periods when prey is abundant.

During the breeding season, many animals such as seabirds are central place foragers, returning to a central location after foraging to provide for young (Orians & Pearson 1979; Ropert-Coudert et al. 2004). As an extension of optimal foraging theory, central place foraging theory predicts that foraging behaviours have evolved in such a way as to increase their fitness by maximizing the rate at which energy is delivered to young (Orians & Pearson 1979). Moreover, life history theory predicts that while breeding, resources are to be allocated between reproduction and body maintenance to ensure survival (Stearns 1976). Consequently, there is a high energy demand on seabirds while breeding. They must be able to maintain a good body condition, regularly provide and care for a brood and, retain energy stores for periods of fasting (e.g. incubation; Furness & Camphuysen 1997; Pinaud & Weimerskirch 2002). Therefore, the temporal and spatial separation between foraging areas and breeding ground imposes an important energetic constraint (Pinaud &

Weimerskirch 2002; Ropert-Coudert et al. 2004; Miller et al. 2010). By maximizing the rate at which energy is delivered to young, the foraging range of parent seabirds is limited. This increases their dependency on local marine resources thus making them particularly sensitive to fluctuation in their marine environments.

1.2. Seabirds

Seabirds are important predators in the marine environment, annually consuming almost 70 million tons of prey from the oceans (Brooke 2004). Their diet represents an important link between themselves and the biotic and abiotic features in their environment (Karnovsky et al. 2012). Thier diet is often confined to a narrow range of trophic levels, mainly consisting of large zooplankton, fish and cephalopods (Quillfeldt & Masello 2013). The distribution and subsequent availability of these prey items is temporally and spatially heterogeneous (Cheung et al. 2009) and it is shaped by biological and physical conditions which are particularly sensitive to fluctuations of physical oceanographic parameters (Pinaud & Weimerskirch 2002; Cheung et al. 2009). This variability is subsquently reflected in their diet and foraging behaviour (Pinaud & Weimerskirch 2002; Baylis et al. 2015).

Seabirds are long lived, have high survival rates, low reproductive rates and deferred maturity (Furness & Camphuysen 1997). Body condition plays a large role in determining allocation of resources towards self-maintenance or chick provisioning (Stearns 1976; Clarke 2001; Ropert-Coudert et al. 2004). When prey availability is insufficient to meet the energy demands faced while breeding, seabirds will favour self-maintenance over chick provisioning leading to a low annual breeding success (Pinaud & Weimerskirch 2002; Frederiksen et al. 2006). As such, annual breeding success (i.e. number of chicks fledged per breeding pair) and population size of seabirds has been strongly correlated with prey availability (Cairns 1988; Bost et al. 1994a; Weimerskirch et al. 2003; Piatt et al. 2007). This often relates to annual fluctuations in breeding population size and success (Cury et al. 2011). This flexibility in annual breeding performance is a trait of seabirds that buffers them against natural cycles and anomalies of physical oceanographic parameters that affects the availability of their prey in their environment (Cury et al. 2011). However, chronic prey scarcity will result in long term low breeding success and negative population growth (Cury et al. 2011).

Understanding the foraging strategies, diet and distribution of a seabird species is fundamental to make inferences of environmental influences on seabird demographics (Pinaud & Weimerskirch 2002; Miller et al. 2010). As recommended by Croll et al. (1998), there are six different types of data that can be used to understand the foraging behaviour of seabirds. (1) The distribution and abundance of the seabird at different spatial and temporal scales, (2) movement of individuals at different temporal scales, (3) either knowledge of regional oceanography or congruent oceanographic sampling, (4) prey availability data, (5) diet of seabirds and (6) fitness measures of foraging success such as growth, survival and breeding success. While any one of these datasets will increase the understanding of seabird foraging ecology, a combination of datasets, that are collected congruently, will be the most rewarding (Duffy & Jackson 1986; Croll et al. 1998). Furthermore, data collection concerning demographics (e.g. Crawford et al. 2003b), foraging distribution (e.g. Baylis et al. 2015) and diet (e.g. Lescroël et al. 2004) of seabirds is greatly facilitated by their annual breeding aggregations on land and high site fidelity (Furness & Monaghan 1987; Monaghan 1996; Piatt et al. 2007).

Through the use of techniques such as: fatty acid analysis (e.g. Iverson et al. 2007), stable isotopes (e.g. Forero et al. 2005) and stomach content samples (e.g. Lescroël & Bost 2005), dietary studies of seabirds have become useful to identify temporal and spatial availability of prey items in the marine environment. However, dietary studies are limited in that they only reflect presence, absence and relative abundance of prey species rather than absolute abundance (Cairns 1988). Furthermore, the extent to which a seabird's diet can reveal information about its environment is dependent on its foraging behaviour and at sea distribution (McCafferty et al. 1999; Iverson et al. 2007). Alternatively, variations in diet may not be a reflection of prey availability. Rather variability may be a reflection of seabirds actively selecting prey with a higher calorific content to compensate for high energy demands during breeding (Williams et al. 1992; Robinson & Hindell 1996).

The miniaturization of tracking instruments through advanced technology has allowed for major advances in tracking the fine scale movement of animals (Cairns 1988; Croll et al. 1998; Grémillet et al. 2004). Devices such as global positioning systems (GPS) are capable of accurately recording spatial and temporal at sea distribution of seabirds, providing important information about their habitat use. When coupled with a temperature-depth recorder (TDR), one gains further understanding into the vertical use of the water column and surrounding environmental characteristics. Therefore, when these devices are deployed concurrently they provide inference about movement which can reflect foraging tactics or behaviours seabirds use in searching for and pursuing prey.

1.3. Study species: gentoo penguin, *Pygoscelis papua*

Figure 1.1. Gentoo penguins guarding chicks at sub-Antarctic Marion Island.

The gentoo penguin, *Pygoscelis papua*, ranges in height from 51-90cm (BirdLife International 2015). It is characterized by black flippers, back and head and white ventral side with characteristic triangular white patches above each eye which often meets on top of the head, and bright orange feet and markings on the bill (Figure 1.1.; BirdLife International 2015). The gentoo penguin is one of the most widespread penguin species owing to its circumpolar distribution, with breeding colonies occurring from the Antarctic Peninsula (65°S) to sub-Antarctic islands (45°S; Bost & Jouventin 1990; Lynch 2013). They breed at fourteen localities worldwide, namely, the Falklands, Staten, Marion, Prince Edward, Heard and McDonald, Macquarie, Kerguelen, Crozet, South Georgia, South Shetland, South Orkney and Sandwich Islands and on the Antarctic Peninsula (Figure 1.2.; Stonehouse 1970; de Dinechin et al. 2012). It is defined as a morphologically single species but is divided into two sub-species, the larger *P. papua papua* which breeds on sub-Antarctic islands at latitudes less than 60°S and the smaller *P. papau ellsworthi* which breeds at the Antarctic Peninsula and its surrounds

(Stonehouse 1970; Bost & Jouventin 1990). However, the current division of the sub-species, which is based on morphology, is unsupported by genetic analysis (de Dinechin et al. 2012). This thesis will focus on the gentoo penguins inhabiting Marion Island at the Prince Edward Island Archipelago (PEIs), a sub-Antarctic colony.

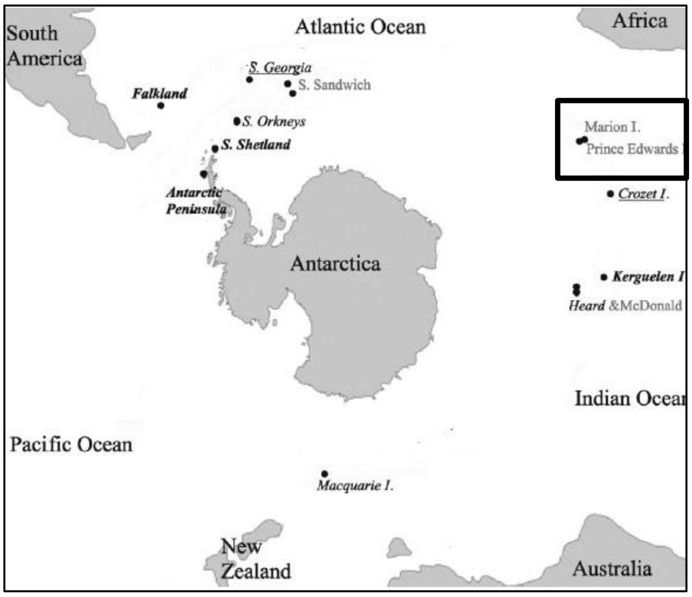

Figure 1.2. Global distribution of gentoo penguins. Figure adopted from de Dinechin et al. (2012).The Prince Edward Island Archipelago is highlighted by the black box.

Compared to other penguin species, the gentoo penguin’s global population is generally small, estimated to include approximately 387 000 breeding pairs, of which the Falklands and South Georgia Islands and the Antarctic Peninsula currently holds approximately 80% of the world’s population (Lynch 2013). Although some colonies are stable or increasing, the gentoo penguin is listed on the IUCN red list as “Near Threatened” (BirdLife International 2015). However this status has been suggested to be unwarranted owing to the fact that the global gentoo penguin population has been stable or increasing over the past two decades (Lynch 2013).

Throughout their distribution gentoo penguins are considered diurnal, inshore foragers feeding over the continental shelf regions (Croxall et al. 1988; Tanton et al. 2004; Lescroël & Bost 2005). While their foraging range is variable across localities, these birds rarely exceed foraging ranges of more than 30km during the breeding period (Croxall et al. 1988; Tanton et al. 2004; Lescroël & Bost 2005) and may retain their inshore foraging ranges or forage further offshore during the non-breeding period (Clausen & Pütz 2003). This limited, inshore foraging during the breeding period makes them highly dependent on the local marine environment (Bost & Jouventin 1990; Clausen & Pütz 2003; Lescroël et al. 2004). To help buffer this dependency they exhibit plasticity in foraging behaviour and are characterized by being opportunistic foragers, often adjusting foraging behaviours to forage for different prey (Lescroël & Bost 2005) which is evident in their diets (Adams & Klages 1989; Clausen & Pütz 2002; Lescroël et al. 2004). Typically, gentoo penguins are benthic-demersal foragers (e.g. Croxall et al. 1988; Wilson et al. 1996; Kokubun et al. 2010), searching the ocean floor for prey (Takahashi et al. 2008) but also foraging on pelagic prey (Bost et al. 1994b; Reid et al. 2005).

1.4. Gentoo penguins at sub- Antarctic Marion Island

This thesis focuses on the gentoo penguins that populate the sub-Antarctic Marion Island (46°54’S, 37°45’E) of the Prince Edward Island Archipelago (PEIs). The PEIs are classified as a special nature reserve, in terms of Section 18 of the Environment Conservation Act 1989 (Act 73 of 1989). Entry to the islands is only permitted for scientific, managerial and other legitimate purposes (Prince Edward Islands Management Plan Working Group 1996). Additionally, since December 2004 the islands have been surrounded by a no fishing zone of 12 nautical miles which prohibits any type of fishing activity (Lomard et al. 2007). The gentoo penguin is one of four penguin species that breed at Marion Island; the other three species being: the southern rockhopper, *Eudyptes chrysocome filholi*; macaroni, *E. chrysolophus* and king, *Aptenodytes patagonicus,* penguins. This is a relatively small gentoo penguin population, consisting of approximately 700 breeding pairs (Crawford et al. 2014). When compared to gentoo penguins at other localities, the breeding season of this population is extended and relatively asynchronous (Bost & Jouventin 1990; Crawford et al. 2014). Initiating breeding during the austral winter at two to three years of age (Bost & Jouventin 1990; Crawford et al. 2003b), chick rearing is shared between parents and can be separated into three distinguishable periods: (1) incubation (2) brooding, guarding chick(s) and (3) crèche, chicks are left alone within a crèche of other chicks while parents forage (Williams 1990; Croxall & Davis 1999). Eggs are laid between mid-June and mid-July, with hatching occurring 35-40 days later. Crèches begin forming from beginning to mid-September and fledging occurs approximately a month later (Crawford et al. 2003b).

Over 18 years (1994-2012) the average breeding success of 0.45 chicks fledged per breeding pair of gentoo penguins at Marion Island has been insufficient to maintain a stable population (Crawford et al. 2003b, 2014). This has resulted in a long term decline in population size, with approximately 52% less breeding pairs on the island during 2012 compared to 1994 (Crawford et al. 2014). Furthermore, the breeding success of these gentoo penguins fluctuates largely from year to year and has been correlated to the date that breeding commences during that respective year (Crawford et al. 2014). The later the onset of breeding, the lower the breeding success is that year. This trend is also evident for the gentoo penguin population at Crozet Island (45° 50′ S, 51° E; Bost & Jouventin 1990). At Marion Island, this correlation has been attributed to eggs and small chicks still being present when the predatory sub-Antarctic Skua, *Catharacta antarctica*, returns to the island in the summer (Bost & Jouventin 1990; Crawford et al. 2003b).

Additional factors are also believed to be partly driving the long term decline and fluctuating annual breeding success. These include: (1) failure to feed and fledge chicks due to decreased prey availability (Crawford et al. 2003; Crawford et al. 2014), (2) reduced survival of young breeders (Williams 1991, Crawford et al. 2014), (3) breeding failure due to inexperience of first time breeders (Williams 1990), (4) adult mortality (Williams and Rodwell 1992), (5) poor annual recruitment of breeding adults during to adults not breeding in successive years (Williams and Rodwell 1992; Crawford et al. 2003), (6) disturbance by humans that either cause failure of breeding attempts or prevent birds from breeding (Crawford et al. 2003; Crawford et al. 2014) and (7) birds moving between colonies (Williams and Rodwell 1992; Crawford et al. 2003). However, different gentoo penguin breeding colonies across the island tend to follow similar fluctuations in annual breeding success (Crawford et al. 2003; Crawford et al. 2014). This suggests ultimate factors, such as changes in local prey availability and extreme weather events may be driving the long term decline in population size (Crawford et al. 2003; Crawford et al. 2014). Which is likely as the breeding success of gentoo penguins at South Georgia (54°25', 36°35'E) was found to be significantly correlated with annual prey availability (Reid et al. 2005). Furthermore, annual fluctuation of breeding commencement date and success and an extended breeding period are typical of a species that are dependent on fluctuating prey availability (Bost & Jouventin 1990; Williams & Croxall 1991; Lescroël et al. 2009). For example, Artic Terns, *Sterna paradisaea*, at the Shethland Islands lay eggs earlier in the season if their primary prey sandeels, *Ammodytes marinus*, become more readily available earlier (Suddaby & Ratcliffe 1997).

Further evidence to substantiate changes in prey availability at Marion Island can be seen in the population of Crozet Shags, *Phalacrocorax [Atriceps] melanogenis*. These birds have congruent annual fluctuations in breeding population and success, with the same general declining trend as the gentoo penguin population at the island (Crawford et al. 2014). Both of these seabirds are thought to be inshore foragers at the PEIs and exhibit considerable amount of overlap in diets (Espitalier-Noël et al. 1988; Adams & Klages 1989; Crawford et al. 2003a). Furthermore, the rockhopper penguins, that forage predominantly inshore during the breeding season, and macaroni penguins, that forage both inshore and offshore during the breeding season, have also been experiencing long term population declines (Brown 1987; Brown & Klages 1987; Crawford et al. 2009). While the breeding populations of seabirds that predominantly forage offshore remain stable or increasing (light-mantled sooty albatross, *Phoebetria palpebrata*, wandering albatross, *Diomedea exulans*, southern giant petrel, *Macronectes giganteus* with the exception of the sooty albatross (*P. fusca*; Ryan et al. 2009).

Previously, the diet of the gentoo penguin at Marion Island has been studied twice (La Cock et al. 1984; Adams & Klages 1989). Their diet was shown to have significant variability throughout the year (Adams & Klages 1989). Crustaceans dominated the diet during the beginning of the year from March to June, whereas fish dominated the diet from June to October (La Cock et al. 1984; Adams & Klages 1989). The species that made up the crustacean component also varied. The benthic crustacean, *Nauticaris marionis*, dominated from March to September, and then a pelagic crustacean, *Euphausia vallentini,* dominated from October to February the following year. The switch from crustacean to fish coincided with peak egg laying and it was inferred that the birds were selecting prey with higher energetic content due to higher energy demands during this time (Adams & Klages 1989).

The at sea distribution of the gentoo penguin at Marion Island has, however, only been studied once, with the use of speedometers to record travelling speed and time (Adams & Wilson 1987). Birds that foraged on benthic crustaceans tended to travel shorter distances, suggesting that foraging behaviour mimicked the restricted distribution of *N. marionis* around the island. The time spent travelling and the estimated distance that was reached away from the colony was dependant on colony location on the island (Adams & Wilson 1987). This suggests that the concentration of gentoo penguin colonies on the eastside of Marion Island may be a consequence of favourable foraging conditions present by the shallow water between Marion Island and Prince Edward Island (Adams & Wilson 1987).

1.5. Oceanographic setting of sub-Antarctic Marion Island

The Antarctic Circumpolar Current (ACC) plays a prominent role in structuring ecosystems within the Southern Ocean. Lying in the direct path of the ACC are the PEIs comprising of two islands approximately 19km apart: Marion Island (240km^2) and Prince Edward Island (45km^2; Lutjeharms 1985). They are positioned in the Indian sector of the Southern Ocean (Lutjeharms 1985). The Antarctic Polar Front (APF) and the sub-Antarctic Front (SAF) are located to the south and north of the islands, respectively, and are separated by a transition zone called the Antarctic Polar Frontal Zone (APFZ; Ansorge & Lutjeharms 2002). Ascending from a depth of 3000m, the islands are separated by a shallow inter-island shelf that ranges from 40m to 200m in depth (Figure 1.3.;

Pakhomov et al. 2000; Ansorge & Lutjeharms 2002). Due to the shallow topography, the PEIs act as an obstacle to the ACC resulting in a unique oceanographic and biological marine environment (Froneman et al. 1999).

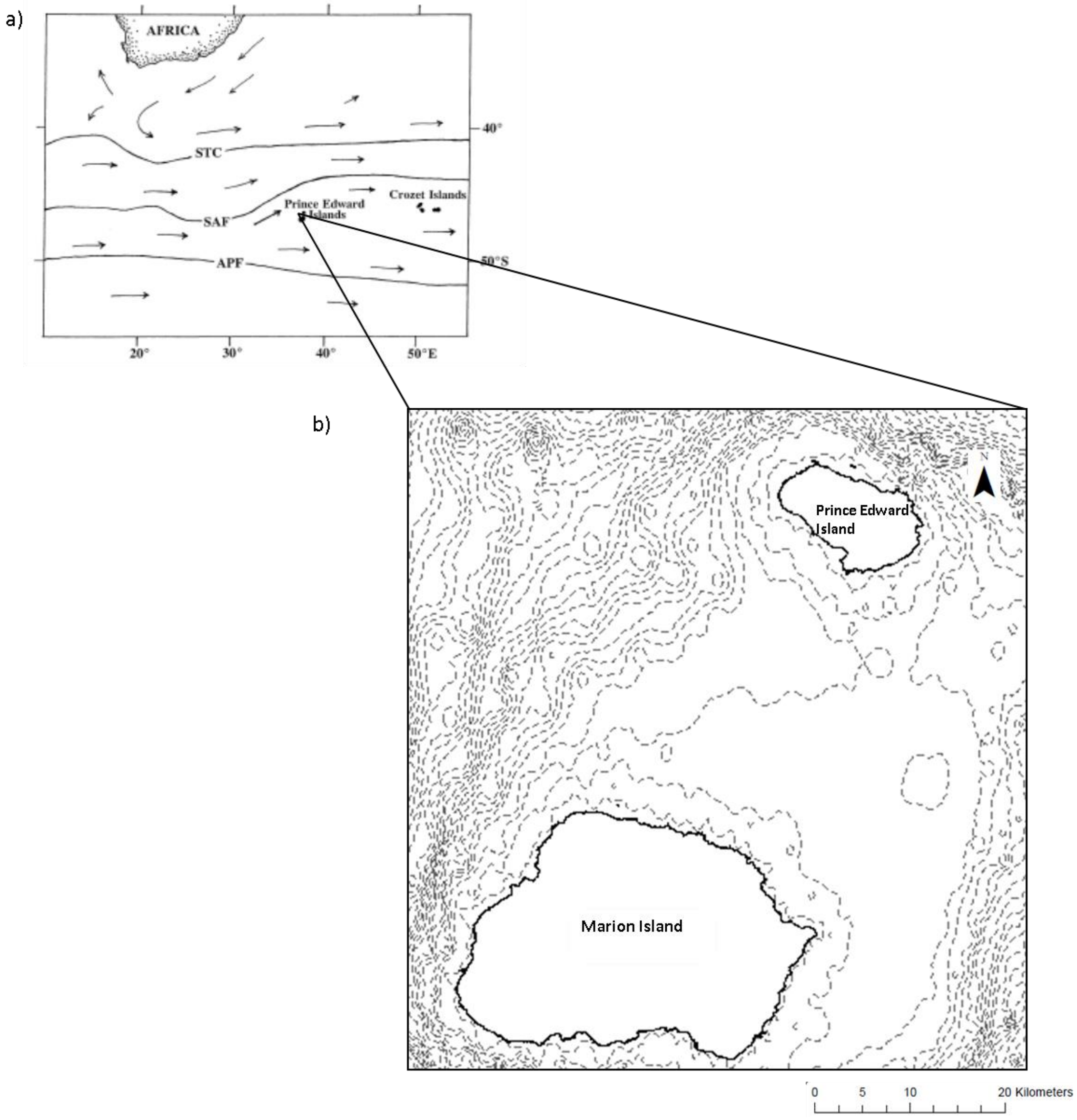

Figure 1.3. a) The position of the Prince Edward Archipelago in relation to the average position of the Antarctic Polar front (APF), the sub-Antarctic polar front (SAF) and the Subtropical Convergence (STC; figure adopted from Pakhomov et al. (1999)) and b) local bathymetry surrounding Marion and Prince Edward Islands. Dashed lines indicate isobaths at 100m intervals.

