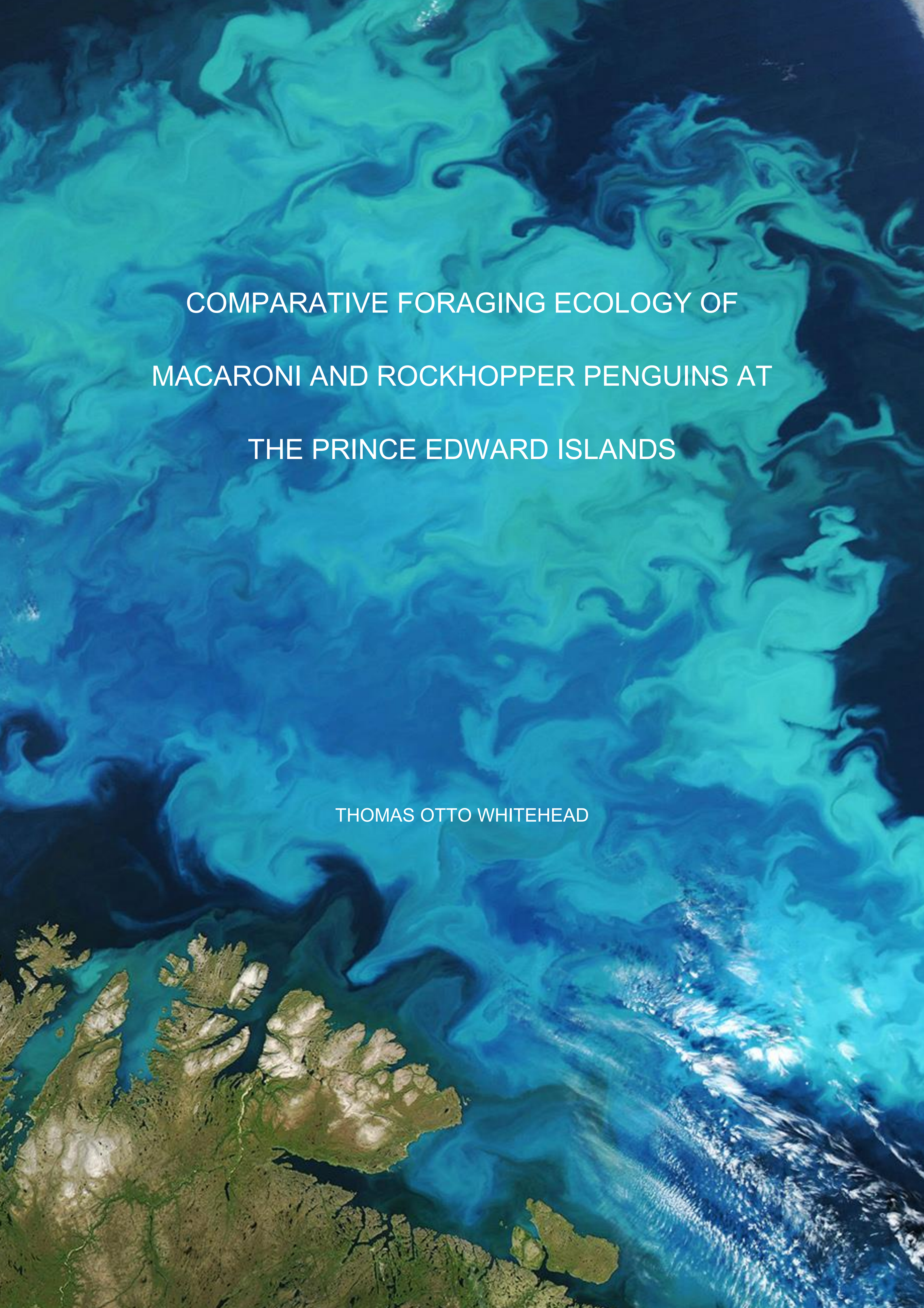

COMPARATIVE FORAGING ECOLOGY OF MACARONI AND ROCKHOPPER PENGUINS AT THE PRINCE EDWARD ISLANDS

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Cover page: Phytoplankton bloom in the Baltic Sea (NASA)

Comparative foraging ecology of macaroni and rockhopper penguins at the Prince Edward Islands

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DECLARATION

I declare that this thesis is my own work and effort, both in concept and execution, with normal guidance and assistance from my supervisors. I, Thomas Otto Whitehead, hereby declare that the work on which this thesis is based is my original work (except where indicated otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I authorise the University to reproduce for the purpose of research either the whole or any portion of the contents in any manner whatsoever.