The macro- and meso- scale oceanographic environments surrounding the island group are strongly influenced by the geographical position of the SAF which varies considerably in latitude (Perissinotto et al. 2000; Ansorge & Lutjeharms 2002; Ansorge et al. 2009). When the SAF lies further to the north of the islands, the flow rate of the ACC in proximity to the islands is relatively slow and allows for formation of anti-cyclonic eddies that become trapped on the shallow inter-island shelf (Perissinotto & Duncombe Rae 1990; Ansorge & Lutjeharms 2002). Furthermore, macronutrients, resourced mainly from guano and moulted remains of land-based marine predators, are transported into the surrounding waters via freshwater runoff (Perissinotto & Duncombe Rae 1990). The resulting retention of freshwater runoff and increased water column stability promotes the development of phytoplankton blooms, a phenomenon known as the "island mass effect" (Perissinotto & Duncombe Rae 1990). This phenomenon provides an important autochthonous food source for the benthic community within the inter-island shelf (Perissinotto & McQuaid 1992; Pakhomov & Froneman 1999a). A study conducted by Kaelher (2000a) provided evidence that this autochthonous source of macronutrients, is an important dietary component within the zookplankton community at PEIs, including the diet of *N. marionis*, which has historically been found to be an important component of the gentoo penguin's diet (Adams & Klages 1989).

In contrast, when the SAF lies further south, in closer proximity to the island group, there is an intensification of flow rates resulting in a flow through system. Thus, there is prevention of both eddy formation and maintenance on the inter-island shelf and development of phytoplankton blooms (Perissinotto et al. 2000; Ansorge et al. 2009). During times when the SAF is in close proximity to the islands, allochthonous prey species, such as the crustacean *E. vallentini,* become an increasingly important food source to marine predators (Perissinotto & McQuaid 1992; Kaehler et al. 2000). Notably too, is the lower allochthonous macrozooplankton biomass and size which have been recorded during times when the SAF lies further away from the island group compared to when the SAF lies in close proximity (Hunt & Pakhomov 2003).

Climate change models have shown that, in response to climate change, the SAF is shifting southward (Ansorge et al. 2009; Downes et al. 2011). The effect of this will result in a permanent flow through system at the PEIs, resulting in autochthonous nutrient loss, which may result in a decline of primary productivity in the proximity of the island group (Pakhomov et al. 2004; Ansorge et al. 2009; Downes et al. 2011; Allan et al. 2013). Already, a decrease in δ^{13}C signatures of the local zooplankton species, such as *N. marionis,* have becoming evident, whereas, δ^{13}C signatures of allochthonous zooplankton, such as *E. vallentini*, remain stable (Pakhomov et al. 2004, Allan et al. 2013). This regional change may have detrimental effects on organisms at higher trophic levels (Pakhomov et al. 2004; Frederiksen et al. 2006; Allan et al. 2013). These organisms are likely experiencing reduced prey availability, which is believed to be behind the declining populations of gentoo penguin and Crozet shag breeding at Marion Island (Allan et al. 2013; Crawford et al. 2014).

1.6. Rationale

The geographic locality, isolation, limited direct human interference on the islands, as well as the abundance of marine predators make the PEIs an ideal locality to study the potential effects of dynamic marine ecosystems on predator foraging behaviour within the Southern Ocean (Bergstrom & Chown 1999; Ryan & Bester 2008). Furthermore, there is evidence to suggest that regional climate change is affecting allochthonous and autochthonous sourced productivity at the PEIs (Kaehler et al. 2000; Pakhomov et al. 2004). This is believed to be reducing the available prey in the inshore environment (Allan et al. 2013). Occurring congruently with this, are the declines of inshore foraging predator populations on Marion Island, while several offshore foraging top predator populations are stable or increasing. This may be a signal that the local marine environment around the islands is changing.

South Africa is an original signatory of the international Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and the PEIs fall within the area of application. Thus, there is a long term study of the gentoo penguins breeding success, chronology and population size in place at Marion Island (Crawford et al. 2003b, 2009, 2014). However, the lack of long term dietary studies has made it difficult to assess the association between breeding success and population changes and shifts in dietary composition and possibly prey availability. Thus, the first objective of this study was to describe and investigate the diet of the gentoo penguin over three years during particular periods of the annual cycle. Related to diet, the second objective was to investigate variation in the diet over approximately 20 years in order to better understand long term changes and fluctuations in dietary composition.

The lack of tracking studies or at sea observations of the gentoo penguin at Marion Island limits inferences about where these birds are foraging and the foraging strategies they may be using. Therefore, the third objective of this study was to, for the first time, record the fine scale movement of these birds during the breeding season using GPSs and TDRs. Chapters 2 and 3 were written in the format of stand-alone papers to facilitate future publishing. There is consequently some repetition between these two chapters.

1.7. Aims

1. To determine and describe the diet of the gentoo penguin at Marion Island using stomach content samples that were collected during five different years (1994-1996; 2012; 2014) and to investigate whether the diet exhibited any intra or inter-annual variability during this time.
2. To investigate, for the first time, the at sea distribution of the gentoo penguin during the brooding period at Marion Island.

1.8. Key Questions

1. What is the diet composition of the gentoo penguins inhabiting Marion Island?

   The gentoo penguin diet on Marion Island is expected to be dominated by Nototheniid fish, specifically *Lepidonotothen squamifrons*, and two crustacean species, *Euphausia vallentini* and *Nauticaris marionis*. Predictions are based on known distribution of prey items (Perissinotto & McQuaid 1990; Hunt & Pakhomov 2003; Pakhomov et al. 2006), expected at-sea distribution of gentoo penguins (Adams& Wilsons 1987; Lescroël & Bost 2005; Kokubun et al. 2010) and previous work by Adams & Klages (1989) and La Cock et al. (1984).

2. Is there temporal variation in the diet of the gentoo penguin at Marion Island?

   Firstly, the diet of the gentoo penguin at Marion Island is expected to exhibited variation among different periods of the annual cycle over three years. Predictions are based on previous work by Adams & Klages (1989) at Marion Island and findings of other work elsewhere (Croxall et al. 1999; Coria et al. 2000; Clausen & Pütz 2002). Additionally, a possible long term change may be evident due to the southward shifting SAF (Downes et al. 2011) which is believed to be influencing prey availability around the islands (Pakhomov et al. 2004; Allan et al. 2013), particularly *N. marionis* (Pakhomov et al. 2004; Allan et al. 2013) and *E. vallentini* (Allan et al. 2013).

3. What is the foraging distribution of gentoo penguins at Marion Island during the brooding period?

    Based on studies at other localities (Robinson & Hindell 1996; Croxall et al. 1999; Tanton et al. 2004; Lescroël & Bost 2005; Miller et al. 2009; Kokubun et al. 2010) and previous inferences of foraging distribution of the gentoo penguin at Marion Island (Adams & Wilsons 1987; Crawford et al. 2014), the foraging distribution is expected to be inshore and concentrated on the shallow inter-island shelf between Marion and Prince Edward Island.

4. What are the dive characteristics of the gentoo penguins at Marion Island during the breeding period?

    Based on the prediction that the birds will be foraging over the inter-island shelf, and their largely benthic foraging characteristics reported elsewhere (Croxall et al. 1988; Wilson et al. 1996; Takahashi et al. 2008; Kokubun et al. 2010), diving depths is expected to reflect the shelf's bathymetry.

1.9. Research license and Ethics

The project was conducted through ethics approval granted by the NMMU Research Ethics Committee (Animal). The ethics clearance reference number is A14-SCI-ZOO-012.

Chapter 2

Temporal variation in the diet of gentoo penguins, *Pygoscelis papua,* at sub-Antarctic Marion Island

2.1. Introduction

Seabirds are linked to the abiotic and biotic features of marine ecosystems (Cairns 1988; Piatt et al. 2007) and understanding the relationship between them and their prey can provide important ecological information (Cury et al. 2011). This is because the distribution and availability of prey species of seabirds can be highly variable owing to spatial and temporal fluctuations in physical oceanographic conditions, such as water temperature and salinity (Cheung et al. 2009). For example, variability in sea surface temperature at Triangle Island, British Columbia, influenced the timing of availability of the Cassin's auklets', *Ptychoramphus aleuticus,* primary prey, the copepod, *Neocalanus cristatus* (Hedd et al. 2002). During years of favourable, cooler, sea surface temperatures and related high copepod availability, the auklet's diet was predominated by copepods, whereas, during years of unfavourable, warmer, sea surface temperatures and related low copepod availability, larval rockfish, *Sebastes* spp., dominated the diet.

The diet of a seabird may also be influenced by the cost of raising offspring. During this period there are increased energy demands (Bevan et al. 2002) which may require selective foraging for prey with higher energetic content or feeding on a greater abundance of prey (Forero et al. 2002; Le Corre et al. 2003; Browne et al. 2011). Consquently, the impact of fluctuating prey availability on annual breeding success of seabirds is well documented (e.g. Suryan et al. 2000; Hedd et al. 2002; Pinaud & Weimerskirch 2002; Browne et al. 2011). If there is low prey availability, then seabirds will allocate resources towards self-maintenance and survival rather than chick provisioning (Stearns 1992; Piatt et al. 2007). For example, the body condition of parent black-browed albatrosses, *Thalassarche melanophris*, at the Kerguelen Islands was low during years of low prey availability which was related to colder sea surface temperatures (Pinaud & Weimerskirch 2002). This consistently resulted in breeding failure and thus overall decrease in breeding success during that respective breeding season.

The breeding performance of the gentoo penguin, *Pygoscelis papua*, has been shown to correlate with prey availability (Croxall et al. 1999; Reid et al. 2005). Perhaps more so in this species as it is an inshore forager (Lescroël & Bost 2005; Kokubun et al. 2010) and its range to search for prey is limited (Saraux et al. 2011). The long term changes in the local marine environment at the Prince Edward Islands Archipelago (PEIs; Allan et al. 2013) seem to be reflected in the breeding success of gentoo penguins (Crawford et al. 2014). The gentoo penguin population at Marion Island, of the PEIs, has been unsuccessful at maintaining a stable or growing population since 1994 (Crawford et al. 2003b, 2009, 2014), with the population experiencing a 52% decrease between 1994 and 2012 (Crawford et al. 2014). This has been suggested to be indicative of a change in the availability of principle prey items of gentoo penguins as a result of long term changes in the local marine environment (Allan et al. 2013; Crawford et al. 2014).

The southward shift of the sub-Antarctic Front (SAF), due to anthropogenic climate change (Gille 2002; Downes et al. 2011), is expected to have major consequences on the PEIs marine ecosystem (Ansorge et al. 2009). The PEIs (46°50’S, 37°50’E) are located in the Indian sector of the Southern Ocean, situated between the SAF and the Antarctic Polar Front (APF), within the Antarctic Circumpolar Current (ACC, Figure 2.1.). The highly variable latitudinal position of the SAF is an important factor in determining local oceanographic conditions and source of food material at the PEIs (Pakhomov & Froneman 1999b; Perissinotto et al. 2000; Ansorge & Lutjeharms 2002; Ansorge et al. 2009). In general, when the SAF is located further north, an autochthonous food source becomes prominent in the marine ecosystem at the PEIs due to a reduced flow rate of the ACC and subsequently formations of anticyclonic eddies and phytoplanktonic blooms occur (Perissinotto et al. 2000). In contrast, when the SAF is located further south, an allochthonous food source is more dominant as a result of increased flow rate of the ACC around the PEIs and advection of allochthonous food source (Perissinotto & Duncombe Rae 1990; Ansorge & Lutjeharms 2002). Therefore, a consequence of a southward shift of the SAF is an increased input of allochthonous food resources into the ecosystem (Allan et al. 2013). This is expected to have long term effects on the marine productivity in the proximity of the PEIs (Allan et al. 2013). For example, since 1984, the δ^{13}C signature of *Nauticaris marionis,* a crustacean species that is dependent on autochthonous food material*,* has been declining (Pakhomov et al. 2004; Allan et al. 2013). Contrastingly, the δ^{13}C signature of another crustacean, *Euphausia vallentini,* an allochthonous food source, has remained stable (Allan et al. 2013). Both were historically key prey items in the diet of gentoo penguins at Marion Island (Adams & Klages 1989).

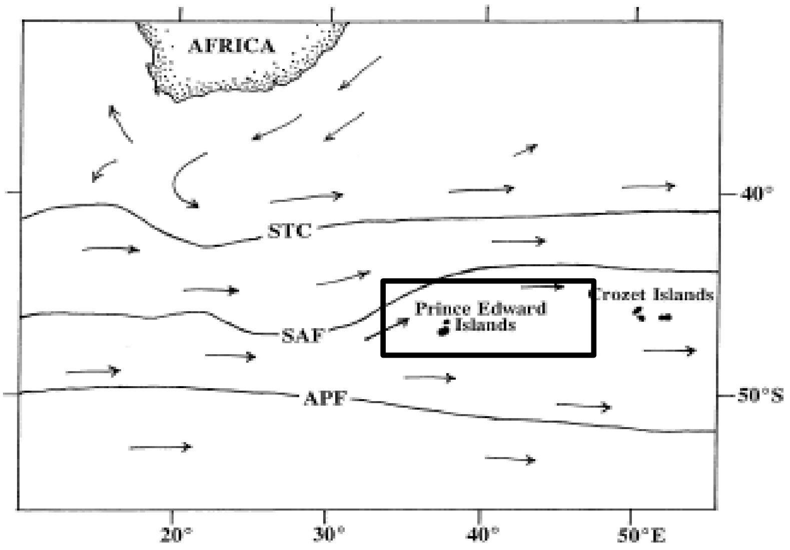

Figure 2.1. The position of the Prince Edward Islands in relation to the average position of the Antarctic Polar front (APF), the sub-Antarctic polar front (SAF) and the Subtropical Convergence (STC; Figure from Pakhomov et al. 1999).

Variation, within and among annual cycles, in the diet of gentoo penguins has been observed at several localities (e.g. Adams & Klages 1989; Robinson & Hindell 1996; Clausen & Pütz 2002; Lescroël et al. 2004; Reid et al. 2005) and has been attributed to changes in the availability of prey rather than increased energy demands during chick rearing. However there may be a suite of factors that may effectively cause changes in diet composition of the gentoo penguin within and among annual cycles. A multiyear comparison of the diet, spanning the range of the breeding and non-breeding cycles, is a useful means to further understand the variation in their diets (Piatt et al. 2007).

With access to historical records and notable decline in the gentoo penguin population at Marion Island (Crawford et al. 2014) a detailed investigation toward the diet of this species is timely. This chapter has two main aims: 1) describe the diet of the gentoo penguin population at Marion Island during different periods of the annual cycle and 2) investigate whether the diet exhibits any variability within and among annual cycles. The diet is described and temporal variability is investigated using stomach content samples that were collected from 1994 to 1996 and periodically during 2012 and 2014. To investigate annual variation and whether a specific period during the annual cycle has an effect on the diet, the dietary composition during different periods of the annual cycle (i.e. pre-moult, post-breeding, pre-incubation, incubation, guarding and crèche periods) over three years (1994-1996) is compared. The proportions of fish, crustaceans and cephalopods, as well as, species composition thereof, are expected to vary in the diet within and among the annual cycles. This expectation is supported, as Adams & Klages (1989) reported significant monthly variation in the diet of this population during 1984/85. It is expected that this variation will reflect temporal changes in available prey. Furthermore, the study investigated whether a long term change in the diet was evident by comparing the diet approximately 20 years apart, from samples collected during 1994-1996 and during 2012 and 2014. It is expected that, due to the effect of the shifting SAF, the diet of the gentoo penguin will reflect an increase in allochthonous prey i.e. an increase in *E. vallentini* and a decrease in *N. marionis*.

2.2. Materials and Methods

2.2.1. Study site and species

Marion Island (240km^2) is one two islands of the PEIs. It lies approximately 19km south-south west of Prince Edward Island (45km^2; Figure 2.2.). Ascending from a depth of 3000m, the islands are separated by a shallow inter-island shelf that ranges from 45m to 260m in depth (Ansorge & Lutjeharms 2002; Lutjeharms & Ansorge 2008). At Marion Island, the gentoo penguin colonies are concentrated along the north and east coasts of the island. Sampling for this study was conducted at four different colonies along the north east coast of Marion Island (Figure 2.2.). Combined, these colonies accounted for 36.1 ± 4.4% (mean ± standard deviation (SD)) of the entire breeding population at Marion Island between 1994/95 and 2002/03 (Crawford et al. 2003a) and 37% in 2014.

Breeding of gentoo penguins at Marion Island is initiated during austral winter opposed to gentoo penguins further south that initiate breeding during summer (Bost & Jouventin 1990; Crawford et al. 2003b). Furthermore, compared to other localities, their breeding season is extended and relatively asynchronous (Bost & Jouventin 1990; Crawford et al. 2014). Incubation and chick rearing is shared between parents and can be separated into three distinguishable periods: incubation, guarding of chick(s) and chicks forming a crèche (Williams 1990; Croxall & Davis 1999). Generally, from the beginning of June adults start returning to nesting sites. Incubation begins in mid-June and is completed by mid-July, with hatching occurring 35-40 days after laying. Crèches start forming from beginning to mid-September and fledging occurs approximately a month later (Crawford et al. 2003b).

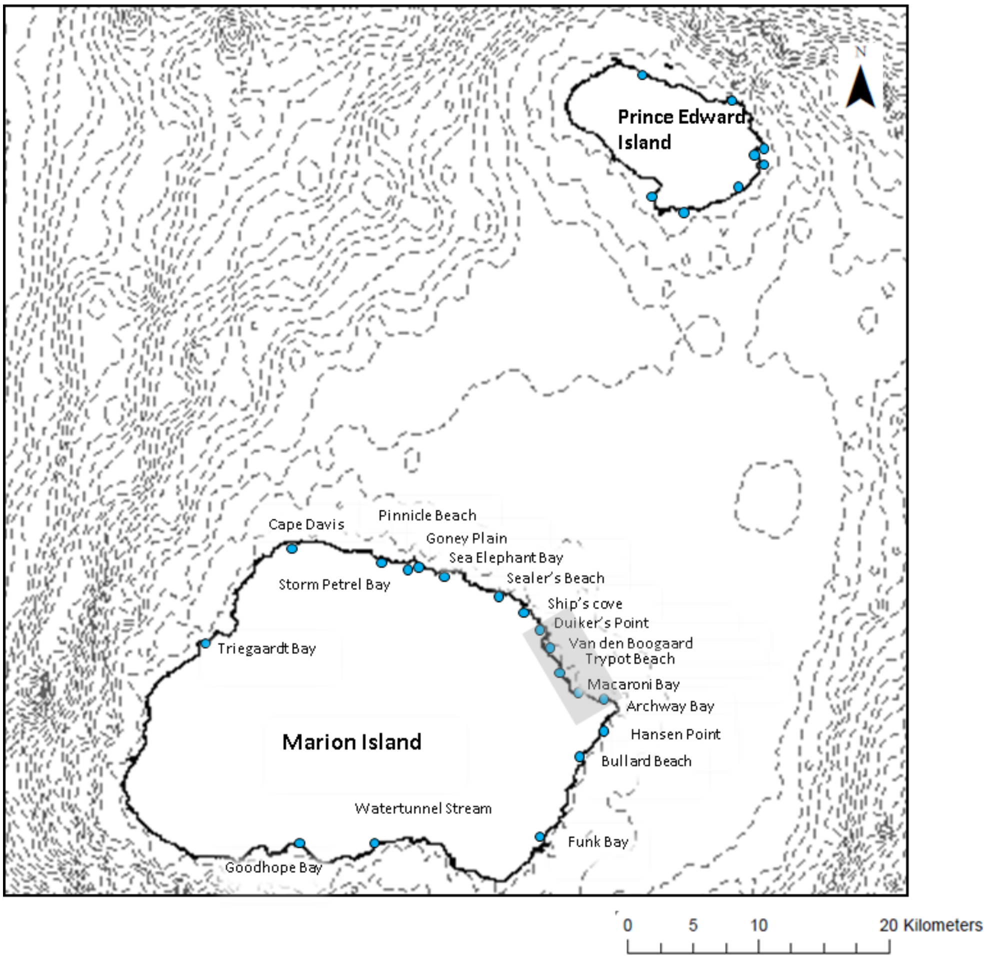

Figure 2.2. Sub-Antarctic Prince Edward Islands showing gentoo penguin colonies (blue dots) and those from which stomach content samples were collected (grey shaded area). Note that samples were not collected from Macaroni Bay. Dashed lines around the island represent isobaths at 100m intervals.

2.2.2. Stomach content sample collection

Stomach content samples were obtained monthly between March 1994 to December 1995 and July to December 1996 to investigate the diet composition of the gentoo penguin within and among annual cycles. More recently, samples were obtained during July and August 2012, and January and August 2014 to investigate long term change in the diet of gentoo penguins at Marion Island.

The CCAMLR Ecosystem Monitoring Program (CEMP) water offloading technique described in SC-CAMLR (2003) for obtaining stomach content samples was applied. This involved restraining the bird and inserting a soft plastic catheter (diameter = 0.4mm) down the oesophagus and into the stomach. Water (solution of seawater and warm freshwater mixed until it reached approximately 37^{o}C) was poured into a funnel connected to the catheter. The catheter was then gently removed and the bird inverted. The beak was held open and the neck massaged until the bird regurgitated its stomach content. The regurgitation was collected in a bucket and drained of excess water over a 0.5 mm sieve before being put into ziplock bags or plastic jars. Typically, stomach content samples were collected in the late afternoon from birds returning from a foraging trip.

2.2.3. Storage and sorting of samples

After collection, stomach content samples were either kept in 70% ethanol or frozen at -20°C until further processing. All samples were sorted according to CEMP procedures (SC-CAMLR 2003). After being drained of water, each sample was weighed and separated into its main prey taxa, which were then individually weighed and counted. Prey species were identified to the lowest possible taxonomical level. Fish were identified from otoliths using available identification guides (Fisher & Hureau 1985; Hecht 1987; Gon & Heemstra 1990; Williams & McEldowney 1990; Smale et al. 1995; Reid 1996) and the number of individuals was taken as the highest number of right or left otoliths present. Cephalopds were identified from their beaks (Clarke 1986; Smale et al. 1993) and the number of individuals taken as the highest number of upper or lower rostrums of that species present in the sample. Crustaceans, from their particular morphology (Branch et al. 1991):

- Euphausiids: spines on the tail segments and the antennular flappet, found on the second segment of the antennae
- Decapods: by their rostrum
- Amphipods: by shape, colour (only if samples had not been stored in ethanol) and spines on segments and legs
- Isopods: by characteristic shapes. Most individuals were identified to genus level

The number of crustaceans in a sample was calculated by dividing the cumulative mass of a species by the weight of one individual of that species (following methods by Adams & Klages 1989).

2.2.4. Data analysis

To assess variation within and among annual cycles, stomach content samples were grouped into six different periods of the annual cycle (Table 2.1.):

1. Pre-incubation: This is considered to be the period when the adults start returning to the breeding colony.
2. Incubation: The period when partners alternate incubating egg(s).
3. Brooding: The period when partners alternate feeding and brooding chick(s).
4. Crèche: The period when the chick is no longer brooded but both partners are feeding the chick.
5. Post-breeding: The gentoo penguins at Marion Island begin to moult in January (Crawford et al. 2003b). Therefore, this period was defined from the end of the crèche period (when the adult is no longer caring for chick(s)) to the beginning of the moult period, which, for the purposes of this study, was defined as 31 December.

Long term variation was investigated using samples from 1994-1996 in conjunction with more recent samples that were restricted to certain periods. Specifically, samples collected during July and August 2012 were collected during the incubation period and samples collected during August 2014 were collected during the brooding period and therefore were compared against samples collected during the respective breeding periods of 1994-1996. However, samples collected during January 2014 did not correspond to any period previously defined and therefore were only compared to samples collected during January and February 1995. As gentoo penguins foraging during this time are most likely to be preparing for moult (Crawford et al. 2003b), this period will be further referred to as the pre-moult period (the sixth period that was grouped).

As stomach content samples were collected from birds returning from the sea the breeding status of sampled birds was unknown. Therefore, timing of the various periods was inferred from the year specific breeding chronology of the birds (Crawford et al. 2003b). The breeding of gentoo penguins on Marion Island is relatively asynchronous (Crawford et al. 2003b). Every year the timing of events is different as well as individual birds are often incubating and brooding chicks at different times (Crawford et al. 2003b, pers obs.). Therefore the grouping of samples into periods is based on the breeding period of most individuals of that respective colony (Crawford et al.2003b). The breeding periods, as defined above, were used as a temporal comparison measure, however, it cannot be said with complete confidence that the inferred breeding status of the birds from which stomach content samples were collected from is accurate.

The diet was described using four measures:

1. Percentage wet mass (%W): the proportion of the mass of major prey taxa
2. Percentage frequency of occurrence (%FO): the proportion of diet samples containing the prey type compared to all diet samples examined.
3. Percentage numerical abundance (%N): the proportion of the total number of individuals of one prey taxa compared to total number of individuals of all prey items per sample
4. Simpson's dominance index (λ"; Molinero & Flos 1992): a measure to estimate a prey type's dominance in the diet, as well as, the expected commonness of a particular prey type in the diet (Formula 1). Formula 2 was used to render the index independent of sample size (z = number of stomach samples). Dominance values were expressed as a percentage using Formula 3 (Molinero & Flos 1992). This index takes into account the %FO and %N of a prey species. Therefore, if a species has a low %N but a high overall %FO it will receive a higher dominance value of a prey item that has a high %N but a low overall %FO.

$(\lambda)=\sum \%N^2$ **Formula 1**

$\lambda'=(\lambda/z) \times 100$ **Formula 2**

$\lambda''=(\lambda'/\sum \lambda') \times 100$ **Formula 3**

To visualize the differences in diet among periods and annual cycles, non-Metric Multidimensional Scaling (nMDS) ordinations (package: vegan; Oksanen et al. 2015) using Bray-Curtis resemblance matrices were used (Anderson et al. 2010). The fit of each ordination was assessed with a stress value > 0.2 being seen as undesirable (Quinn & Keough 2002). The ordispider function (package: vegan) was used to plot ordinations. This function plots the weighted mean or centroid for each treatment with higher dissimilarity amongst centroids being indicated by greater distance between them.

To test for differences in species assemblages within and among annual cycles an ADONIS test was used (package: vegan). The ADONIS test is analogous to a non-parametric permutational multivariate analysis of variance (PERMANOVA) but is considered to be more robust. This test is used for the analysis and partitioning of sums of squares using distance matrices as a response variable (Anderson 2001). It describes the strength and significance that a predictor variable may be having on the variance of the response variable. A Bray-Curtis resemblance matrix of %N of the species assemblages in the diet was used as the response variable and periods and years, as well as their interaction were the predictor variables to test for difference within and among years. Only year was used as a predictor variable to test for difference in the diet over the long term.

Variation of major prey taxa in the diet was investigated for by grouping the prey species into four major categories: fish, crustaceans, cephalopods and other. The “other” category comprised prey items that were rarely recorded in diet samples. Following this, variation of prey species that were identified as dominant prey items was investigated. To identify dominant prey items in the diet the dominance indices (i.e. λ” values) of each prey item were ranked and a cumulative contribution curve was plotted. The dominant prey items were identified as those for which the slope of the cumulative curve was at least 10% of that at the origin; prey species after this point were excluded from analyses as they contributed relatively little to the diet (Appendix A; Landman et al. 2013).The motivation for investigation of the most dominant prey items was based on the observation that 90% of the prey species in the diet during the sampling periods had a dominance value of less than 1%. Furthermore, the number of prey species that had a dominance value of less than 1% accounted for 3.5% of the total number of prey items eaten. Therefore, these prey species were presumed to have been of minor significance.

Analysis of variance procedures (one-way ANOVA) followed by Tukeys' HSD post-hoc tests were used to test for differences in major prey taxa and dominant prey items across periods and years (Mecenero et al. 2006). Where appropriate, data were arcsine-transformed to meet assumptions of normality and homoscedasticity of variances (Zuur et al. 2009).

All data analyses were performed using R version 3.1.1 (R Core Team 2014). All values are reported as means ± standard deviation, unless otherwise stated, and significance is specified as $p <0.05$.

2.3. Results

A total of 195 stomach content samples were collected over the entire study period. During 1994-1996, 133 samples, 10 ± 4 stomach content samples per period, were used to assess annual variation in the diet (Table 2.1.). To assess for long term variation in the diet the study compared stomach content samples collected in pre-moult 2014, incubation 2012 and brooding 2014 to the corresponding periods of 1994 to 1996. In total, 93 stomach content samples, 9 ± 2 stomach content samples per period were used for this comparison (Table 2.1.). Over the entire sampling period of this study, stomach content samples weighed on average 109.18 ± 98.93g. Of the 195 samples, stones and seaweed occurred in a total of 52 and 19, respectively. However, they were not included in analyses (following Adams & Klages 1989).

Table 2.1. The number of stomach content samples collected from gentoo penguins at sub-Antarctic Marion Island during the different periods during the annual cycles of 1994-1996, 2012 and 2014.

Annual cycle	1994						1995					1996				2012	2014	
Period	Pre-Incubation	Incubation	Brooding	Crèche	Post-breeding	Pre-moult	Pre-Incubation	Incubation	Brooding	Crèche	Post-Breeding	Incubation	Brooding	Crèche	Post- breeding	Incubation	Pre-moult	Brooding
Beginning date of period	31/05/1994	27/06/1994	07/08/1994	15/09/1994	24/10/1994	01/01/1995	15/06/1995	02/07/1995	21/08/1995	26/09/1995	07/11/1995	11/07/1996	15/08/1996	15/09/1996	07/11/1996	05/07/2012	01/01/2014	01/08/2014
Number of stomach content samples	4	15	8	12	10	9	5	11	7	16	13	10	6	6	10	5	11	10

2.3.1. General diet composition

During the course of the study, a total of 54 prey species were identified from the stomach content samples (Table 2.2.). A total of 20 294 individual prey items were found in the stomach content samples during the course of the study, of which 20.5% were fish, 76.7% were crustaceans, 2.5% were cephalopods and the remaining 0.3% of species found consisted of gastropods, bivalves and one sea urchin. Fish, crustaceans and cephalopods were present in the diet during every period (Table 2.2.). The most frequently occurring species were *Lepidonotothen larseni* and *N. marionis,* which was found in the diet during every period and *Otopus* sp. which was also found in every period except during the brooding period of 1995 and the incubation period of 2012. In those samples collected during the more recent part of the study (2012 and 2014), four species were identified that had not been recorded during the earlier period (1994-1996). These included amphipods from the genus: *Vibilia* and from the infraorder: Gammarida; the euphausiid: *E. longirostra*; and one unidentified crab.

Table 2.2. Prey species identified in the diet of gentoo penguins at sub-Antarctic Marion Island during 1994 to 1996, 2012 and 2014. Species are categorised by order and then family. Sampling periods are P= pre-incubation, I = incubation, B = brooding, C = crèche, PB = post breeding and M = Pre-Moult of that respective year. Species are presented as %FO. Percentage mass (%W) is only reported for as a cumulative figure for each major taxa found during each period.

Sampling period	1994					1995						1996				2012	2014	
	P	I	B	C	PB	M	P	I	B	C	PB	I	B	C	PB	I	M	B
	n=4	n=15	n=8	n=12	n=10	n=9	n=5	n=11	n=7	n=16	n=13	n=10	n=6	n=6	n=10	n=5	n=11	n=10
Fish %W	(103.36 ± 104.30)	(81.65 ± 85.66)	(138.35 ± 92.14)	(107.45 ± 77.98)	(86.71 ± 72.99)	(181.13 ± 114.79)	(8.42 ± 11.03)	(36.18 ± 36.17)	(118.23 ± 132.68)	(112.68 ± 116.77)	(46.85 ± 77.00)	(34.84 ± 46.76)	(64.17 ± 66.54)	(32.39 ± 64.75)	(8.86 ± 8.20)	(19.63 ± 13.51)	(82.03 ± 76.86)	(89.77 ± 73.61)
Nototheniidae																		
Dissostichus eleginoides	-	6.67	37.5	8.33	-	-	-	-	-	-	-	10	16.67	-	-	-	-	10
Gobionotothen angustifrons	-	6.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gobionotothen cyanobrancha	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gobionotothen gibberifrons	25	-	-	-	-	-	-	-	-	6.25	-	-	-	-	-	-	-	-
Gobionotothen marionensis	25	-	50	25	20	-	-	9.09	-	6.25	15.38	20	33.33	16.67	30	-	9.09	10
Lepidonotothen squamifrons	-	-	-	-	-	33.33	-	-	-	-	7.69	-	-	-	-	-	-	-
Lepidonotothen larseni	100	73.33	75	83.33	70	100	80	90.91	100	93.75	76.92	90	66.67	50	70	80	36.36	90
Paranotothenia magellanica	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trematomus sp.	-	-	-	-	-	-	-	-	-	6.25	-	-	-	-	-	-	-	-
Unidentified juvenile	-	-	-	8.33	20	88.89	-	-	-	-	-	-	-	-	-	-	90.91	-
Unidentified Nototheniid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
Myctophidae																		
Electrona carlsbergi	25	20	-	-	-	11.11	20	-	-	-	-	-	-	-	-	-	-	-
Electrona subaspera	-	6.67	12.5	-	-	-	-	-	-	-	-	10	16.67	-	-	-	-	-
Electrona spp.	-	-	-	-	-	-	-	-	14.29	-	-	-	-	-	-	-	-	-
Gymnoscopelus braueri	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus fraseri	-	13.33	25	-	10	11.11	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus nicholsi	-	26.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus opisthopterus	-	6.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus piabilis	25	13.33	12.5	-	-	11.11	20	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus sp.	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Krefftichthys anderssoni	-	6.67	25	16.67	-	22.22	-	-	-	6.25	-	-	-	-	-	-	-	-
Lampichthys procerus	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Metelectrona ventralis	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protomyctophum bolini	25	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
Protomyctophum choriodon	-	13.33	-	8.33	10	22.22	-	9.09	-	-	-	10	-	-	-	-	-	-
Protomyctophum tenisoni	-	6.67	12.5	25	20	11.11	-	-	-	-	-	10	-	-	-	-	-	-
Myctophid sp.	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
Bathylagidae																		
Bathylagus antarcticus	-	6.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paralepididae																		
Arctozenus risso	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified fish	25	-	-	-	-	-	-	9.09	-	-	-	-	-	-	-	-	-	-

Sampling period	1994					1995						1996				2012	2014	
	P	I	B	C	PB	M	P	I	B	C	PB	I	B	C	PB	I	M	B
Crustacean %W	(5.66 ± 11.25)	(23.18 ± 41.50)	(16.99 ± 42.23)	(33.88 ± 103.79)	(28.59 ± 45.98)	(0.68 ± 0.90)	(0.50 ± 1.12)	(1.63 ± 4.53)	(0.66 ± 1.65)	(8.14 ± 18.27)	(73.54 ± 124.54)	(12.96 ± 21.63)	(20.26 ± 16.16)	(24.91 ± 37.33)	(41.24 ± 51.68)	(8.50 ± 14.29)	(0.80 ± 2.17)	(5.84 ± 10.17)
Decapoda																		
Hippolytidae																		
Nauticaris marionis	50	80	75	83.33	40	77.78	20	27.27	14.29	31.25	15.38	50	100	33.33	30	20	9.09	-
Euphausiidae																		
Euphausia vallentini	25	-	-	16.67	20	-	-	-	14.29	25	46.15	10	-	16.67	80	80	-	50
Thysanoessa vicina	-	-	-	-	-	-	-	-	-	-	7.69	-	-	-	-	-	18.18	30
Euphausia longirostra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-
Euphausiid spp.	50	6.67	25	16.67	40	11.11	-	-	-	31.25	23.08	10	-	33.33	-	-	-	-
Amphipoda																		
Hyperiidae																		
Themisto gaudichaudii	-	26.67	37.5	16.67	40	22.22	-	9.09	-	-	-	-	-	-	-	20	9.09	-
Vibilia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
Phrosinidae																		
Gammarida sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-
Calliopioidea																		
Paramoera fissicauda	-	-	-	-	-	-	-	-	-	-	-	-	16.67	-	-	-	-	-
Phrosinidae																		
Primno macropa	-	-	-	-	-	-	-	-	-	-	7.69	-	-	-	-	-	-	-
Unidentified Amphipod	-	-	12.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda																		
Sphaeromatidae																		
Cymodocella sp.	-	-	-	-	-	-	-	-	-	-	7.69	-	-	-	-	-	-	-
Unidentified Isopod	25	-	12.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified crab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.09	-
Cephalopods %W	(1.66 ± 2.56)	(0.32 ± 0.49)	(0.89 ± 1.65)	(1.01 ± 2.84)	(0.87 ± 2.00)	(19.78 ± 33.60)	(19.50 ± 26.7)	(1.40 ± 4.24)	(0.01 ± 0.04)	(10.37 ± 33.37)	(0.48 ± 1.13)	(0.06 ± 0.16)	(0.04 ± 0.08)	(0.48 ± 1.13)	(0.08 ± 0.18)	- -	(1.56 ± 1.49)	(0.05 ± 0.13)
Octopodidae																		
Octopus sp.	100	60	37.5	66.67	60	33.33	40	9.09	-	6.25	7.69	10	16.67	16.67	50	-	36.36	20
Onycoteuthidae																		
Moroteuthis ingens	-	-	-	8.33	10	33.33	40	54.55	-	12.5	23.08	-	-	-	-	-	-	-
Kondakovia longimana	-	-	-	-	-	-	-	-	-	-	15.38	-	-	-	-	-	-	-
Unidentified squid	-	20	25	16.67	50	22.22	20	9.09	14.29	50	23.08	10	16.67	16.67	-	-	72.73	-
Other %W	-	-	(0.03 ± 0.07)	(0.39 ± 0.70)	(0.02 ± 0.04)	(0.38 ± 0.99)	-	-	(0.20 ± 0.53)	(0.03 ± 0.07)	(0.067 ± 0.20)	(0.08 ± 0.25)	(0.49 ± 0.70)	-	(0.08 ± 0.13)	(0.01 ± 0.03)	(0.01 ± 0.05)	- -
Gastropoda																		
Calliostomatidae																		
Margarella expansa	-	-	12.5	33.33	20	22.22	-	-	14.29	6.25	15.38	10	66.67	-	20	-	-	-
Borsoniidae																		
Typhlodaphne platamodes	-	-	-	8.33	-	-	-	-	-	-	-	-	16.67	-	-	-	-	-
Muricidae																		
Trophon septus	-	-	-	-	-	-	-	-	-	-	-	-	16.67	-	-	-	-	-
Bivalvia																		
Limidae																		
Limatula pygmaea	-	-	-	8.33	-	-	-	-	-	6.25	-	-	-	-	-	-	-	-
Echinodermata																		
Echinoidea																		
Sterechinus agassizii	-	-	-	-	-	-	-	-	-	-	-	-	16.67	-	-	-	-	-

2.3.2. Annual and long-term variation in diet composition

Among the different periods during the annual cycles of 1994-1996, the ADONIS test revealed that the interaction between year and period was significant (F_4=1.71, R^2=0.05, p=0.03), where period (F_4=4.33, R^2=0.11, p<0.01) was responsible for 11% and year (F_1=4.15, R^2=0.02, p<0.01) was responsible for 2% of the variation. These significant differences were difficult to discern from the nMDS ordination (Figure 2.3.) as no clear pattern could be conceived. However, the diet during the post breeding periods of 1995 and 1996 looked to be the most dissimilar to the diet during any other period. The centroids of pre-incubation, incubation, brooding and crèche of the different annual cycles showed no overlap indicating that the diet during the same period of different annual cycles were not similar to one another, except for the crèche period of 1995 and 1996. Brooding and incubation during 1995 and pre-incubation and post-breeding period of 1994 showed overlapping centroids indicating greater similarity of diet during these periods compared to any other.