Signed by candidate

Thomas Otto Whitehead

Cape Town, July 2017

‘In conclusion, it appears to me that nothing can be more improving to a young naturalist than a journey in distant countries … to teach him good-humoured patience, freedom from selfishness, the habit of acting for himself, and of making the best of every occurrence.’

Charles Darwin, *The Voyage of the Beagle*

‘The penguins’ by Owen Davey

ABSTRACT

Penguins are one of the largest consumers of marine resources in the Southern Ocean and spend most of their lives at sea. Although the last four decades have seen technological advancements that have considerably expanded our knowledge about their at-sea behaviour, there is still much to be learned. Given the rapid ongoing ecosystem changes in the Southern Ocean, it is vital to better understand, firstly, how penguins respond to environmental variability, and secondly, how such changes alter ecological relationships between sympatric species.

Being flightless, travel is slower and more costly for penguins than flying seabirds. This constrains their ability to find resources, particularly during the breeding season when they must regularly return to the colony to provision offspring. As penguins are colonial nesters, high foraging pressure near the colony can limit available resources, enhancing potential intra- and interspecific competition. At many localities, ecologically similar penguin species breed sympatrically. In such cases, co-existence is only thought possible through ecological segregation in space, time and/or diet.

At the Prince Edward Islands, approximately 302,000 pairs of macaroni *Eudyptes chrysolophus* and 80,000 pairs eastern rockhopper *E. chrysocome filholi* penguins breed sympatrically. These populations are closer to parity than at any other locations where two eudyptid species breed sympatrically. Populations of both species at the Prince Edward

Islands have declined in the last two decades, but drivers of these declines are poorly understood. The primary aim of this thesis was to better understand the foraging strategies of macaroni and rockhopper penguins at the islands and identify aspects of their ecology that allow them to co-exist. The secondary focus was to investigate how each species responds to environmental variability and assess how ecological interactions between species might be altered in an era of rapid global change. To study the at-sea habitat use and diving behaviour of penguins during chick-rearing and pre-moult periods, I used GPS loggers and time-depth recorders. To track penguins during the winter I used geolocation loggers and satellite transmitters. Stable isotope analyses were used to investigate trophic ecology during late winter, summer and pre-moult periods.

During the breeding season, both species primarily foraged in pelagic waters beyond the shelf break (> 3000 m), with macaroni penguins foraging slightly farther offshore on average. However, rockhopper penguins breeding adjacent to the inter-island shelf foraged in shallow waters (< 200 m) over the shelf. Both species dived to similar depths (40 to 60 m), but macaroni penguins dived deeper more often. The diet of both species was dominated by two krill species (*Thysanoessa vicina* and *Euphausia vallentini*). Diving behaviour varied between years, with both species diving deeper when the SAF was located farther away and geostrophic flow was reduced. During these conditions, macaroni penguins fed on a larger proportion of myctophids whereas rockhopper penguins resorted to less energy-dense nototheniids. This highlights contrasting responses to periods of low krill availability.

During the pre-moult period, habitat preferences were similar between species, with penguins travelling up to 1000 km south to forage in Antarctic Zone waters (SST 3-4 °C). However, a three-week difference in departure dates minimised spatiotemporal overlap between species. Diving behaviour was similar between species, but macaroni penguins performed more deep dives and encountered thermoclines more often. Stable isotope analyses revealed that macaroni penguins fed on a greater proportion of fish than rockhopper penguins, and revealed species-specific spatial responses to changes in primary productivity, with macaroni penguins travelling farther south in less productive years.

During the 6-month long winter sojourn, macaroni penguins generally foraged in cooler waters (SST ~ 3 °C) compared to rockhopper penguins (5-6 °C). However, stable isotope analyses revealed that trophic and spatial overlap were high during late winter. Both species associated with mesoscale eddies and submesoscale filaments, suggesting that these features play an important role in aggregating prey during the resource-limited winter months.

In summary, it appears that subtle differences exist to minimise competitive overlap between macaroni and rockhopper penguins. The three-week difference in the onset of breeding is integral to minimising competitive overlap during late winter, brood-guard/crèche, pre-moult and immediately following the moult. This allochrony staggers the peak energy demands of rockhopper penguins to reduce overlap with macaroni penguins. The larger-bodied macaroni penguins are capable of diving deeper, for longer and more efficiently than rockhopper penguins, which increases their behavioural flexibility and fitness by minimising stresses associated with reduced krill availability. Such differences in diving behaviour may explain contrasting population trends at the islands and suggests that rockhopper penguins may continue to decline at a faster rate than macaroni penguins if ongoing climate change continues to reduce prey availability around the Prince Edward Islands.

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TABLE OF CONTENTS

ABSTRACT .... **VI**

ACKNOWLEDGEMENTS .... **VIII**

CHAPTER 1 **General introduction** **1**

CHAPTER 2 **Study site, species and methods** **20**

CHAPTER 3 **Habitat use and diving behaviour of sympatric crested penguins during the breeding season** **60**

CHAPTER 4 **Habitat use and diving behaviour of sympatric crested penguins during the pre-moult period** **109**

CHAPTER 5 **Trophic ecology of sympatric crested penguins during the pre-moult period** **165**

CHAPTER 6 **Where do crested penguins go in winter? Insights from tracking and stable isotopes** **190**

CHAPTER 7 **Synthesis** **230**

REFERENCES **264**

CHAPTER 1

General introduction

Figure 1.1. Macaroni penguins *Eudyptes chrysolophus* (foreground) and king penguins *Aptenodytes patagonicus* (background) at Kildalkey Bay, Marion Island

Competition and co-existence

In nature, species rarely occur in isolation. The interactions between species have therefore long fascinated ecologists. These interactions – facilitative, neutral or antagonistic – shape the structure and functioning of ecosystems and drive diversification. In facilitative interactions, the presence of one species may positively affect the fitness of another, such as the mutualism between many plants and pollinators (Bascompte and Jordano 2007) or the commensalism between some seabirds and the dolphins/gamefish that push their prey to the surface (Bruno et al. 2003; Vaughn et al. 2008). Conversely, in antagonistic interactions, the presence of another species may negatively affect the fitness of another, such as with predator-prey interactions or competition for a shared resource.

In *The Origin of Species*, Charles Darwin wrote, "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera" (Darwin 1859, p. 79). When closely related or ecologically similar species share a common resource, competition may negatively affect foraging success and lower reproductive performance (Hunt et al. 1986). In such cases, the principle of competitive exclusion predicts that in order to maintain co-existence, sympatric species must segregate aspects of their ecology to minimise competitive overlap (Gause 1934; Hardin 1960). For example, sympatric warblers living in coniferous forests manage to co-exist by foraging at different heights in the canopy (MacArthur 1958). Beyond the single dimension, Hutchinson's (1957) concept of the ndimensional niche hypervolume states that niche differentiation can occur along multiple ecological axes. Competitive overlap may still occur, but trade-offs between physiological, morphological and/or behavioural traits allow co-existence despite interspecific competition. For example, many stretches of the North Pacific sub-Arctic coastline support up to six species of alcid; three of which feed on different resources, whereas the other three, which share a common resource, rely on contrasting foraging areas, bill morphology and energy requirements to minimise competition (Cody 1973).