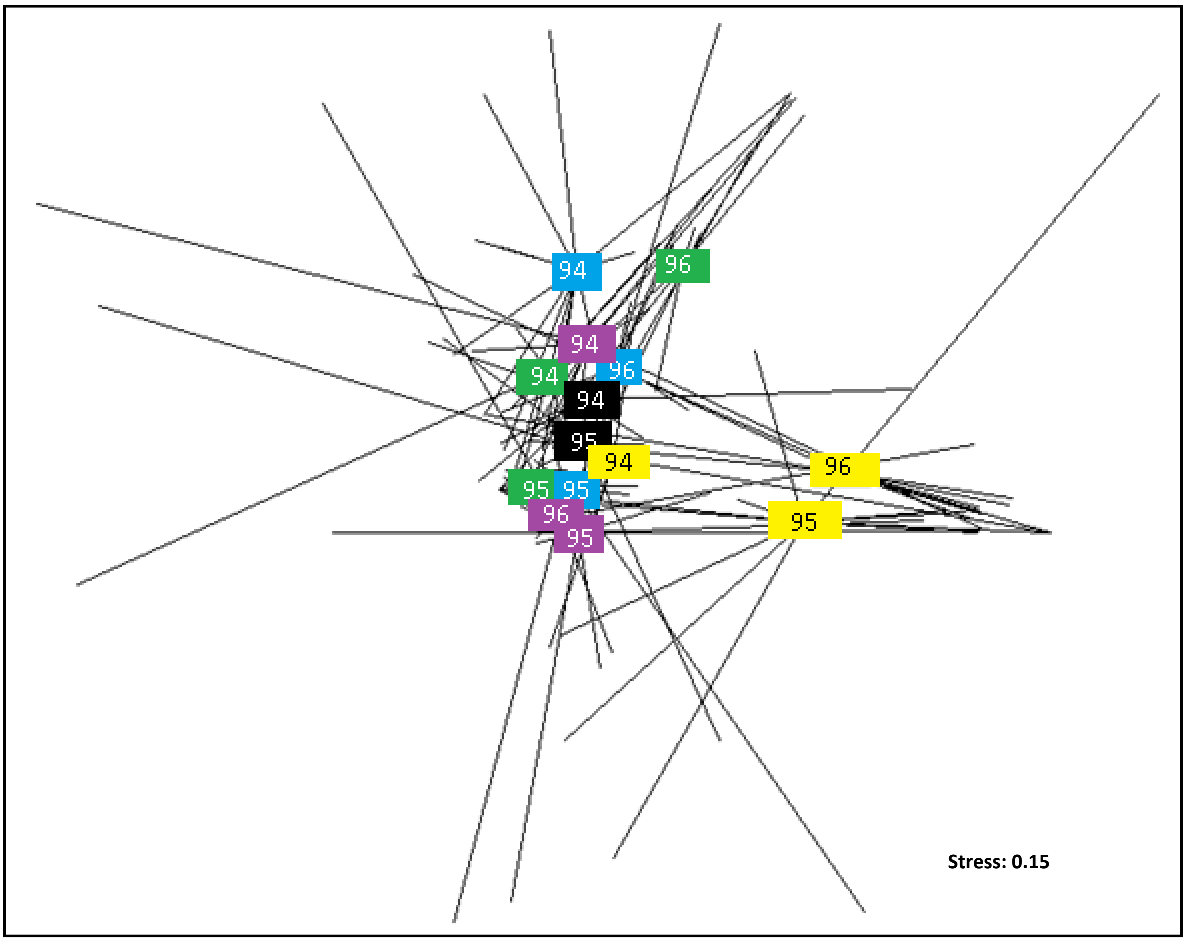

Figure 2.3. Non-metric multidimensional scaling ordination of percentage numerical abundance showing the differences in prey composition in the diet of gentoo penguins at sub-Antarctic Marion Island during periods (pre-incubation (black), incubation (blue), brooding (green), crèche (purple) and post breeding (yellow)) over three annual cycles (1994-1996).

With regard to long term variation, the ADONIS test revealed that the diet was not significantly different during the pre-moult period (F_1=2.81, R^2=0.14, p=0.08) but was significantly different among the incubation (F_1=3.93, R^2=0.09, p<0.01) and brooding periods (F_1=3.65, R^2=0.11, p<0.01). Based on the nMDS ordination the diet during incubation looked to most dissimilar during 2012 compared to the diet during incubation of 1994 to 1996 (Figure 2.4.a.). However, no clear pattern or groups were conceivable between brooding (Figure 2.4.b.) and pre-moult (Figure 2.4.c.) periods over the different annual cycles.

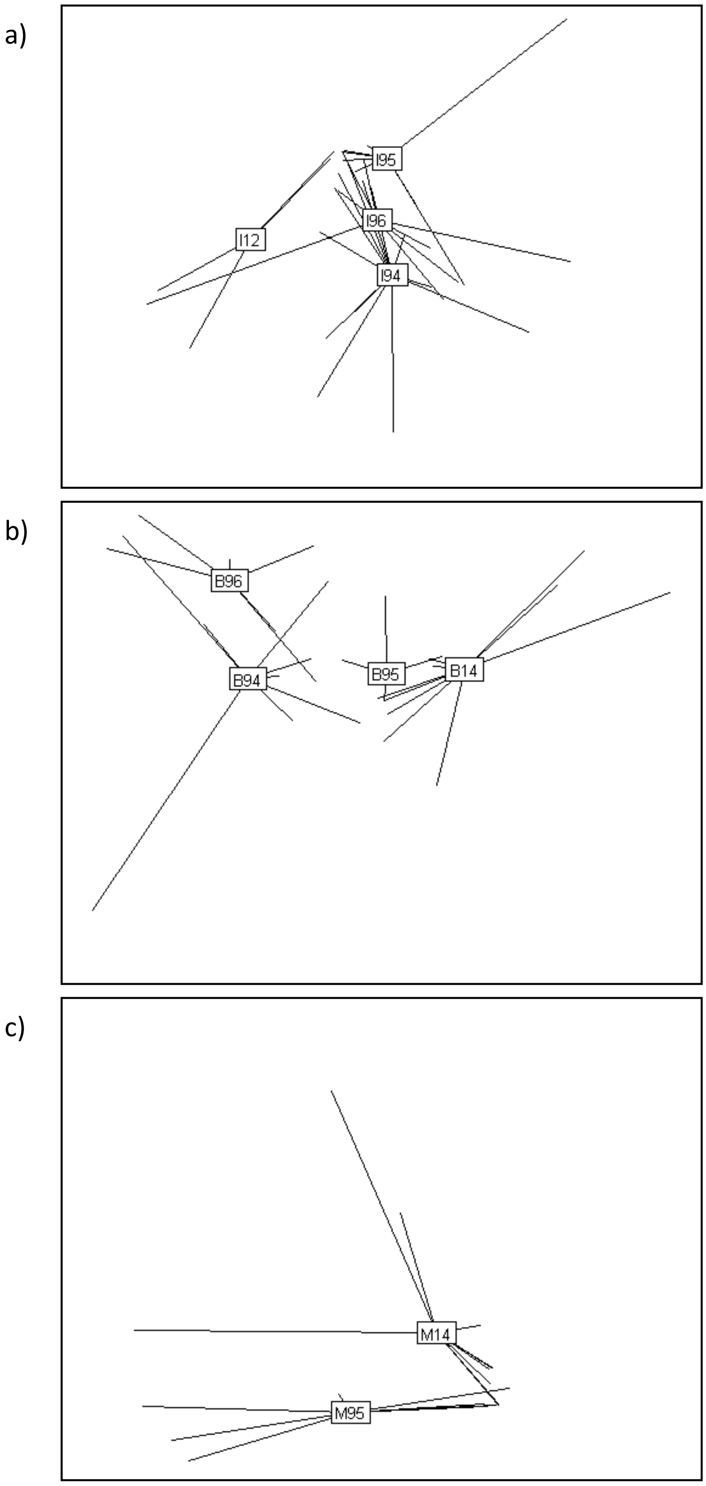

Figure 2.4. Non-metric multidimensional scaling ordination of percentage numerical abundance showing the differences in prey composition in the diet of gentoo penguins at sub-Antarctic Marion Island during the periods a) incubation (I), b) brooding (B) and c) pre-moult(M) of 1994- 1996 and 2012 and 2014. Pre-moult samples are only available for the years of 1995 and 2014.

2.3.3. Major prey groups

2.3.3.1. Annual variation

In 1994-1996, the diet of the gentoo penguins at Marion Island varied within and among annual cycles (Figure 2.5.). The proportion of the fish in the diet consistently increased from pre-incubation and peaked in the brooding period across annual cycles. Where after, the proportion of crustaceans in the diet increased and peaked in the post-breeding period. However, after the crèche period of 1995 and throughout 1996, fish contributed less and crustaceans contributed more to the diet than during the 1994 and 1995.

An ANOVA, revealed that the fish and crustacean components of the diet significantly changed among periods (fish: F_{13}=2.78, p<0.01, crustaceans: F_{13}=2.52, p<0.01), whereas the cephalopod and other components did not (cephalopods: F_{13}=1.34, p=0.20; other: F_{13}=1.25, p=0.25). Fish contributed least to the diet during the immediate post-breeding period of 1995 and 1996 (significantly less than the incubation and brooding period of 1995). Furthermore, during the post breeding period of 1996 the birds ate significantly more crustacean than during the incubation and brooding period of 1995. When comparing these results to the nMDS ordination (Figure 2.3.) the clear dissimilarity of diet composition of the post breeding periods (1995 and 1996) seems to be driven by the large increase of crustaceans in the diet during these periods.

2.3.3.2. Long term variation

The quantities of major taxa of the diets collected more recently (2012 and 2014) did not significantly differ from the quantities of major prey found in the diets from respective breeding periods from the earlier part of the study (1994-1996, Figure 2.5.). However, during the brooding period of 1995 there were noticeably more fish and fewer crustaceans than during the brooding periods of all other years.

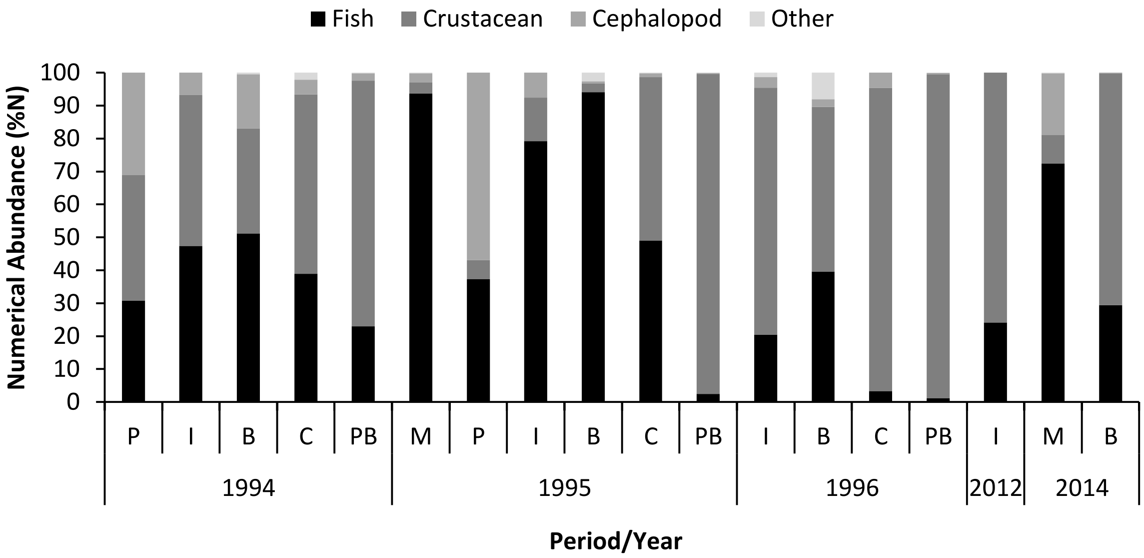

Figure 2.5. Relative contributions, in terms of percentage numerical abundance, of major prey taxa to the diet of the gentoo penguins at sub-Antarctic Marion Island during different periods (pre-incubation (P), incubation (I), brooding (B), crèche (C), post breeding (PB)and pre-moult (M)) within different years (1994-1996; 2012; 2014).

2.3.4. Dominant prey items

The dominance index of species in the diet varied over annual cycles and among periods (Appendix B). From the dominance index three species were identified as dominant prey items. These included, in order of dominance: the rockcod fish, *L. larseni* (λ“ = 79.73), the pelagic crustacean, *E. vallentini* (λ“ = 9.20) and the benthic crustacean *N. marionis* (λ“ = 7.44). Supporting the decision to only include these three species for within and among annual cycle comparisons of the diet is the fact that *L. larseni* was consistently found as a dominant species in the diet over all periods, and throughout most periods either *N. marionis* or *E vallentini* were present as dominant prey.

For the investigation into long term variation in the diet, juvenile nototheniid fish (1995: λ“ = 73.91; 2014: λ“ = 93.00) and *L. larseni* (1995: λ“ = 24.25;) were identified as dominant prey items during the pre-moult period, however *L. larseni* was not a dominant prey item in 2014. The dominant prey items during the incubation period of 2012 were *L. larseni* (λ“ = 39.55) and unidentified squid (λ“ = 5.21), and *L. larseni* (λ“ = 77.84) and *E. vallentini* (λ“ = 20.25) during the brooding period of 2014. However, to investigate long term variation in the diet, comparisons were made between dominant prey items that were identified during the earlier part of the study (1994-1996) i.e. *L. larseni, E. vallentini* and *N. marionis.*

2.3.4.1. Annual variation

The proportion of the dominant prey items found in the diet, *L. larseni*, *E. vallentini* and *N. marionis,* fluctuated within and among annual cycles of 1994 to 1996 (Figure 2.6). An ANOVA revealed that all dominant prey items were significantly different among periods (*L. larensi*: $F_{13}=2.88$, $p<0.01$; *N. marionis*: $F_{13}=4.36$, $p<0.01$; *E. vallentini*: $F_{13}=4.60$; $p<0.01$).

Lepidonotothen larseni followed the same general trend as fish observed during the comparison of major prey groups, i.e. the proportion of *L. larseni* in the diet consistently increased from pre-incubation and peaked during the brooding period. *Nauticaris marionis* was generally found in higher proportions throughout 1994 compared to other years. *Euphausia vallentini* occurred consistently in greater proportions during the post-breeding periods of all annual cycles. The proportion of *E. vallentini* and *N. marionis* were never found in similar proportions in the diet. The dominance of one crustacean species in the diet during a period consistently related to the other crustacean species being found in small quantities.

Following post-hoc testing, the diet during the post-breeding period of 1995 and 1996 were found to have significantly more *E vallentini* and significantly less *L. larseni,* compared to the diet during the brooding period of 1995. Furthermore the diet during the post-breeding period of 1996 had significantly more *E. vallentini* compared to the diet during the incubation, brooding and crèche periods of all annual cycles and the pre-incubation period of 1995*. Nauticaris marionis* was found in significantly higher proportions in the diet during the brooding period of 1996 compared to the diet during all post-breeding periods, the crèche period during 1995 and 1996 and the incubation and brooding period of 1995.

When comparing these results to the nMDS ordination (Figure 2.3.), the dissimilarity of the diet composition amongst the same period over the different annual cycles seems to be driven by unequal proportions of dominant prey items, with the most dissimilar diets during a period looking to be as a result of unequal proportions, presence or absence of either *N. marionis* or *E. vallentini*. To elaborate, the diet during the brooding period 1994 was equally dissimilar to the diet during brooding period of 1995 and 1996, however, the diet during brooding periods of 1995 and 1996 were more dissimilar, discerned from the distance of centroids (Figure 2.3.). The diet during brooding periods contained different amounts of *L. larseni* over the different annual cycles (Figure 2.6)*,* but not significantly so. However, the diet during the brooding period of 1994 and 1996 contained *N. marionis,* whereas the diet during the brooding period of 1995 did not contain but did contain a small proportion of *E. vallentini.* Furthermore, the greater similarity of diets between crèche periods of 1995 and 1996 and dissimilarity of both these periods to the crèche period of 1994 seems to be driven by similar proportions of *E. vallentini* and the greater proportion of *N. marionis* during 1994. In addition, the dissimilarity of the post breeding periods (1995 and 1996), and similarity of the two periods to one another, seems to be further driven by significantly less *L. larseni* and *N. marionis* and significantly more *E. vallentini* during these periods compared to any other period. The greater similarity of the post breeding of 1994 to all other periods seems to be driven by the greater proportion of *L. larseni* during this period compared to the post breeding periods of 1995 and 1996.

2.3.4.2. Long term variation

Over the long term part of the study, the diet from 1994-1995 was different from the diet during 2012 and 2014 (Figure 2.6). An ANOVA revealed that the diet during the pre-moult period of 1995 consisted of significantly less *L. larseni* than during the pre-moult period of 2014 (F_1=9.77, p=0.01). However, the proportions of juvenile Nototheniid fish were consistent between these periods. This is most likely why the ADONIS test was non-significant for this period.

An ANOVA revealed that the proportion of *L. larseni* in the diet during incubation of 1994-1996 and 2012 was not significantly different (F_3=1.98, p=0.13). However, it revealed that the proportion of *L. larseni* was significantly different among brooding periods of 1994-1996 and 2014 (F_3=3.84, p=0.02), and a post hoc analysis revealed that this significant difference was between the brooding periods of 1995 and 1996. Thus, there was no indication of a long term change in the proportion of *L. larseni* in the diet. However, the proportions of *N. marionis* (brooding F_3=9.96, p<0.01) and *E. vallentini* (incubation: F_3=9.01, p<0.01 and brooding F_3=3.75, p=0.02) were significantly different over the long term. No *N. marionis* was found during the brooding period of 2014 compared to the brooding period of 1994 and 1995. With significantly greater proportions of *E. vallentini* being present in diet during the incubation and brooding period of 2012 and 2014, respectively than during the incubation periods and brooding periods of 1994 and 1996.