Of seabirds and penguins

Among avian groups, seabirds are distinguished by their adaptations to feeding at sea and breeding on land. Most are monogamous, long-lived and produce few offspring (Schreiber and Burger 2002). For example, many offshore foraging seabirds only produce one egg, compared to clutch sizes of four to eight eggs typical of terrestrial passerines in temperate regions (Schreiber and Burger 2002; Jetz et al. 2008). The small clutch sizes of seabirds are thought to have evolved in response to the relatively low productivity of marine environments, coupled with long commutes enforced by central-place foraging, which place energetic limitations on the number of offspring each pair can adequately provision (Lack 1968). Being central place foragers, the survival of offspring is largely determined by the parents' ability to regularly find sufficient resources and return to the nest within a limited time period. This is particularly challenging in the pelagic marine environment, as resources are often distant, limited and/or patchily distributed in space and time (Ashmole 1971;

Furness and Birkhead 1984; but see Weimerskirch 2007). In response to such heterogeneity, many seabirds have evolved high phenotypic plasticity, which refers to the ability of an organism to adapt its physiological state and/or behaviour according to environmental conditions (West-Eberhard 1989). For instance, common murres *Uria aalge* maintain adequate provisioning rates during periods of poor prey availability by limiting their resting time (Burger and Piatt 1990) and great cormorants *Phalacrocorax carbo* have a generalist diet that allows them to exploit virtually any fish species that is small enough to be swallowed (Grémillet et al. 2001).

Of all seabirds in the Southern Ocean, penguins (Sphenisciformes) are the most abundant group, consuming more than 23 % of the estimated 70 metric tonnes consumed by all seabirds annually, superseded only by Procellariiformes (Brooke 2004). Being flightless, travel is slower and more energetically costly for penguins compared to flying seabirds (Schmidt-Nielsen 1972), limiting the distance they can travel to find resources. Furthermore, because most penguins are colonial nesters, foraging pressure near the colony is high, often limiting resource availability (Ashmole 1971; Ballance et al. 2009). These foraging constraints appear to reduce the ability of penguins to respond to environmental variability (Grémillet and Charmatier 2010). For example, the reproductive performance of Adélie penguins *Pygoscelis adeliae* is highly sensitive to changes in local sea-ice cover, with few chicks surviving during years when extensive fast ice forces parents to travel farther (Emmerson and Southwell 2008). Reduced flexibility makes penguins ideal environmental indicators (Grémillet and Charmantier 2010) and enhances their vulnerability to global climate change (Canale and Henry 2010).

In the last century, penguin populations have experienced dramatic changes throughout their range. Initial declines were mainly attributed to direct human exploitation, such as guano and egg harvesting and the killing of adults and chicks for meat (Roberts et al. 2005). Since then, commercial fishing (Crawford et al. 2007; Boersma 2009), introduced predators (King et al. 2012), oil spills (Barham et al. 2007) and bycatch (Darby and Dawson 2000) have contributed to their continued decline and, more recently, many species have been and continue to be affected by climate-driven ecosystem changes (Cunningham and Moors 1994; Hilton et al. 2006; Boersma 2009). As a result, penguins are second only to albatrosses (Diomedeidae) in terms of the proportion of a bird family that is globally threatened. In an age of rapid environmental change, it remains unclear how penguins will respond to such changes, emphasising the need to better understand how environmental variation influences their foraging behaviour and alters the ecological relationships between sympatric species (Forcada et al. 2006; Lewison et al. 2012).

Ecological segregation in penguin communities

Contemporary niches may reflect the outcome of past environments and/or competitive interactions, i.e. 'the ghost of competition past' (Connell 1980). Thus, it is important to consider the historical constraints associated with a species' niche when interpreting ecological relationships within a community. The earliest penguin fossils dates back to ~60 Ma (Mayr et al. 2017). Molecular dating indicates the early divergence of *Aptenodytes* and *Pygoscelis* penguins on the Antarctic continent, with the divergence of *Eudyptula*, *Spheniscus*, *Eudyptes* and *Megadyptes* being more recent (Baker et al. 2006). It is hypothesised that this recent diversification occurred during two major cooling events in the Miocene, which strengthened the Antarctic circumpolar current and assisted in the northward dispersal of Antarctic penguins to widely separated islands and continents in sub-Antarctic and temperate regions (Baker et al. 2006). Geographic isolation promotes allopatric speciation, and likely accounts for the diversity of penguin genera that we see today. However, the evolutionary pathways of congeneric species are less clear, especially given that many breed sympatrically. Did these species evolve in isolation and later converge at the same localities through dispersion? Or did local pressures, such as competition and/or the availability of contrasting niches, drive sympatric speciation? Given the paucity of examples of sympatric speciation in island birds (Coyne and Price 2000; but see Ryan et al. 2007), it is more likely that the within-genus diversification of penguins was driven by allopatric speciation.

Today, many breeding localities support two or more penguin species. For example, the Prince Edward Islands support king *Aptenodytes patagonicus*, gentoo *Pygoscelis papua*, macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins (Crawford et al. 2009). Due to contrasting ecologies, there is clear segregation in the diets of the three genera, but the eudyptids overlap considerably (Adams and Brown 1989). When resources are limited, the presence of closely related species may negatively affect foraging success through competition (Hunt et al. 1986). In such cases, the principle of competitive exclusion predicts that species must evolve to exploit different parts of the resource or one will exclude the other (Gause 1934; Hardin 1960). Thus, at localities where congeneric penguin species breed sympatrically, it is expected that they should minimise competition through morphological, physiological and/or behavioural adaptations within their limited phenotype. Potential mechanisms of segregation in penguin communities include differences in the type and/or size of prey taken, breeding phenology, and horizontal and/or vertical habitat use (Trivelpiece et al. 1987; Lynnes et al. 2002; Thiebot et al. 2012; Blanchet et al. 2013). Differences in dive depth efficiency have also been identified as important mechanisms in reducing competition between sympatric penguin species feeding on the same prey (Mori and Boyd 2004; Wilson 2010).

Among extant penguins, crested penguins (genus *Eudyptes*) are the most abundant and diverse group (Fig. 1.2), containing seven of the 18 recognised penguin species (IUCN 2017). Their distribution ranges from temperate to Antarctic climates (Williams 1995), with the highest species diversity located in the New Zealand sub-Antarctic (Baker et al. 2006). Eudyptids are unique among penguins in that, of the two eggs laid, the second egg is considerably larger and almost always produces the only surviving chick (Warham 1975). Furthermore, only females provision the chick during brood-guard, compared to biparental provisioning observed in other genera.

Eudyptids breed sympatrically at many localities – usually involving the smaller eastern rockhopper and the larger royal *E. schlegeli*, erect-crested *E. sclateri* or macaroni penguins (Warham 1975) – but it is uncommon for large numbers of both species to co-exist (Table 1.1). Generally the more common species outnumbers the less common by an order of magnitude or more; the Prince Edward Islands are the only island group where two Eudyptes populations differ by less than a five-fold difference in abundance (Table 1.1). It is thus the ideal site to assess mechanisms that might have evolved to reduce competition by differing in some aspects of their ecology (Gause 1934). Studies focusing on the foraging ecology of sympatric eudyptids have been largely limited to diet (Brown and Klages 1987; Ridoux 1994; Hull 1997) but foraging areas and diving behaviour of rockhopper and royal penguins *E. schlegeli* at Macquarie Island have been studied in detail (Hull 1997, 1999, 2000). The latter two species exhibit differences in breeding chronology, diet and vertical habitat use (Hull 1997, 1999, 2000).