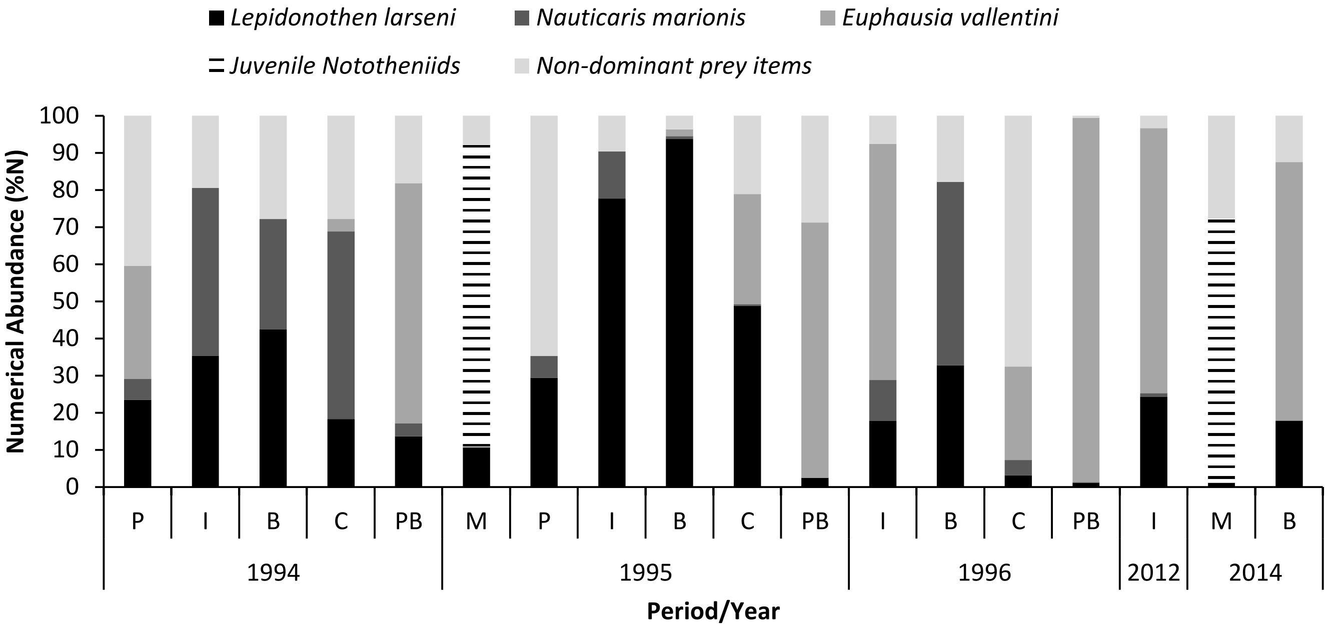

Figure 2.6. Relative contributions, in terms of percentage numerical abundance, of dominant prey items in the diet of the gentoo penguins at sub-Antarctic Marion Island during different periods (pre-incubation (P), incubation (I), brooding (B), crèche (C), post breeding (PB)and pre-moult (M)) within different years (1994-1996; 2012; 2014).

2.4. Discussion

This study investigated the temporal variability in the diet of gentoo penguins at Marion Island over three consecutive years during the 1990’s and then more recently during 2012 and 2014. Significant differences in diet composition were evident among years, as well as, among periods within the annual cycle. This latter variation was, however, not consistent over years. As per expectation, there was evidence to support a change in prey assemblage within the diet of gentoo penguins at Marion Island since the 1990’s.

2.4.1. General diet description

The diet of the gentoo penguin at Marion Island was relatively heterogeneous in terms of major taxa within the diet. It comprised of crustaceans, fish and cephalopods which varied in importance throughout the study period. These results are in agreement with the findings of Adams & Klages (1989) and LaCock et al. (1984) whom studied diet of the gentoo penguin at Marion Island during 1984/85 and 1982, respectively. Furthermore, with Marion Island representing the northern most limit of the gentoo penguin’s distributional range (Lynch 2013), the results reflect similar diet composition seen across more northern, sub-Antarctic localities. Typically, diet across these areas is more heterogeneous than southern localites, comprising of fish, crustacean and cephalopods with the fish component ranging from partial to complete dominance (Adams & Klages 1989; Robinson & Hindell 1996; Clausen & Pütz 2002; Lescroël et al. 2004). At Antarctic localities the diet is almost completely dominated by crustaceans (Croxall & Prince 1980; Volkman et al. 1980; Williams 1991).

Regarding more detailed dietary items, the gentoo penguin population at Marion Island had a strong dependence on two benthic prey items: the fish, *L. larseni*, and the crustacean, *N. marionis,* and one pelagic prey item: the crustacean, *E. vallentini.* Throughout the gentoo penguin’s distributional range Nototheniid fish form an important component of these birds’ diet e.g. South Georgia (Williams 1991), Macquarie Island (Robinson & Hindell 1996), Kerguelen Islands (Lescroël et al. 2004), Heard Island (Klages et al. 1990), and South Orkney Islands (Coria et al. 2000). However, in terms of the crustacean component, the crustacean species found in the diet of gentoo penguin is better explained by the biogeography of the crustacean species. For example, *Nauticaris marionis* is unique in the diet of the gentoo penguins at Marion Island (this study; La Cock et al. 1984; Adams & Klages 1989). The sub-Antarctic crustacean, *E. vallentini,* is more commonly found in the diet of gentoo penguins at more northern localities e.g. Kerguelen Island (Bost et al. 1994a; Lescroël et al. 2004), Heard Island (Klages et al. 1990) and Marion Island (Adams & Klages 1989). Whereas gentoo penguins at more southern localities tend to feed mainly on Antarctic crustacean, *E. superba,* e.g. South Orkney Islands (Coria et al. 2000), South Georgia (Croxall & Prince 1980; Kato et al. 1991), King George Island (Volkman et al. 1980); South Shetland Islands (Miller et al. 2010).

The high occurrence of Nototheniid fish, *N. marionis* and *E. vallentini* in the diet at Marion Island seems to be supported by the local bathymetry. Commonly known as rockcod, Nototheniid fish are widely distributed across the Southern Ocean, found most commonly in neritic waters and form important components of both benthic and pelagic ichthyofauna (Dewitt et al. 1990). The benthic *N. marionis,* commonly known as the swimming shrimp, is restricted to the shelf regions of sub-Antarctic and forms an important part of the benthic biomass on the inter-island shelf at the PEIs (Perissinotto & McQuaid 1990; Branch et al. 1993). In addition, the pelagic crustacean *E. vallentini*, together with *Thysanoessa vicina*, dominates the Euphausiid community on the inter-island shelf (Hunt & Pakhomov 2003). The foraging behaviour of gentoo penguins has been described as opportunistic, displaying the ability to forage on demersal, benthic and pelagic prey (Bost et al. 1994b; Robinson & Hindell 1996; Lescroël et al. 2004; Lescroël & Bost 2005; Takahashi et al. 2008; Miller et al. 2010). Elsewhere, the key determinants of gentoo penguin foraging behaviour and subsequently diet composition have been shown to be local oceanography (Lescroël & Bost 2005), bathymetry (Kokubun et al. 2010) and spatial and temporal availability of prey (Lescroël et al. 2004). At Kerguelen Island, the contrasting oceanographic settings that two different colonies of gentoo penguin faced was shown to have a large impact on the at-sea distribution (Lescroël & Bost 2005) and the diet (Lescroël et al. 2004) of the gentoo penguins from the respective colonies.

Therefore, by examining the composition of the diet of the gentoo penguin at Marion Island, the shallow inter-island shelf between Prince Edward Island and Marion Island provides ideal habitat for the birds to forage on demersal and benthic prey at accessible depths, as well as, encounter pelagic species. Adams & Wilson (1987) reached similar conclusions with concurrent use of speedometers and stomach content analysis. Furthermore, this conclusion is supported in Chapter 3 of this thesis, wherein the inter-island shelf is shown to be an important foraging area of gentoo penguins at Marion Island.

2.4.2. Within and among annual variation (1994-1996)

The diet exhibited large variation in the ratios of fish and crustacean over three years (1994-1996) within and among the different periods of the gentoo penguin's annual cycle at Marion Island. During 1994, fish and crustacean were present in the diet in relatively equal proportions; this then progressed to fish dominating the diet for the majority of 1995 and crustaceans dominating the diet during 1996. However, the proportion of fish was always greatest during the brooding period of the gentoo penguins. These finding complement those of Adams & Klages (1989) for the gentoo penguin at Marion Island, whom too found variation in major taxa in the diet over a year with the proportion of fish increasing during the breeding season. This variation in the proportion of crustacean and fish in the diet, throughout and among years, for the gentoo penguin has been noted beyond Marion Island too e.g. South Georgia (Croxall et al. 1999), Antarctic (Coria et al. 2000) and the Falkland Islands (Clausen & Pütz 2002).

Lepidonotothen larseni, which represented the majority of the fish component in the diet, is a benthic species with a pelagic larval phase (Dewitt et al. 1990). At Marion Island this larval phase lasts throughout spring and summer shifting to benthic life during autumn or winter (Dewitt et al. 1990). The shift to the benthic life of *L. larseni* coincides with the increase in appearance of these fish in the diet during the breeding season of the gentoo penguins. Furthermore, the diet during the pre-moult period of 1995 and 2014 (a time that corresponds to summer) was dominated by juvenile Nototheniids. This is similar to the findings and conclusions of Adams & Klages (1989), whom also noted an increase of juvenile Nototheniid fish in the diet of the gentoo penguin during summer and attributed the increase to the increase in availability of adult Nototheniid fish during the breeding season due to maturation of juveniles.

Seabirds will often select for prey with higher energetic value during an energetically demanding time like the brooding period. Even though this argument has been supported for other seabirds (e.g. yellow-eyed penguin *Megadyptes antipodes* (Browne et al. 2011), black-legged kittiwakes, *Rissa tridactyla* (Suryan et al. 2000) and pigeon guillemots, *Cepphus columba* (Golet et al. 2000)) this does not seem to be the case for the gentoo penguins at Marion Island. The temporal variability of fish in the diet seems to be more strongly supported by becoming more temporally available during the brooding period. In support of this argument, an increase in fish in the diet of the gentoo penguins at Kerguelen Island coinciding with the peak egg laying period was also not attributed to changing energetic demands during the breeding period but rather fish becoming more temporarily available due to spawning migrations (Lescroël et al. 2004).

From 1994 - 1996, the crustacean component in the diet of the gentoo penguins changed from predominantly *N. marionis* during 1994 to *E. vallentini* during 1995 and 1996. Neither, crustacean species were found congruently in similar quantities in the diet; rather the dominance of either species in the diet during a period related to the other being completely absent or found in relatively small quantities. A similar temporal change of these crustacean species was observed in the diet of the gentoo penguins at Marion Island during 1984/5 (Adams & Klages 1989).

It has been shown that the varying latitudinal position of the SAF is an important contributing factor in determining the macrozooplankton community of the inter-island shelf between the PEIs (Pakhomov & Froneman 1999a; Hunt & Pakhomov 2003). Historically, during times when the SAF lay further to the north a significantly lower macrozooplankton biomass and size, with special mention to *E. vallentini*, was observed on the inter-island shelf compared to years when the SAF lay further south (Hunt & Pakhomov 2003). This decrease was attributed to the reduced advection of *E. vallentini* onto the shelf due to increased water stability induced by the occurring anticyclonic eddies (Pakhomov & Froneman 1999a; Hunt & Pakhomov 2003). Due to increased water stability and formation of anti-cyclonic eddies, when the SAF lies further north, autochthonous phytoplanktonic blooms occur on the inter-island shelf which are an important dietary component of *N. marionis* (Pakhomov et al. 1999). It has been suggested that during these times *N. marionis* increases in abundance and availability on the inter-island shelf (Perissinotto & McQuaid 1990). The large effect that the latitudinal positioning of the SAF has on the crustacean composition of the inter-island shelf may be a major driving factor in the variation of the crustacean species in the diet of the gentoo penguin at Marion Island. However, it is hard to reach a concrete conclusion without concurrent data on prey availability in the area during the same period as this study. Bost et al. (1994) provided some evidence (however not conclusive due to different sampling methods used), that the proportion of *E. vallentini* in the diet of gentoo penguins at Kerguelen Island is related to the availability of crustaceans in their foraging range. In contrast, gentoo penguins at King George Island, Antarctica, did not exhibit any changes in prey species over a one year period and consistently preyed upon Antarctic crustacean, a readily available prey item for this locality (Volkman et al. 1980).

The within and among season changes in diet composition of gentoo penguins during this study is most likely representative of changes in the availability of the respective prey items in the inshore and inter-island shelf region at the PEIs. These results are comparable to those of Miller et al. (2010) and Lescroël et al. (2004) who found that changes in diet were linked to variability in oceanography, prey life cycles and resulting prey availability. The lack of information on prey availability during the study makes it difficult to relate oceanographic variability to changes in prey availability and resulting changes in the diet.

2.4.3. Long term

This study found evidence to support long term change in the diet of gentoo penguins at Marion Island between 1994-1996 and 2012 and 2014. The dominant fish species in the diet, *L. larseni*, remained the same over the long term during this study. However, there has been an evident change in the dominant fish species since the 1984/5 when Adams & Klages (1989) reported the fish *Notothenia squamifrons* to be the dominant fish species in the diet of the gentoo penguin at Marion Island. The identification of fish during this study and that of Adams & Klages (1989) was done through the identification of otoliths. It is a difficult process, especially if the otoliths are damaged or eroded leading to the misidentification of species. For example, LaCock (1984) misidentified *L. squamifrons* as *Harpagifer georgianus* (Adams & Klages 1989). However, during the entire period of this study the otoliths were consistently identified by Dr. N. T. Klages and later Mr. B. M. Dyer, an apprentice of Dr N.T. Klages. Therefore, it can be assumed that the decrease of *L. squamifrons* in the diet is a true reflection and not as a result of human sampling error or misidentification of otoliths. Furthermore, a similar change of dominant fish species has occurred in the diet of the Crozet shag at Marion Island. During 1984/ 85 the dominant fish in the diet of the Crozet shag was *L. squamifrons* (Espitalier-Noël et al. 1988) which also changed to *L. larseni* during the late 1990s and early 2000s (Crawford et al. 2003a). Thus, the change of near complete dominance of *L. squamifroms* to the near absence in the diet of gentoo penguins and Crozet shags suggests that there were changes in availability of these fish around the PEIs. Both Allan et al. (2013) and Crawford et al (2014) suggest that the abundance of these fish have decreased in the local marine environment at the PEIs due to industrial fishing that occurred around the islands from the mid-1990s to 2004 (Lombard et al. 2007). If so, this is being reflected in the diet of the gentoo penguin and Crozet shag.

The proportions of *E. vallentini* and *N. marionis* in the diet showed change over the long term investigation of this study. The diet during incubation and brooding of 2012 and 2014, respectively, had significantly less *N. marionis* and significantly more *E. vallentini* than during the respective period during 1994-1996. In addition, *N. marionis* was also observed to contribute more to the diet of these birds than *E. vallentini* approximately 30 years ago during 1984/85 (Adams & Klages 1989). *Nauticaris marionis* contributed 26.7% and 38.1% of wet mass to the diet of the gentoo penguin on Marion Island during August and September during 1984, respectively, months that correspond to the approximate time of the brooding period. Whereas, *E. vallentini* contributed 8.9% and 17.9% of wet mass, respectively, to the diet during August and September during 1984. The $\delta^{13}C$ signature of benthos species around the island, including *N. marionis*, has decreased from 1984 to 2009 (Pakhomov et al. 2004; Allan et al. 2013). In contrast, the $\delta^{13}C$ signature of the pelagic macrozooplankton, with special mention of *E. vallentini,* has remained stable over the same time period (Allan et al. 2013). These contrasting findings have been attributed to the long term southward migration of the SAF and the resulting increase of allochthonous food sources, which includes *E. vallentini* and decreased occurrence of phytoplanktonic blooms, an important autochthonous food source for the benthos species, such as *N. marionis,* at the PEIs (Pakhomov et al. 2004; Allan et al. 2013). These findings suggest that there has been a decrease in availability of *N. marionis* at the PEIs (Allan et al. 2013) and is supported by the decrease of presence and abundance of this species in the diet of the gentoo penguin at Marion Island. However, the significant changes that were observed during the course of this study maybe due to a relatively small sample size. Also, in more recent years, collection of stomach content samples was confined to one period of the annual breeding cycle per year. To fully understand whether the observed changes in this study are due to long term changes in prey availability or if they are just a reflection of temporal fluctuations in the diet, collection and analyses of this population's diet should continue over a longer period.

2.5. Conclusion

This study has provided further evidence of the high degree of plasticity in the diet of gentoo penguins and their opportunistic foraging behaviour, as they were able to forage on benthic, demersal and pelagic species. Highlighted in this study was the high within and among annual variability in the diet of gentoo penguins at Marion Island. In all likelihood, the variation was associated with prey life cycles and the highly dynamic oceanographic conditions at the PEIs. To better understand the trophic ecology of gentoo penguins would require improved understanding of foraging distribution as well as temporal prey availability within these areas. This study provides some evidence that the declining population numbers of gentoo penguins at Marion Island is linked to a change in prey availability due to changes in the local environment. However, further studies involving diet, at sea distribution and the influence of changing oceanographic parameters on spatio-temporal availability of prey is needed to reach a concrete conclusion about the ultimate factors causing the decline of the gentoo population on Marion Island. Furthermore, this study highlights the necessity for the continuation of long term dietary studies of these birds.

Chapter 3

Foraging behaviour, with a unique strategy, in breeding gentoo penguins, *Pygoscelis papua*, at sub-Antarctic Marion Island

3.1. Introduction

Foraging provides the link between marine predators, lower trophic levels and the environment (Kokubun et al. 2011). Therefore, knowledge about the diet and at sea distribution of marine predators is essential to understand a predator's foraging ecology and its' role in the marine ecosystem (Barlow & Croxall 2002; Baylis et al. 2015). Such knowledge is important for predicting responses of marine predators to global climate change and other anthropogenic pressures (Gremillet & Charmantier 2010).

One such group of marine predators are seabirds, which are central place foragers during the breeding period (Furness & Camphuysen 1997). To achieve maximum fitness, central placed foragers maximize the rate at which they feed their young (Orians & Pearson 1979). However, a delicate balance must be found between self and chick provisioning of resources. Therefore, adults have increased energy demands while breeding as they need to maintain body condition, regularly feed broods and retain reserves for periods of fasting (Furness & Camphuysen 1997; Pinaud & Weimerskirch 2002). Thus seabirds face important energetic and time constraints, and trade-offs between caring for themselves and their chicks (Trivers 1974). To achieve this balance it has been suggested that seabirds alternate between short, regular foraging trips, close to the breeding colony, for chick provisioning and periodically perform long trips, to distant reliable prey patches, for self-maintenance (Weimerskirch 1998; Saraux et al. 2011). This behaviour has been observed for several families of seabirds including shearwaters (Weimerskirch 1998; Paiva et al. 2010), albatrosses (Weimerskirch et al. 1997) and penguins (Clarke 2001; Saraux et al. 2011).

Gentoo penguins, *Pygoscelis papua,* are inshore foragers, rarely exceeding 30km from the colony while breeding (Bost & Jouventin 1990), making them particularly dependent on local marine resources and sensitive to fluctuations in prey availability (Lescroël & Bost 2005; Reid et al. 2005). To help buffer against these fluctuations, they exhibit considerable plasticity in foraging strategies within and between localities across their range (Croxall et al. 1988; Lescroël & Bost 2005; Miller et al. 2009). This flexibility has also been shown to be a function of local habitat features such as bathymetry (Lescroël & Bost 2005), the characteristics of prey which are locally available (Croxall et al. 1988; Lescroël & Bost 2005) and the temporal changes in locally available prey (Miller et al. 2009). An example of this is seen in the diet items consumed where they often switch from preying upon benthic fish to pelagic crustaceans within a breeding season (Chapter 2; Adams & Klages 1989; Lescroël et al. 2004; Lescroël & Bost 2005). Prey items can further be reflected in the diving behaviour of gentoo penguins which has been studied throughout most of its distribution including Macquarie (Robinson & Hindell 1996), Kerguelen (Lescroël & Bost 2005), South Shetland (Miller et al. 2009, 2010), King George (Kokubun et al. 2010) and the Falkland (Masello et al. 2010) Islands. Typically they have been described as benthic-demersal foragers (e.g. Croxall et al. 1988; Wilson et al. 1996; Kokubun et al. 2010), searching the ocean floor for prey (Takahashi et al. 2008) but also foraging for pelagic prey (Bost et al. 1994b; Reid et al. 2005).