Figure 1.2. Crested penguins of the world: (a) royal *Eudyptes schlegeli*, (b) macaroni *E. chrysolophus*, (c) Fiordland crested *E. pachyrhynchus*, (d) Snares *E. robustus*, (e) erect-crested *E. sclateri*, (f) southern rockhopper *E. chrysocome* and (g) northern rockhopper *E. moseleyi* (illustrations adapted from Marchant and Higgins 1990)

Table 1.1. Populations of sympatric eudyptids at localities where numbers of both species > 1000 pairs

Locality	Species	Population (pairs)	Ratio	References
Ildefonso	Macaroni	5,660	1:15	Kirkwood et al. (2007)
	Southern rockhopper	86,400		
Diego Ramirez	Macaroni	15,600	1:8.5	Kirkwood et al. (2007)
	Southern rockhopper	132,721		
Prince Edward Islands	Macaroni	302,000	3.8:1	Crawford et al. (2009)
	Eastern rockhopper	80,000		
Crozet Islands	Macaroni	2,200,000	14:1	Jouventin et al. (1984)
	Eastern rockhopper	152,800		
Kerguelen Islands	Macaroni	1,812,000	21:1	Weimerskirch et al. (1988)
	Eastern rockhopper	85,000		
Heard and McDonald Islands	Macaroni	1,000,000	100:1	BirdLife International (2017a, b)
	Eastern rockhopper	10,000		
Macquarie Island	Royal	850,000	23:1	Copson and Rounsevell (1987); BirdLife International (2017b)
	Eastern rockhopper	37,500		
Antipodes Island	Erect-crested	34,226	14:1	Hiscock and Chilvers (2014)
	Eastern rockhopper	2,475		

Macaroni and rockhopper penguins at the Prince Edward Islands

The divergence of macaroni and rockhopper penguins *sensu lato* is estimated to have occurred during the early Pleistocene ~1.8 Ma (de Dinechin et al. 2009). Given the relatively young age of the Prince Edward Islands (~0.5 Ma), macaroni and rockhopper penguins would have colonised the islands as separate species. Due to the limited phenotypic plasticity of penguins, local adaptation to climate shifts is not always possible, making dispersion fundamental to the preservation of a species (Forcada and Trathan 2009). The first macaroni and rockhopper penguins to arrive at the Prince Edward Islands were most likely from the Crozet Islands, which first emerged some 8 Ma (Thiebot et al. 2013). Crested penguins at the Crozet Islands travel thousands of kilometres during the winter months, when they forage in Polar Frontal Zone waters near the Prince Edward Islands (Thiebot et al. 2013). Phylogenetic comparisons of rockhopper penguins at Crozet and Kerguelen Islands indicate that gene flow still exists between these populations (de Dinechin et al. 2009), suggesting that this may also occur at the Prince Edward Islands.

The Prince Edward Islands consist of the larger Marion Island and smaller Prince Edward Island. These islands support approximately 302,000 pairs of macaroni penguins and 80,000 pairs of the eastern race of southern rockhopper penguins, comprising 4% and 7% of global populations, respectively (Crawford et al. 2009). In 2008/09, population estimates at Marion Island were 30 and 70 % less, respectively, than they were in 1994/95 (Crawford et al. 2009). Similar declines have been observed throughout their distributions, resulting in both species being listed as *Vulnerable* (IUCN 2017). Declines at Marion Island have been attributed to inadequate breeding success, as both species produced fewer chicks than needed to maintain a stable population (Crawford et al. 2003a, b). Changes in prey availability at winter foraging areas may have influenced declines, as poor breeding success was related to mass on arrival (Crawford et al. 2006, 2008) but drivers of declines remain poorly understood. Given the increase in local sea surface temperatures (SST, Melice et al. 2003) and shifts in the marine food web (Kaehler et al. 2000; Hunt et al. 2001), it seems likely that changes in local prey availability during the breeding season or at winter foraging areas may have affected the ability of macaroni and rockhopper penguins to adequately provision offspring. However, little is known about their at-sea behaviour and how they respond to fluctuations in prey availability at the Prince Edward Islands.

Within the framework of competition theory (Gause 1934; Hardin 1960), it is predicted that macaroni and rockhopper penguins should segregate aspects of their ecology in order to co-exist. Studies of their diet at Marion Island indicate that both species feed primarily on swarming crustaceans, such as *Euphausia vallentini* and *Thysanoessa vicina*, and to a lesser extent on myctophid fish and cephalopods (Brown and Klages 1987; Cooper et al. 1990; Crawford et al. 2003a, b). There are no apparent differences in the size of prey taken, but macaroni penguins tend to more regularly feed on greater proportions of fish (Cooper et al. 1990; Crawford et al. 2003a, b). To some extent, it appears that different breeding site preferences may minimise interspecific competition, as macaroni penguins typically breed in large colonies with relatively easy beach access (Fig. 1.1), whereas the more agile rockhopper penguins breed in smaller colonies scattered along less accessible stretches of coastline (Fig. 1.3). However, this may only reduce interspecific competition if foraging ranges are highly restricted. In the 1970s, a study of chick provisioning rates indicated that most foraging trips were limited to a few days and were similar between species (Williams 1982). Later estimates of foraging ranges using speed meters indicated that macaroni penguins foraged farther offshore than rockhopper penguins (Brown 1987a) but estimates were obtained at different stages of the breeding season and therefore differences may have reflected contrasting energy demands of chicks. Brown (1987a) concluded that the only major difference between the two species at Marion Island was that rockhopper penguins started breeding three to four weeks after macaroni penguins (see Chapter 2). This results in partial spatiotemporal segregation of the marine environment that either minimises potential competition for resources when energy demands are highest (Brown 1987a) or reflects a temporal difference in the optimal period to exploit different preferred niches. Diving behaviour has only been studied in macaroni penguins (Pichegru et al. 2010), precluding interspecific comparisons of vertical habitat use.

Figure 1.3. Rockhopper penguins breeding along the northeast coast of Marion Island

In this thesis I investigate the foraging ecology of macaroni and eastern rockhopper penguins breeding at the Prince Edward Islands to better understand how these species partition their environment. Furthermore, I explore how foraging behaviour and interactions change in response to environmental variability.

Thesis aims and structure

The focus of this chapter is to introduce the theoretical concepts central to the questions in this thesis. Chapter 2 introduces the study site, species and methods. The data chapters (Chapters 3 to 6) are written in the style of stand-alone scientific journal articles: I refer between these chapters, but some repetition may occur. Chapter 7 summarises key findings and provides suggestions for future research.

Chapter 3 – Habitat use and diving behaviour of sympatric crested penguins during the breeding season

During the breeding season, the distance a penguin can travel is limited by the need to regularly return to the nest to provision offspring. This results in high foraging pressure near the colony and increases potential competition for resources. Investigating where and how sympatric macaroni and rockhopper penguins at the Prince Edward Islands find resources during this period is integral to understanding mechanisms that allow them to co-exist. Furthermore, given that environmental variation may influence ecological relationships between sympatric species, it is also important to investigate links between foraging behaviour and environmental conditions. This may also provide insights into potential drivers of population dynamics. GPS loggers and time-depth recorders (see Chapter 2) were deployed over three years at three sites and used to:

1. Describe seasonal variation in foraging strategies in relation to changing energy demands of chicks;
2. Assess spatiotemporal overlap in foraging areas between species;
3. Describe diving behaviour and compare vertical habitat use between species;
4. Determine how foraging strategies vary between sites with different penguin densities;
5. Explore environmental drivers of variation in foraging strategies and diving behaviour.

I hypothesize that:

1. Penguins should forage farther from the colony and spend longer at sea as energy demands of chicks increase;
2. Contrasting foraging ranges and a three-week difference in departure dates should result in minimal spatiotemporal overlap;
3. Larger-bodied macaroni penguins should forage at greater depths than rockhopper penguins;
4. Foraging effort should be lower at colonies with fewer penguins;
5. Given that greater concentrations of the main krill species *E. vallentini* are associated with the close proximity of the Sub-Antarctic Front (SAF), penguins should exhibit reduce foraging effort and dive more efficiently during years when the SAF is closer to the islands.