However, neither the diving behaviour nor the at-sea distribution of the relatively small population of gentoo penguins at sub-Antarctic Marion Island has received previous attention. At Marion Island, one of two islands making up the Prince Edward Islands Archipelago (PEIs), the gentoo penguin population was recently estimated to consist of about 700 breeding pairs in 2012 (Crawford et al. 2014). The population has experienced a considerable decline in breeding success and breeding pair numbers since 1994, which have approximately halved in size between 1994 and 2012 (Crawford et al. 2003b, 2014). Apart from chick predation by skuas (Crawford et al. 2003; Crawford et al. 2014), this decline is thought to be partly linked to decreased prey availability in the inshore waters, particularly on the inter-island shelf between Marion and Prince Edward Island (Allan et al. 2013; Crawford et al. 2014). It is therefore important to quantify the dive and at-sea distribution along with diet (Chapter 2) of this population to aid in understanding what is driving their decline. This study achieves this for the first time, by investigating the fine scale foraging behaviour of gentoo penguins at Marion Island with the use of GPS and TDR loggers during the brooding period. It is anticipated that these birds will forage over the shallow inter-island shelf between Marion and Prince Edward Island following predictions made by Adams & Wilson (1987).

3.2. Material and Methods

3.2.1. Data collection

Field work was conducted at Trypot Beach (46°53'14.33"S, 37°52'1.66"E) on sub-Antarctic Marion Island between 20 and 30 August 2014. The resident gentoo penguin colony is the largest of 18 colonies on the island and consisted of 99 breeding pairs during the 2014 breeding season. At time of instrument deployment, 74 breeding pairs were brooding small chicks and 25 breeding pairs were incubating eggs. The brooding period lasts from approximately mid-July to mid to late September (Crawford et al. 2003b) when adult birds perform solo diurnal foraging trips while partners tend to chicks (Adams & Wilson 1987). During the brooding period, partners are relieved daily with most partner change-overs occurring during the late afternoon (Adams & Wilson 1987).

Ten adult gentoo penguins brooding a recently hatched chick were equipped with GPS loggers (IgotU120, Mobile action technology) packaged in heat-shrink tubing (44.5mm x 28.5mm x 13mm) programmed to sample locations every two minutes and TDR loggers (G5 long life, CEFAS Technology Limited, England, 11.5mm x 35.5mm; cumulative weight of TDR and GPS: 29.01g) programmed to sample data every two seconds. The TDR loggers were attached to the bottom of the GPS logger with black waterproof TESA® tape (Beiersdorf, AG, GmbH, Hamburg, Germany; Figure 3.1.), before these were attached. Targeted nests were observed from approximately 14:00 until sunset, as this is the approximate time period that the birds return from foraging to their colonies to relieve their partners from nest duties (Adams & Wilson 1987). Once nesting adults were relieved and moved a small distance away from the colony the bird was captured using a modified hook on the end of a two meter pole. One observer restrained the bird by securing the head firmly between their body and upper arm, restraining the feet with both hands and supporting the body of the bird on their legs, while another observer attached the loggers using TESA® tape, to the caudal position of the bird’s back (Figure 3.2.; Bannasch et al. 1994). Cable ties and cyanoacrylate glue (Loctite 401®) were used to help secure the instruments to the study birds. Specifically, attachment involved three strips of tape (approximately 10 centimetres long) being placed underneath the feathers perpendicular to the bird’s midline with the adhesive side of the tape facing upwards. Strips were placed parallel to one another and approximately half a centimetre apart. The data logger was then placed in the middle of the strips and alternatively each end of the tape pulled over. Two cables ties were then fastened around the data logger, tape and feathers with the ends secured by cyanoacrylate glue. In addition, and to facilitate recapture, each bird was marked on the white chest feathers with porcimark dye. Attachment of data loggers took approximately 10 minutes, where after the bird was immediately released. To facilitate recording of multiple foraging trips, retrieval of devices occurred approximately five days after deployment. Retrieval of devices was done at the beach where birds exit the sea to minimise disturbance around the colony. The retrieval of data loggers took approximately five minutes.

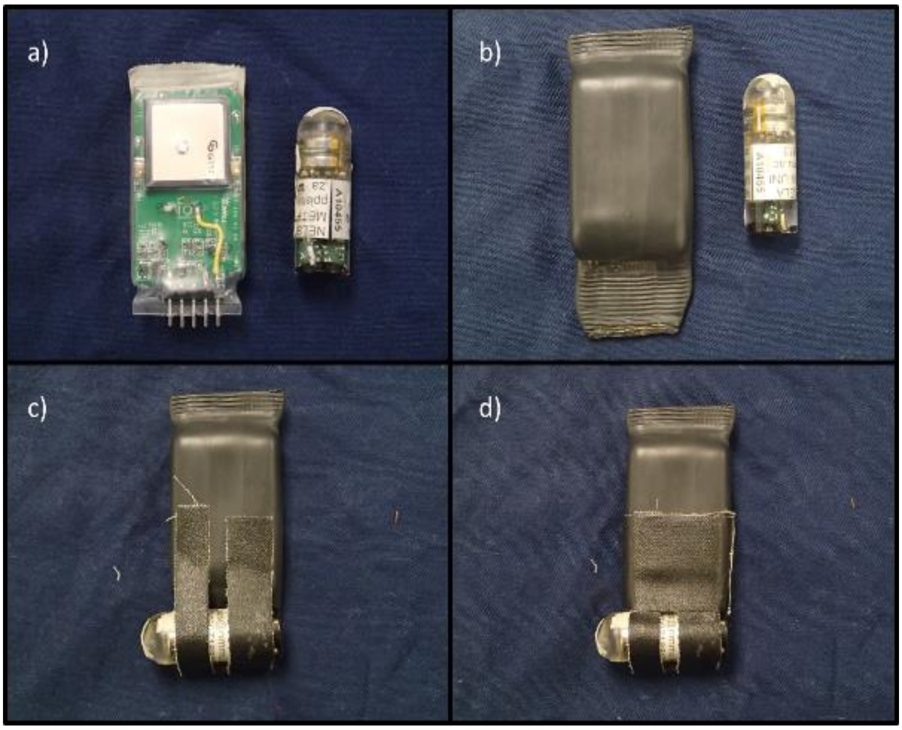

Figure 3.1. Example of the a) GPS and TDR units that were deployed on gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014. b) GPS covered in heat shrink tubing and clamped at either end with pliers to ensure a waterproof package. c) TDR was fastened to the GPS unit with two thin strips of TESA ® tape and d) secured to the GPS by wrapping a thicker piece of tape tightly around the thinner strips of tape and the GPS

Figure 3.2. Position of device deployment on a gentoo penguin at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014.

3.2.2. Processing of data

All data processing and analyses were conducted in R version 3.1.2. (R Core Team 2014) and ArcMap 10.2. software (ESRI). All values are reported as means ± standard deviation, unless otherwise stated, and significance is specified as $p < 0.05$.

3.2.2.1. TDR data

The pre-processing of TDR data from each bird track was achieved using the *diveMove* package (Luque 2007) and involved: (1) zero offset correction, which was done by visually inspecting the dive tracks of each bird and finding a feasible offset value. Zero offset correction is a method used to calibrate the depth measurements of TDRs (Luque & Fried 2011). Selecting a feasible offset value is facilitated by the return of these birds to land (Luque & Fried 2011). Additionally, (2) correction of time budget summaries (i.e. whether the bird was in the water or on land) of each dive trace, were done through manual edits by viewing the dive trace using the features within the *diveMove* package. When the birds exited the water there was an evident increase in temperature therefore providing a reference for correction and visual comparison with the GPS data using ArcMap 10.2. software (ESRI).

Only dives that were greater than a depth of five meters were considered for analysis as dives shallower than five meters were considered to be travelling dives without active foraging (Miller et al. 2009; Kokubun et al. 2010). The dive parameters that were extracted from TDR data included: (1) time of dive (2) total duration of dive, (3) total number of dives greater than five meters per foraging trip, (4) depth of each dive (calculated as the deepest point reached during a dive) and (5) duration of bottom time of the dive (Berlincourt & Arnould 2014; Chilvers et al. 2014).

3.2.2.2. GPS data

Analyses were performed on complete foraging trips, defined as the time between when the birds departed from land, i.e. the last sampled location on land, and when they returned to land, i.e. the first known location on land following a foraging trip (Masello et al. 2010; Berlincourt & Arnould 2014).

Using an algorithm derived by McConnell et al. (1992), erroneous GPS locations based on a transit speed of greater than 8 km.h^{-1} (following Lescroël & Bost 2005) were filtered from the data (package: *trip,* Sumner 2014). The GPS data loggers access to satellites were interrupted every time the bird went underwater which caused irregular time intervals between positional fixes of the birds resulting in gaps in the tracks potentially biasing estimates of travelling speed and path movement (Johnson et al. 2008). Following Baylis et al. (2015), the filtered data were therefore processed using a non-stop continuous time correlated random walk model (package: *crawl*, Johnson 2013) to estimate the approximate foraging track. Dive locations were then interpolated on this track at time intervals defined by the onset of a dive which was determined during the processing of TDR data.

Additionally, locations were interpolated for one minute intervals in order to determine foraging parameters for each individual trip (package: *Move;* Kranstauber & Smolla 2014). Foraging parameters included: (1) the total path length (calculated as the sum between all interpolated fixes), (2) maximum distance from the colony (calculated as the greatest distance reached from last point on land for that trip), (3) trip duration (calculated as the time between the last and first point on land before and after a foraging trip) and (4) average travelling speed.

3.2.3. Statistical analyses

3.2.3.1. At sea distribution

Dives were assumed to be related to foraging activity (Kokubun et al. 2010). Therefore, interpolated dive locations were used to define important foraging areas which were estimated using kernel density plots (Worton 1989; Pelletier et al. 2014; Robertson et al. 2014). The 25%, 50% and 95% kernel density contours were calculated and plotted using the *kernel.UD* function (package: *adehabitatHR*, Calenge 2006) and were considered to represent areas of prey encounter or "hot-spot", core use and active foraging areas, respectively (Kokubun et al. 2010; Pelletier et al. 2014). To visually examine the difference in foraging areas between the different types of provisioning trips (see results), the contours were plotted separately for different trip types. All kernel density plots were plotted against the bathymetry contours that were generated by integrating data from General Bathymetric Charts of the Oceans (GEBCO; 0.0167 degree resolution;www.gebco.net) and fine-scale in situ data collected by the South African Navy (SAN; www.sanho.co.za). All maps were projected in PGS WGS 1984 World Mercator. The surface area (km^2) that was utilized in the areas of "hot- spot", core and active use foraging areas was calculated using the *kernel.area* function (package: *adehabitatHR,* Calenge 2006).

3.2.3.2. Consistency in dive parameters

To assess for within versus between individual differences in dive parameters, as well as, between the different types of provisioning trips (see results), linear mixed effects models (LME, package: *nlme;* Pinheiro et al. 2015) were used with a restricted maximum likelihood (REML, Beck et al. 2003; Zuur et al. 2009). The following dive parameters were assessed using LMEs and were included in the models as response variables: dive depth, total duration of dive and duration of bottom time (Beck et al. 2003; Austin et al. 2006; Kokubun et al. 2010). The models only included one fixed effect which was different types of provisioning trips (see results). Each foraging trip of each individual was given a unique number and thus the trip number nested within individual identification was included as a random effect (Ratcliffe et al. 2013).

LMEs are ideal to assess variation in dive parameters between individuals as they allow one to account for any temporal autocorrelation associated with dive parameters (Beck et al. 2003). Furthermore, by including individual identification as a random effect, within and between individual differences are taken into account by assuming different intercepts and/or slopes for each individual. This facilitates avoidance of pseudoreplication associated with having multiple responses from the same individual (Seltman 2010).

LMEs follow strict assumptions about the data, i.e. normality, independence and homoscedasticity of variance of the response variable and lack of collinearity among fixed effects (Zuur et al. 2009). Therefore, homoscedasticity and normality were tested for by creating an observed and fitted values plot, a histogram, Q-Q plot and box plot of the residuals of each response variable. If data violated these assumptions, an appropriate variance structure was fitted to the model and selected for by minimizing the Akaike information criterion value (AIC) and selecting the most significantly different model (Zuur et al. 2009). An autocorrelation function (ACF) was then applied to the data to investigate temporal autocorrelation (a violation of the independence assumption). Data were visually judged to be auto-correlated if the result of the ACF plot were not within the 95% confidence intervals (Zuur et al. 2009). All response variables were found to be auto-correlated. Consequently, all varying combinations of the random effects were fitted with the autoregressive variance matrix (corAR1) representing an autocorrelation structure of order 1 (Beck et al. 2003; Austin et al. 2006; Zuur et al. 2009). The best combination of random effects and their respective autocorrelation structure was accomplished, as above, by selecting the model with the lowest AIC value and that which was most significantly different via a one-way analysis of variance (ANOVA). Then by using the model with the random effects structure that best explained the variability in the model, the validity of the fixed effect was tested against the null model (i.e. a model that excludes the fixed effect).

3.2.3.3. Consistency in GPS derived foraging parameters

The GPS derived parameters violated the assumption of normality and homogeneity of variance that are assumed my LMEs (Zuur et al. 2009). Therefore, following methodology of López-López et al. (2013), a Kruskal Wallis test with 9999 Monte Carlo permutations and a stratification defined by bird identification (to control for repeated measure for individuals) was used to investigate consistency in GPS parameters between different types of trips (package: coin; Hothorn et al. 2008). However, average speed was found to be normally distributed and therefore differences were investigated using a nested one-way analysis of variance (ANOVA).

3.3. Results

3.3.1. Data outcome and quality

Instruments were successfully retrieved from nine study birds after multiple trips. From these retrievals, TDR data from 58 complete trips (6 ± 2 trips per individual) were obtained but only during 32 trips were concurrent GPS data obtained (4 ± 1 trips per individual). On all accounts the number of trips recorded by the GPS loggers was limited by the life span of the battery, with one exception where the GPS was removed before the battery went flat. During the 58 trips recorded by the TDRs, 5067 dives greater than five meters were recorded (563 ± 256 per individual). Visualization of the GPS tracks revealed that the birds were alternating between two classes of foraging trips. The first entailed birds not returning to the colony after being at sea. Instead, these birds remained near the point of exit to the sea until departure for a foraging trip the next day. Gentoo penguins can digest the flesh of fish within eight to 16 hours (Gales 1985) and therefore it was assumed that all food consumed during these trips was digested by adults and not provided to their chicks.

Therefore, such foraging trips, were assumed to be for self-maintenance. The second class entailed birds returning to the colony after being at sea for chick provisioning. Directly after device deployment in the late afternoon, three birds departed to sea and returned to the beach (but not the colony) later that day, therefore these trips were considered to be for self-maintenance. The remaining six birds returned to the colony after deployment and then departed to sea the next day, all executing a longer chick provisioning trip.

Of the 32 GPS tracks obtained, a total of 31 complete trips were recorded of which 20 were defined as chick provisioning trips (where they returned to the colony) and 11 were defined as self-maintenance trips. Of the 58 TDR tracks 41 were defined as being during chick provisioning (a total of 4902 dives) and 17 during self-maintenance trips (a total of 598 dives). On average birds performed 104 ± 34 dives during a chick provisioning trip and 35 ± 14 dives during a self-maintenance trip. For trips that were only recorded by TDR devices and not GPS devices, chick provisioning trips were defined by whether a foraging trip was preceded by a day of non-foraging activity (i.e. no dives were recorded). It was assumed that during this time the adult had returned to the nest and was performing nest duties. This division of trips is supported as this behaviour was observed for foraging trips that were recorded by GPS and TDR data. Furthermore, gentoo penguins are rarely seen on the beach during day light hours during the breeding season (pers. ob). If a bird returns from a foraging trip during daylight hours it almost immediately returns to the colony where chick provisioning occurs (pers. obs). Seven study birds exhibited both self-maintenance and chick provisioning trips, whereas the remaining two only exhibited chick provisioning trips.

3.3.2. At sea distribution

Birds exclusively headed in a north-east direction from the Trypot beach study colony and almost always remained on the inter-island shelf above the 150m isobath (Figure 3.3). After all but one foraging trip the birds returned to the same beach they departed from. All trips that were classified as chick provisioning trips extended further away from the island (Figure 3.3a) than any of the self-maintenance trips (Figure 3.3b).

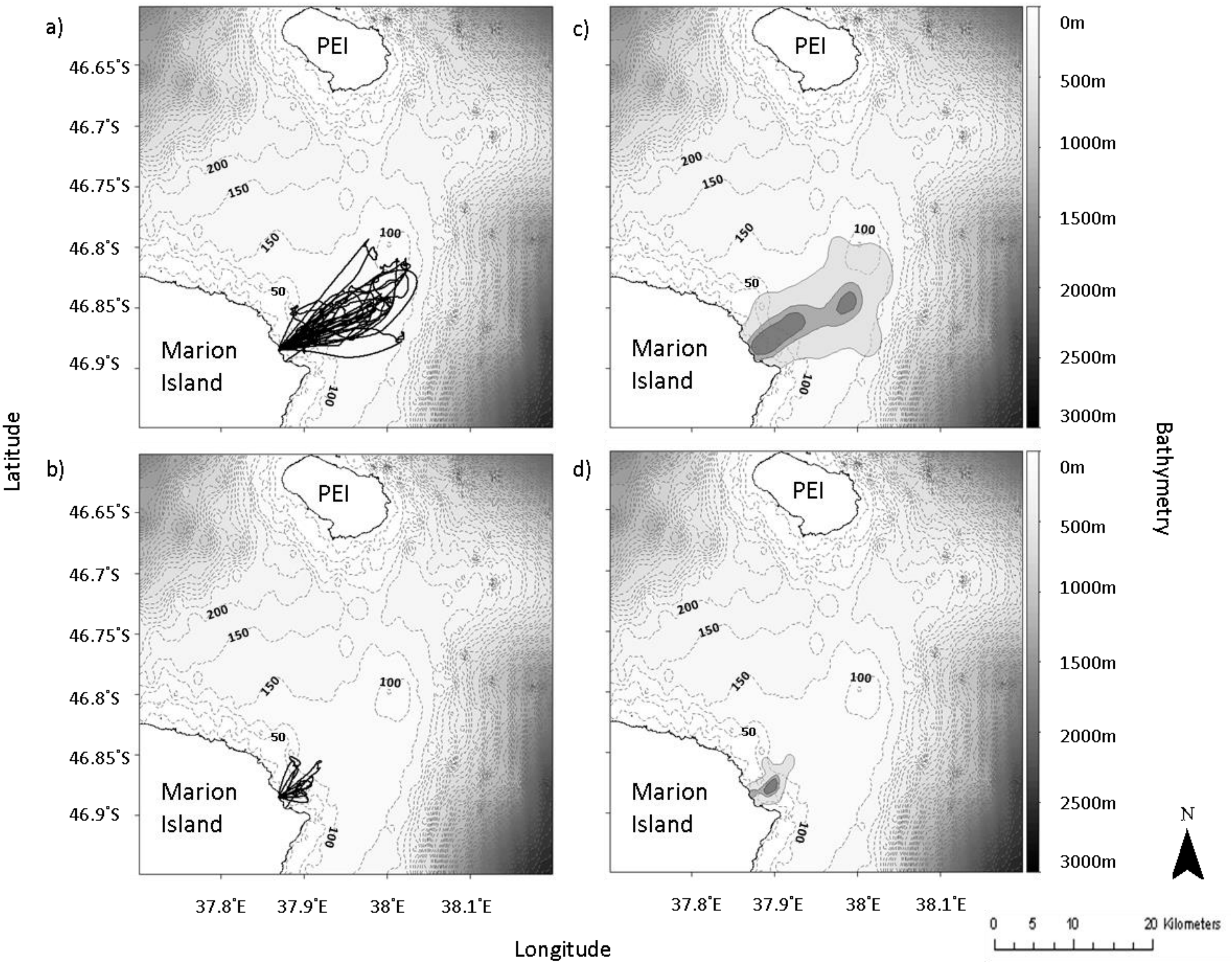

Figure 3.3. Tracks of gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014 for penguins executing a) chick-provisioning and b) self-maintenance trips and the kernel density of the diving locations for c) chick provisioning and d) self-maintenance trips. The “hot spot”, core, and active foraging areas (25%, 50% and 90% kernel density contours, respectively) have been indicated (from darkest to lightest grey, respectively). Dashed lines indicate isobaths at 50m intervals between Marion and Prince Edward (PEI) Islands.

The “hot-spot”, core, active foraging area for these birds were noticeably smaller during self-maintenance trips compared to chick provisioning trips (Table 3.1, Figure 3.3 c and d). During chick provisioning trips, the kernel density indicated that the birds’ had two “hot spot” foraging areas. The first was confined closer to the island over a broad depth range of 0 – 150m and the second was concentrated further from the coast within 100 to 150m depths (Figure 3.3.c). Self-maintenance trips indicated one “hot spot” foraging area closer to the coast and were confined between 0 and 100m from the land (Figure 3.3.d).

Table 3.1. Area of “hot spot”, core and active foraging areas (25%, 50% and 90% kernel density contours, respectively) of gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014. n = number of foraging trips.

Foraging parameter	**Self-maintenance (n=11)**	**Chick provisioning (n=20)**
"Hot spot" foraging area (km^2)	1.19	10.47
Core foraging area (km^2)	2.92	26.18
Active foraging area (km^2)	14.87	97.35

3.3.3. Consistency in dive parameters

Diving depth (L.Ratio=98.79, df=5, p<0.01) and total dive duration (L.Ratio=28.23, df=5, p<0.01) of the birds was found to be significantly different between different types of foraging trips (Table 3.2.). During self-maintenance trips the depth reached by birds was 39.05 ± 14.76m shallower and 37.16 ± 28.08 seconds shorter than during chick provisioning trips (Table 3.3.; Figure3.4.). Time spent at the bottom of dives was not significantly different between different types of provisioning trips (L.Ratio=0.60, df=6, p=0.44; Figure 3.4.).

Bird identification as the only random factor was found to be the most parsimonious model for all response variables (Table 3.2.). The standard deviation of diving depth, total dive duration and bottom time between birds was ± 13.16m, ± 24.38 and 10.95 seconds, respectively. For dive depth, total dive duration and bottom time, 5.61%, 8.01% and 7.01% of the variance, respectively, was explained by between bird differences; however, 94.38%, 91.99% and 92.92% of the variance, respectively was explained by within bird differences.

Table 3.2. Linear mixed effects models fit to dive parameters of gentoo penguin at sub-Antarctic Marion Island. The models are ranked from lowest to highest AIC value for each response variable. * Represent the most significantly different model.

Model	AIC
Bottom time ~ trip type + 1|Bird *	48 531.17
Bottom time~ 1 + 1|Bird	48 538.35
Bottom time ~ trip type + 1|Bird /Trip number	48 549.90
Bottom time ~ trip type + 1|Trip number	48 575.46
Bottom time ~ trip type	48 645.31
Diving depth ~ trip type + 1|Bird *	50 816.46
Diving depth ~ trip type + 1|Bird /Trip number	50 919.52
Diving depth ~ trip type + 1|Trip number	50 921.46
Diving depth ~ 1 + 1|Bird	50 922.53
Diving depth ~ trip type	50 969.29
Dive duration ~ trip type + 1|Bird *	56 834.02
Dive duration ~ 1 + 1|Bird	56 871.98
Dive duration ~ trip type + 1|Bird /Trip number	56 940.68
Dive duration ~ trip type + 1|Trip number	56 954.88
Dive duration ~ trip type	57 014.15

Table 3.3. Mean ± SD dive parameters calculated for each trip of gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014. n = number of foraging trips.

Dive parameter	**Self-maintenance (n= 17)**	**Chick provisioning (n=41)**
Dive depth (m)	66.71 ± 48.70	103.00 ± 52.38
Dive duration (sec)	163.78 ± 90.15	201.31 ± 85.19
Bottom time (sec)	89.60 ± 48.69	91.32 39.77

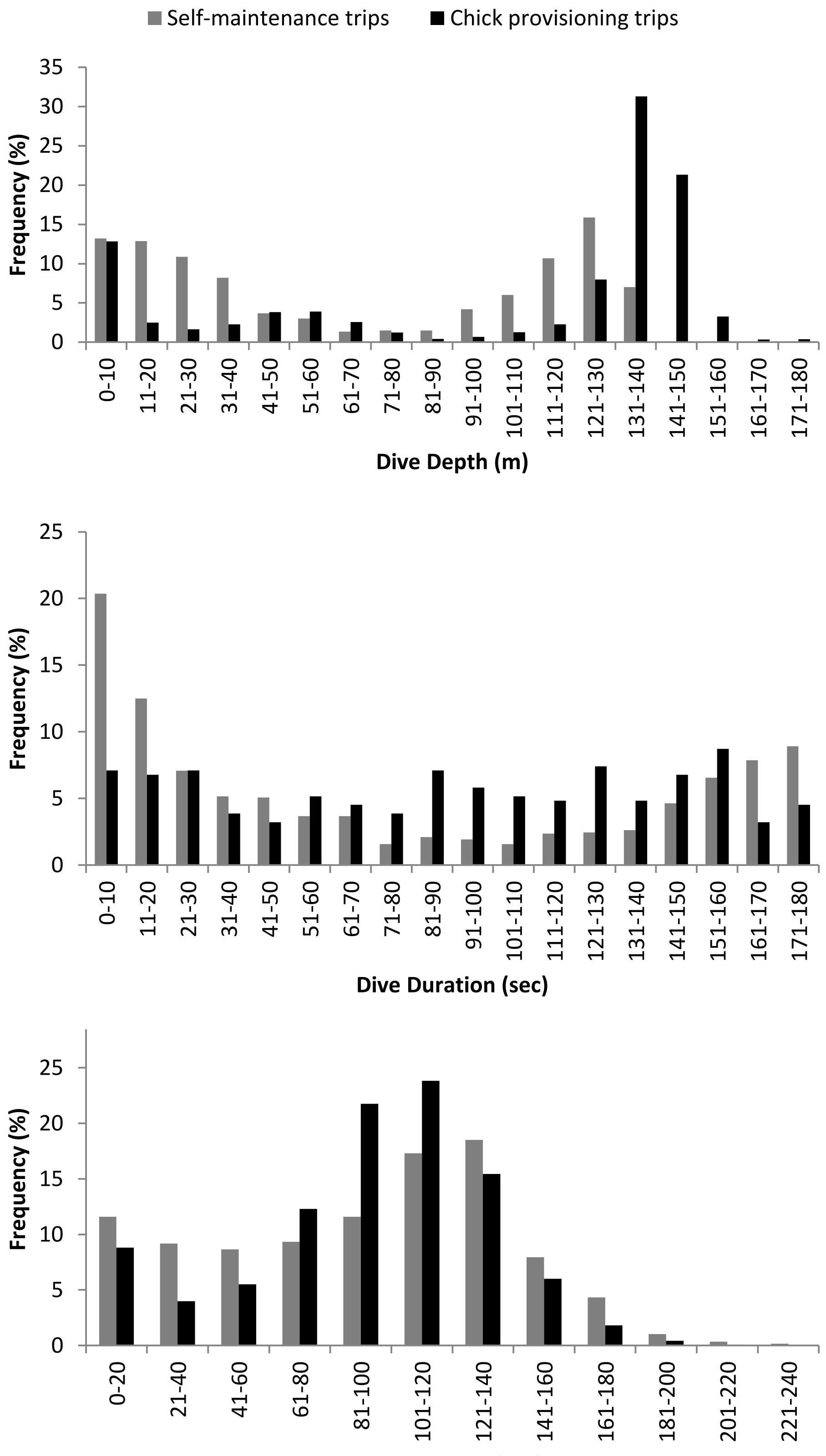

Figure 3.4. Frequency histogram of dive parameters for gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014 for self-maintenance and chick provisioning trips.

3.3.4. Consistency in GPS parameters

All birds performed single day foraging trips and only foraged during the day (Figure 3.5.). Different departure times were observed between self-maintenance and chick provisioning trips. Birds that departed for a chick provisioning trip largely left between 6:00 and 7:00, whereas, birds that departed for a self-maintenance trip largely left between 15:00 and 16:00. The time that birds returned from a chick provisioning trip varied more (13:00 – 19:00) compared to birds returning from self-maintenance trips (18:00 – 19:00). Shortly after returning from a chick provisioning trip the birds returned to the colony. Conversely, birds returning from a self-maintenance trip remained near the point of exit until the following morning where they all proceeded to perform a longer chick provisioning trip. Chick provisioning trips were further and longer than during self-maintenance trips as path length, maximum distance reached away from the colony and trip duration was found to be significantly less during self-maintenance trips (Table 3.3., Figure 3.6.). Only mean travelling speed during trips were found to be consistent between different types of provisioning trips (Table 3.4., Figure 3.6.).

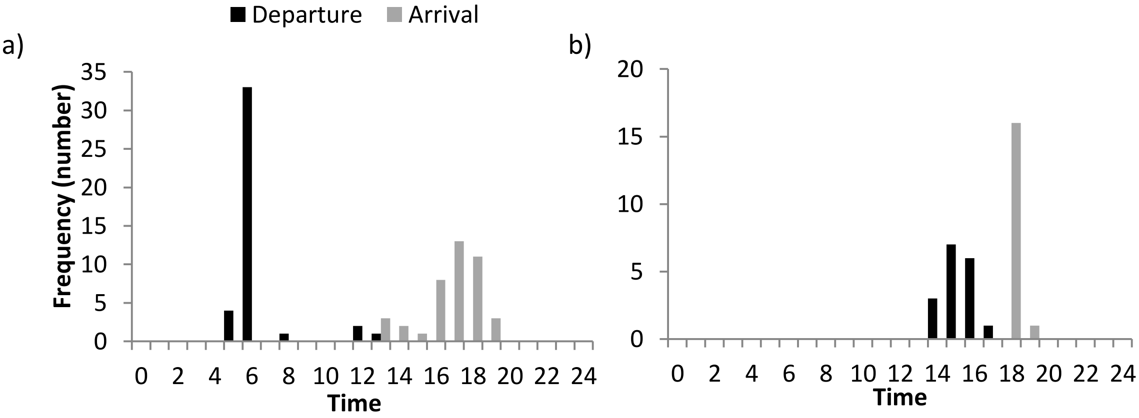

Figure 3.5. Departure and arrival times for a) chick provisioning and b) self-maintenance foraging trips for all tracked gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014.

Table 3.4. Mean ± SD GPS parameters, calculated for each foraging trip of gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014, comparing chick provisioning trips (n = 20) and self-maintenance trips (n = 11), with results of Kruskal Wallis with 9999 Monte Carlo permutations test and nested ANOVA tests. Results of nested ANOVA are underlined.

GPS Parameter	Self-maintenance	Chick provisioning	χ2	F value	P-value
Path length (km)	7.14 ± 2.61	22.72 ± 8.20	12.94		<0.01
Maximum Distance reached (km)	3.17 ± 0.97	9.95 ± 3.60	12.07		<0.01
Trip Duration (h)	2.96 ± 0.78	10.01 ± 1.92	14.64		<0.01
Average Travelling speed ($km.h^{-1}$)	2.64 ± 0.59	2.24 ± 0.62		0.61	0.81

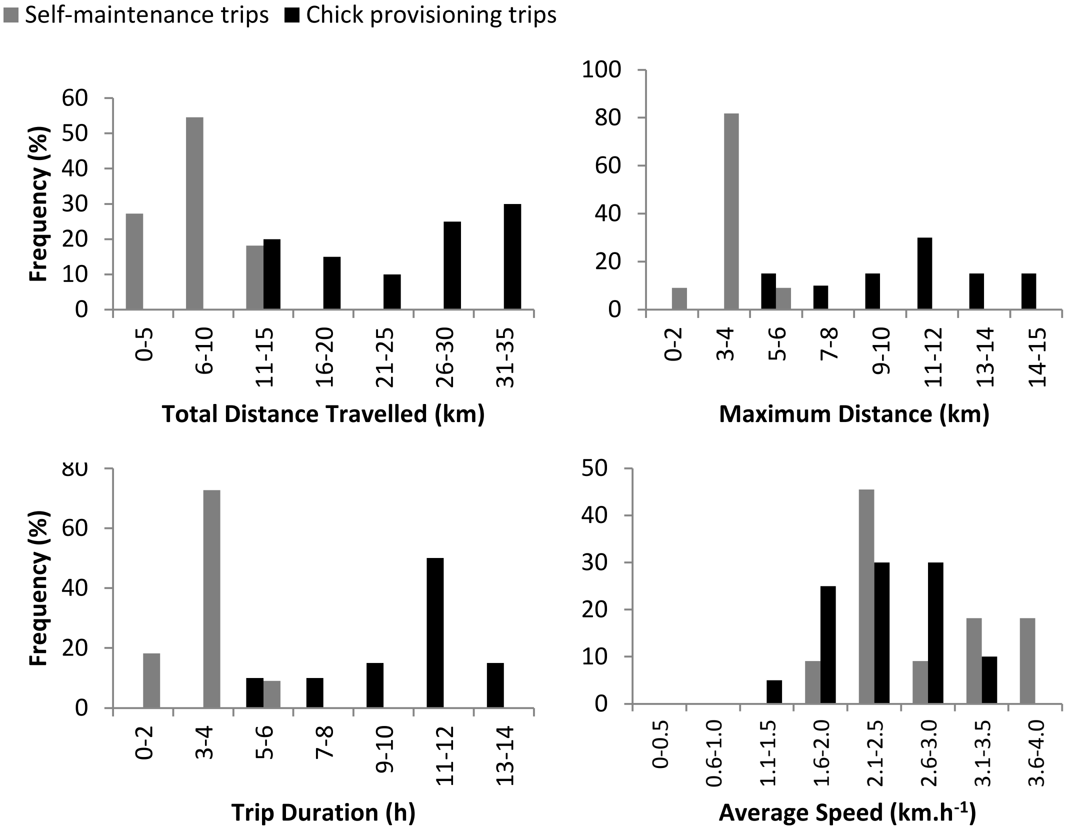

Figure 3.6. Frequency histogram comparing GPS parameters of chick provisioning and self-maintenance trips for gentoo penguins at Trypot Beach colony at sub-Antarctic Marion Island during 20 – 30 August 2014.

3.4. Discussion

For the first time, this study described the fine scale foraging behaviour of gentoo penguins at Marion Island. The birds foraged diurnally, spending the night either roosting on the beach or brooding chicks. Additionally, the shallow inter-island between Marion Island and Prince Edward Island was identified as an important foraging area for these birds. Interestingly, a new type of foraging strategy was identified during the course of the study. The birds were found to be alternating between long chick-provisioning trips and short trips self-maintenance trips.

The gentoo penguins alternated between two different types of foraging trips during this study: chick provisioning and self-maintenance trips. Chick provisioning trips were significantly longer and further away from the breeding colony than self-maintenance trips. A number of breeding seabirds (Tveraa et al. 1997; Weimerskirch 1998), including some penguin species (Clarke 2001; Taylor et al. 2002; Ropert-Coudert et al. 2004; Kato et al. 2008; Saraux et al. 2011), alternate between short and long foraging trips during chick rearing in an attempt to try compensate for increased energy demands during chick rearing. While breeding, animals face important energy trade-offs between self-maintenance and provisioning for their young (Trivers 1974; Saraux et al. 2011). Chicks benefit from frequently being fed but this is at the cost of the parents' stored energy reserves (Weimerskirch 1998; Clarke 2001; Ropert-Coudert et al. 2004). Therefore, regular short trips have been reported before in other seabirds, in relatively close proximity of their breeding colonies so to regularly feed chicks (Weimerskirch 1998; Ropert-Coudert et al. 2004; Kato et al. 2008). However, to compensate for energy loss in the adults, some species have periodically been noted to perform longer foraging trips, to further, more predictable and profitable prey patches for self-maintenance to restore body stores. For example, Clarke (2001) speculated that foraging trips closer to the breeding colony of the Adélie penguins, *Pygoscelis adeliae,* from Béchervaise Island, Antarctica, did not yield enough energy to maintain the parent's body condition as well as regular feeding of the chick. Thus, periodically, adults would perform longer, often overnight, foraging trips and travel further to a prey patch that is known to be more profitable and remain in the foraging area longer than would be required to only meet chick resource requirements.

The longer chick provisioning and shorter self-maintenance foraging trips exhibited during this study seem to be unique among seabirds. Other studies have associated shorter foraging trips with chick provisioning and longer trips with self-maintenance (Weimerskirch 1998; Clarke 2001; Ropert-Coudert et al. 2004; Kato et al. 2008; Saraux et al. 2011). The chick provisioning trips are comparable to the single day trip durations of chick rearing gentoo penguins at the South Shetland (Miller 2010), King George (Kokubun 2010), Falkland (Masello et al 2010) and Macquarie Islands (Robinson and Hindell 1996), however, the short afternoon trips for gentoo penguins appears to be unique to Marion Island. Previously, Adam and Wilson (1987) reported that out of 100 birds monitored, only 13 departed for the sea in the afternoon, of which 11 spent the night at sea and two returned the same day after spending 4.8 hours and 3.7 hours at sea. This falls in line with most birds being diurnal foragers as they are visual predators and cannot detect prey in low light conditions (Wilson et al. 1993, 1996). In this study both short and long trips only occurred during the day. Taylor et al. (2002) speculated that by remaining out at sea during an overnight trip the cost of thermoregulation and risk of predation for the Humbolt penguin, *Spheniscus Humboldt,* was less than the cost to travel back to land and return to the sea the following morning. For gentoo penguins at Marion Island the relatively close proximity of their foraging area to land means that the cost of remaining out at sea overnight might outweigh the cost of returning to land to rest which gives rise to the unique short self-maintenance trips these birds are executing.

Important to note is that tracked birds in this study were brooding chicks. Gentoo penguins at Marion Island consume more fish while brooding than during any other time of their breeding cycle (Adams & Klages 1989; Chapter 2). During this time the majority of their diet is made up of benthic Nototheniid fish, with the remainder of their diet consisting of the crustaceans *Nauticaris marionis* and *Euphausia vallentini*, which vary in proportion between years (Chapter 2). The inter-island shelf between Marion and Prince Edward Island provides favourable habitat for Nototheniid fish (Dewitt et al. 1990; Pakhomov et al. 2006) and both species of crustacean are readily found here (Perissinotto & McQuaid 1990; Hunt & Pakhomov 2003). Thus, taking into consideration the diet composition of these gentoo penguins, the fact the birds foraged exclusively on the inter-island shelf between Marion and Prince Edward Island largely below the 150m isobaths for the duration of this study, the inter-island shelf area may provide predictable prey utilized by breeding gentoo penguins.

Considering the benthic nature of the key prey group, Nototheniid fish (Dewitt et al. 1990), eaten during the brooding period (Adams & Klages 1989; Chapter 2), these birds are most likely demersal foragers. “Hot spot” and core foraging areas during self-maintenance dives and chick provisioning were largely confined to areas above the 100m isobaths, and an additional “hot spot” and core foraging area during chick provisioning trips between the 100m and 150m isobaths. The additional foraging area during chick provisioning is an indication of an increased area searched for prey as a function of increased trip duration. In order to optimize their foraging efficiency, a demersal foraging species aim to maximize the amount of time spent at the bottom of dives where prey is encountered (Wilson et al. 1996; Tremblay & Cherel 2000; Zimmer et al. 2010). However, bottom time was similar between chick provisioning and self-maintenance trips indicating that the birds may have been foraging at a constant effort per dive during the different types of trips.

Dives were deeper and longer during chick provisioning trips compared to that of self-maintenance trips. However, bottom time of the different types of trips was similar. Therefore, the longer dives performed during chick provisioning are most likely an artefact of the greater amount of time it takes to reach greater depths (Zimmer et al. 2010. Average diving depths during chick provisioning trips were noticeably deeper than those observed for gentoo penguins at Kerguelen (Lescroel et al 2005); Shetland (Miller 2009) and King George Islands (Kokubun 2010), with the exception of dives at Macquarie Island (Robinson and Hindell 1996.). However, average dive depths during self-maintenance trips were comparable to dive depths at other localities (Trivelpiece et al. 1986; Robinson & Hindell 1996; Lescroël & Bost 2005; Miller et al. 2009). However, during both types of trips, the diving depths followed a bimodal distribution. Both self-maintenance and chick provisioning trips favoured depths ≤10 meters, however the second depth to be favoured was greater for chick provisioning trips (131-140m) than self-maintenance trips (121-130m). This bimodal distribution in dive depth has previously been noted for gentoo penguins elsewhere (Williams & Rothery 1990; Williams et al. 1992; Robinson & Hindell 1996; Lescroël & Bost 2005) and it has been suggested to be due to dives having different functions (Williams et al. 1992; Lescroël & Bost 2005). Thus, the dives shallower than 10 meters were most likely travelling or exploratory dives and deeper dives were most likely feeding dives.

A larger proportion of the variation in diving depth and duration was found to be due to within bird variability rather than between bird variations. This may reflect the diving depth of birds becoming increasingly deeper as they travel further out to sea into deeper areas and vice versa as the birds return to land. As previously noted, the gentoo penguin is an opportunistic forager displaying a high degree of plasticity in foraging behaviour (Robinson & Hindell 1996; Croxall et al. 1999; Tanton et al. 2004; Lescroël & Bost 2005; Miller et al. 2009). It has been shown to reflect the distribution and characteristics of available prey and locality characteristics (e.g. bathymetry; Lescroël & Bost 2005). At the Kerguelen Islands, the foraging behaviour and diet of gentoo penguins were compared between an open sea and closed sea locality (Lescroël et al. 2004; Lescroël & Bost 2005). Birds at the open sea locality foraged demersally for benthic fish, increasing their foraging effort by spending more time at the bottom of dives. However, birds at the closed sea locality that foraged pelagically for crustaceans increased their foraging effort by diving more frequently and limiting time spent at the bottom of dives (Lescroël & Bost 2005). Therefore, the gentoo penguins at Marion Island are most likely foraging dermersally, as time spent at the bottom of dives at Marion Island is comparable to that of the open sea locality at Kerguelen.

The fine scale movement of gentoo penguins at Marion Island studied using GPS and TDR data loggers during this study. These could potentially have had adverse effects on foraging birds as the drag of the device may impede swimming speed and therefore affect diving depth, foraging range and prey encounter, thus influencing the overall foraging efficiency (Wilson et al. 1986).

However, Kokubun et al. (2010) found that larger loggers than the ones used in this study did not have any effect on the foraging efficiency of gentoo penguins at South Shetland Islands. Additionally, the devices were placed on the caudal position of the birds, a placement that has been found to minimize the amount of drag caused by a device (Bannasch et al. 1994). Therefore, it is likely that the loggers in this study did not affect the foraging behaviour of instrumented birds. Furthermore, comparisons were only made between instrumented birds and therefore the effect of loggers on the birds foraging behaviour, if any, is unlikely to affect the outcome of the results.

3.5. Conclusions

The inter-island shelf between Marion and Prince Edward Island was identified as an important foraging area for the gentoo penguins breeding at the Trypot Beach colony. These birds exhibit a unique foraging strategy among seabirds as they were found to perform shorter self-maintenance trips and longer chick provisioning trips. These findings do, however, reflect the behaviour for a single gentoo penguin colony at Marion Island. For a more holistic understanding of how the gentoo penguins are utilizing their habitat an inter-colony and inter-year comparison of tracking data should be conducted for this population in the future.

Chapter 4

General Discussion

As an extension of optimal foraging theory (Emlen 1966; MacArthur & Pianka 1966), the foraging behaviours of central placed foragers have evolved in such a way as to increase individual fitness by maximizing the rate at which energy is delivered to offspring (Orians & Pearson 1979). Therefore, being central place foragers, seabirds should show preference for prey items that are most energetically profitable and only consume less profitable items in situations where more profitable prey are not available (Stephan & Krebs 1986). The prey items of seabirds are often confined to a narrow range of trophic levels, mainly consisting of large zooplankton, fish and cephalopods (Quillfeldt & Masello 2013). The spatial and temporal distribution of these prey items is dynamic and related to fluctuating oceanographic parameters (Cheung et al. 2009). This relates to variable prey availability and predictable prey patches and is subsquently reflected in the diet and foraging behaviour of seabirds (Pinaud & Weimerskirch 2002; Baylis et al. 2015). The effect of fluctuating prey availability on seabird breeding success is well documented (e.g. Pinaud & Weimerskirch 2002; Weimerskirch et al. 2003; Reid et al. 2005). During years of low prey availability seabirds will favour self-maintenance over chick provisioning leading to decreased breeding success (Pinaud & Weimerskirch 2002; Frederiksen et al. 2006).

Understanding the diet and distribution of a seabird species is fundamental to make inferences of environmental influences on seabird demographics (Pinaud & Weimerskirch 2002; Miller et al. 2010). Therefore, this study investigated the foraging ecology of gentoo penguins at sub-Antarctic Marion Island. In particular, this study investigated the temporal variation in the diet with the use of stomach content samples and for the first time described the fine scale at sea distribution of this population during the brooding period using temperature depth recorders (TDRs) and global positioning system (GPS) loggers. Temporal variation in the diet was firstly investigated within and among the different periods of three annual cycles (1994-1996) and secondly, long term variation was investigated by comparing diet approximately 18 years apart.

4.1. The diet and foraging behaviour of gentoo penguins at sub-Antarctic Marion Island

The diet of the gentoo penguins exhibited considerable plasticity over three years (1994-1996). The importance of fish and crustaceans in their diet varied throughout the year. Nototheniid fish, and in particular *Lepidonotothen larseni*, represented the majority of the fish component in the diet. Their importance grew steadily from the beginning of the breeding season and peaked during the time that the gentoo penguins were brooding chicks. The increase of these fish in the diet corresponded to the approximate time of transition from the larval phase to the adult phase (Dewitt et al. 1990). Therefore, it was speculated that the increased importance of this fish during breeding is related to increased availability rather than selective foraging for prey with higher energetic content.

Nauticaris marionis and *Euphausia vallentini* represented the majority of the crustacean component in the diet. However, these species were never found in similar quantities in the diet, rather when one species featured prominently the other was poorly represented or absent. The latitudinal position of the SAF has historically been shown to play an important role in determining the availability of these species at Marion Island (Pakhomov & Froneman 1999a; Hunt & Pakhomov 2003). In general when the SAF lies further to the north, the development of *N. marionis* is favoured (Perissinotto & McQuaid 1990) and the advection of *E. vallentini* is impeded (Pakhomov & Froneman 1999a; Hunt & Pakhomov 2003). However, when the SAF lies further to the south, flow rates around the island group are increased and there is greater advection of *E. vallentini* in the proximity of the islands (Pakhomov & Froneman 1999a; Hunt & Pakhomov 2003). The large effect that the latitudinal position has on the crustacean composition of the inter-island shelf may be a driving factor in the variation of the crustacean species in the diet of the gentoo penguin at Marion Island. However, in the absence of concurrent data on prey availability this remains speculative.

Across five sampling periods spanning 18 years, the diet of the gentoo penguin at Marion Island now has significantly less *N. marionis* and more *E. vallentini*. This is thought to be as a result of the southward shift of the SAF as a result of climate change (Downes et al. 2011) and resulting in changes in these key prey items of gentoo penguins (Allan et al. 2013; Crawford et al. 2014). Comparison over the long term, was however unfortunately only confined to one period within the annual cycle.

The inter-island shelf between Marion Island and Prince Edward Island clearly represented an important and possibly predictable prey patch for the gentoo penguin population inhabiting the island. This was demonstrated through tracking of gentoo penguins but also stomach content samples taken during this study in which identified prey items are characteristically available in coastal shelf waters (Dewitt et al. 1990; Perissinotto & McQuaid 1990; Hunt & Pakhomov 2003). Furthermore, an important and perhaps unique foraging strategy was identified. The birds alternated between short self-maintenance foraging trips and long chick provisioning trips during chick rearing. Alternating between foraging trips during chick-rearing has previously reported for seabirds (Weimerskirch 1998; Clarke 2001; Ropert-Coudert et al. 2004; Kato et al. 2008; Saraux et al. 2011). Many seabirds will frequently perform short trips in close proximity of breeding ground to maximize provisioning rates of chicks. However, this is at the expense of the adult’s own energy reserves. Therefore, periodically, to restore energy reserves, parent seabirds will perform longer self-maintenance trips, increasing trip duration to reach further, more predictable prey patches. The foraging strategy for gentoo penguins at Marion Island is unique in that shorter trips were associated with self-maintenance and longer trips were associated with chick provisioning. The driving factor behind this behaviour was speculated to be that these penguins do not have to travel further to reach a predictable foraging patch. It was speculated that the cost of returning to land and remaining on the beach until foraging the following day outweighed the cost of thermoregulation and the risk of predation than remaining at sea.

4.2. Implications and future directions

Seabirds, including penguins, are often considered as being marine sentinels (Hughes et al. 2005; Piatt et al. 2007; Boersma 2008; Gremillet & Charmantier 2010) and have been used as indicators of marine ecosystem health. This is largely enabled by the fact that they are central placed foragers during the breeding season making data collection concerning demographics, diet and at sea distribution relatively easy (Furness & Monaghan 1987; Piatt et al. 2007). The observation that the population and breeding success of gentoo penguins and Crozet shags at Marion Island have experienced declines over the past two decades are therefore symptomatic of ecosystem changes (Crawford et al. 2003a, 2003b, 2014). Although in the current study significant changes in diet over the long term were evident, these conclusions would have been strengthened if comparisons over the long term were possible over the entire (rather than one period) annual cycle. Therefore, long term study into the diet of these penguins at Marion Island is suggested with sampling spread across the year so as to help elucidate causal factors behind the long term decline of this population. If collection of stomach content samples is limited per annual cycle it is suggested that collection of sample is confined to the brooding period so that future comparisons can be made with the findings reported in this study. Furthermore, long term changes in foraging effort, in addition to demographic parameters (such as breeding success and population numbers) and diet composition can be indicative of changes in prey availability (Gremillet & Charmantier 2010). Therefore, it is furthermore suggested that the study of fine scale at sea movement of the gentoo penguin at Marion Island continues concurrently with dietary studies.

4.3. Final thoughts

This study has provided valuable information towards understanding the foraging ecology of gentoo penguins and provided a platform for future comparisons. As for the gentoo penguins at Marion Island, it is the first study to provide knowledge of diet over three consecutive years, as well as, the first to investigate any long term variation in the diet. Furthermore, it provided the first fine scale movements of brooding gentoo penguins breeding on the island. Despite advances made in our understanding of the foraging ecology of gentoo penguins at Marion Island, reasons associated with declining numbers still remain largely speculative. This study has provided important detailed knowledge of the at-sea distribution and temporal variation in the diet and of these birds which will help to elucidate the factors that are driving the long term decline that this population is facing.

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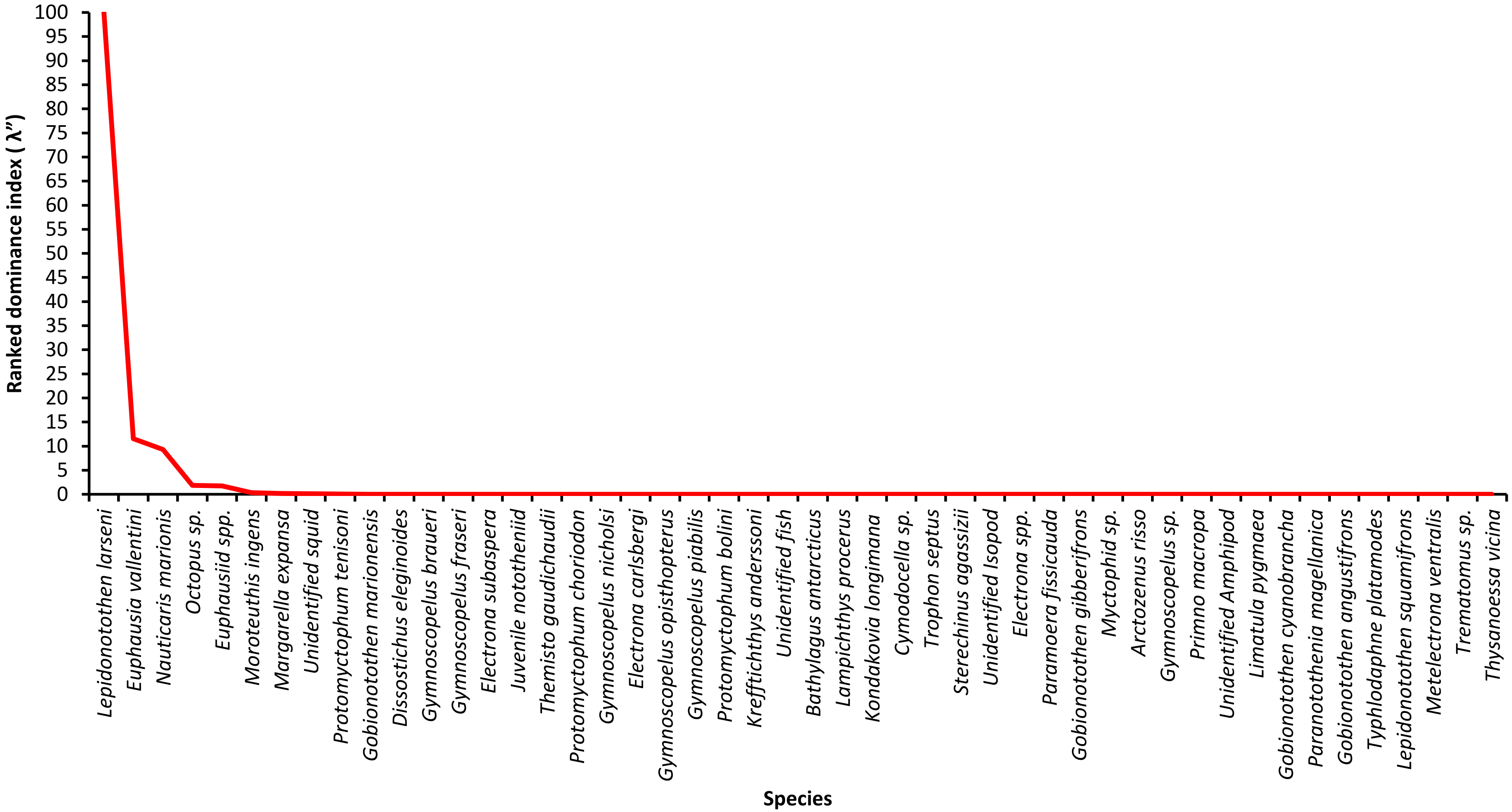

Appendix A. Cumulative contribution curve of ranked Simpson’s dominance index (λ”) of prey items that were found in the diet of the gentoo penguin at sub-Antarctic Marion Island between 1994 and 1996, 2012 and 2014.

Appendix B. Complete list of prey items found in the diet of the gentoo penguin at sub-Antarctic Marion Island, over the course of the study (1994-2014), showing their overall contribution to the diet in terms of Simpson's dominance index (λ"). Values in bold indicate prey items that were found to be dominated prey species during that period. Species are categorised by order and then family. Sampling periods are P= pre-incubation, I = incubation, B = brooding, C = crèche, PB = post breeding and M = Pre-Moult of that respective year.

Sampling period	1994					1995						1996				2012	2014	
	P	I	B	C	PB	M	P	I	B	C	PB	I	B	C	PB	I	M	B
Fish																		
Nototheniidae																		
Dissostichus eleginoides	-	<0.01	0.02	<0.01	-	-	-	-	-	-	-	1.53	<0.01	-	-	-	-	<0.01
Gobionotothen angustifrons	-	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gobionotothen cyanobrancha	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gobionotothen gibberifrons	0.03	-	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-	-	-
Gobionotothen marionensis	<0.01	-	0.05	0.03	0.02	-	-	0.01	-	<0.01	<0.01	<0.01	1.42	0.01	<0.01	-	-	-
Lepidonotothen squamifrons	-	-	-	-	-	0.06	-	-	-	-	<0.01	-	-	-	-	-	-	-
Lepidonotothen larseni	**63.99**	**56.03**	**47.04**	**63.91**	**64.42**	**24.25**	**78.18**	**94.56**	**99.15**	**89.73**	**18.66**	**81.47**	**25.55**	**51.54**	**5.15**	**39.55**	0.33	**77.84**
Paranotothenia magellanica	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trematomus sp.	-	-	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-	-	-
Unidentified juvenile	-	-	-	<0.01	1.02	**73.91**	-	-	-	-	-	-	-	-	-	-	**93**	-
Unidentified Nototheniid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.34
Myctophidae																		
Electrona carlsbergi	<0.01	0.14	-	-	-	<0.01	0.11	-	-	-	-	-	-	-	-	-	-	-
Electrona subaspera	-	<0.01	0.52	-	-	-	-	-	-	-	-	<0.01	0.01	-	-	-	-	-
Electrona spp.	-	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-	-	-	-
Gymnoscopelus braueri	-	0.93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus fraseri	-	0.02	0.81	-	0.11	<0.01	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus nicholsi	-	0.28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus opisthopterus	-	0.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus piabilis	0.02	0.03	0.03	-	-	<0.01	0.01	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus sp.	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Krefftichthys anderssoni	-	<0.01	0.01	0.01	-	<0.01	-	-	-	<0.01	-	-	-	-	-	-	-	-
Lampichthys procerus	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Metelectrona ventralis	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protomyctophum bolini	<0.01	-	-	-	0.21	-	-	-	-	-	-	-	-	-	-	-	-	-
Protomyctophum choriodon	-	0.12	-	<0.01	<0.01	<0.01	-	<0.01	-	-	-	0.01	-	-	-	-	-	-
Protomyctophum tenisoni	-	<0.01	0.03	3.02	2.04	<0.01	-	-	-	-	-	0.02	-	-	-	-	-	-
Myctophid sp.	-	-	-	-	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
Bathylagidae																		
Bathylagus antarcticus	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bathylagus sp.	-	-	-	-	-	<0.01	-	-	-	-	-	-	-	-	-	-	-	-
Paralepididae																		
Arctozenus risso	-	-	-	-	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified fish	<0.01	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-

Sampling period	1994					1995						1996				2012	2014	
	P	I	B	C	PB	M	P	I	B	C	PB	I	B	C	PB	I	M	B
Crustacean																		
Decapoda																		
Hippolytidae																		
Nauticaris marionis	0.35	**34.48**	**18.9**	**27.28**	4.33	1.61	4.67	1.77	0.02	0.02	<0.01	**13.41**	**71.84**	0.28	<0.01	0.77	0.77	-
Euphausiidae																		
Euphausia vallentini	4.64	-	-	3.07	**20.01**	-	-	-	0.13	5.02	**63.87**	2.98	-	**7.87**	**91.36**	-	-	**20.25**
Thysanoessa vicina	-	-	-	-	-	-	-	-	-	-	<0.01	-	-	-	-	0.01	0.01	1.57
Euphausia longirostra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphausiid spp.	0.26	<0.01	0.02	0.04	7.16	<0.01	-	-	-	3.97	**13.27**	0.02	-	**30.93**	-	-	-	-
Amphipoda																		
Hyperiidae																		
Themisto gaudichaudii	-	0.02	0.05	0.01	0.08	<0.01	-	<0.01	-	-	-	-	-	-	-	0.67	0.67	-
Vibilia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<0.01	<0.01	-
Phrosinidae																		
Gammarida sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calliopioidea																		
Paramoera fissicauda	-	-	-	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-
Phrosinidae																		
Primno macropa	-	-	-	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-	-
Unidentified Amphipod	-	-	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda																		
Sphaeromatidae																		
Cymodocella sp.	-	-	-	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-	-
Unidentified Isopod	<0.01	-	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified crab	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<0.01	-
Cephalopods																		
Octopodidae																		
Octopus sp.	**30.59**	**7.73**	0.7	2.36	0.34	0.06	3.69	<0.01	-	<0.01	<0.01	0.23	0.04	**9.34**	3.49	0.02	0.02	<0.01
Onycoteuthidae																		
Moroteuthis ingens	-	-	-	0.01	<0.01	0.04	**11.9**	3.64	-	<0.01	1.35	-	-	-	-	-	-	-
Kondakovia longimana	-	-	-	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-	-
Unidentified squid	-	0.03	<0.01	<0.01	0.22	<0.01	1.44	<0.01	0.02	1.25	0.03	0.02	0.01	0.03	-	**5.21**	5.21	-
Other																		
Gastropoda																		
Calliostomatidae																		
Margarella expansa	-	-	<0.01	0.25	0.02	<0.01	-	-	0.68	<0.01	2.78	0.29	1.07	-	<0.01	-	-	-
Borsoniidae																		
Typhlodaphne platamodes	-	-	-	<0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Muricidae																		
Trophon septus	-	-	-	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-
Bivalvia																		
Limidae																		
Limatula pygmaea	-	-	-	<0.01	-	-	-	-	-	-	-	-	-	<0.01	-	-	-	-
Echinodermata																		
Echinoidea																		
Sterechinus agassizii	-	-	-	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-