Chapter 4 – Habitat use and diving behaviour of sympatric crested penguins during the pre-moult period

The pre-moult period is a critical stage in the annual cycle of adult penguins, as failure to accumulate sufficient resources may threaten survival during and after the moult fast ashore. Knowledge of where and how macaroni and rockhopper penguins find such resources is vital to better understand their susceptibility to environmental changes during this critical period. In this chapter GPS loggers and time-depth recorders (see Chapter 2) were used to investigate habitat use and diving behaviour. Specifically I:

1. Model travel speed in relation to environmental covariates to determine whether habitat preferences differ between species;
2. Quantify spatiotemporal overlap between species;
3. Describe diving behaviour and compare vertical habitat use between species.

I hypothesize that:

1. Macaroni and rockhopper penguins should target areas of predictable resources (i.e. fronts, eddies) but in different water masses;
2. Contrasting broad-scale habitat preferences and a three-week difference in departure dates should minimise spatiotemporal overlap;
3. Larger-bodied macaroni penguins should forage at greater depths than rockhopper penguins.

Chapter 5 – Trophic ecology of sympatric crested penguins during the pre-moult period

As knowledge of how penguins respond to fluctuations in the marine environment is vital to better understand their susceptibility to ecosystem changes, this chapter explores inter-annual variation in the trophic ecology of macaroni and rockhopper penguins in relation to at-sea conditions during the pre-moult period. This complements investigations of habitat use and diving behaviour undertaken in Chapter 4 to provide a more holistic perspective of ecological segregation during this critical period. Stable isotope analysis of feathers (see Chapter 2) were used to:

1. Describe the trophic niche of each species and quantify overlap to assess niche differentiation;
2. Investigate inter-annual variation in diet and foraging areas in relation to environmental conditions.

I hypothesize that:

1. Larger-bodied macaroni penguins should feed at a higher trophic level (i.e. consume more fish) than rockhopper penguins;
2. Trophic niche overlap should decrease during years of reduced prey availability.

Chapter 6 – Where do crested penguins go in winter? Insights from tracking and stable isotopes

Given that resource availability at winter foraging areas may influence population dynamics (Crawford et al. 2006, 2008), it is important to identify habitat preferences and better understand the diet of penguins during this resource-limited time. Furthermore, because the lack of provisioning constraints during this period allows greater flexibility in terms of habitat selection, it provides an opportunity to investigate whether fundamental differences in habitat preferences exist between macaroni and rockhopper penguins. Tracking techniques (geolocation loggers and satellite transmitters) and stable isotope analysis of blood (see

Chapter 2 for details) were used to:

1. Model presence/absence of macaroni and rockhopper penguins in relation to environmental covariates;
2. Assess spatiotemporal overlap between species using sea surface temperatures;
3. Describe trophic niches and quantify niche overlap between species;
4. Compare trophic niches between winter and summer;
5. Determine whether mass on arrival is related to winter foraging areas and/or diet.

I hypothesize that:

1. Penguins should target areas of predictable resources (i.e. fronts, eddies) but in different water masses;
2. Due to their larger size and greater ability to maintain body temperature, macaroni penguins should be able to exploit cooler waters than rockhopper penguins;
3. Macaroni penguins should feed at a higher trophic level (i.e. consume more fish) than rockhopper penguins due to their deeper-diving ability;
4. Due to reduced availability of fish, penguins should feed at a lower trophic level during winter compared to summer;
5. Penguins that feed at a higher trophic level (i.e. more fish) should be heavier on arrival to the colony the following breeding season.

Chapter 7 – Synthesis

In this chapter I summarise the key findings of Chapters 3 to 6, focusing on how sympatric macaroni and rockhopper penguins at the Prince Edward Islands partition the marine environment throughout their annual cycle. I discuss potential top-down and bottom-up drivers of population dynamics and foraging behaviour. I make suggestions for how to incorporate macaroni and rockhopper penguins into the current Marine Protected Area management plan and I discuss the potential for future research at the Prince Edward Islands.

CHAPTER 2

Study site, species and methods

This chapter introduces the study site (Prince Edward Islands), study species (macaroni and rockhopper penguins) and methods used throughout this thesis.

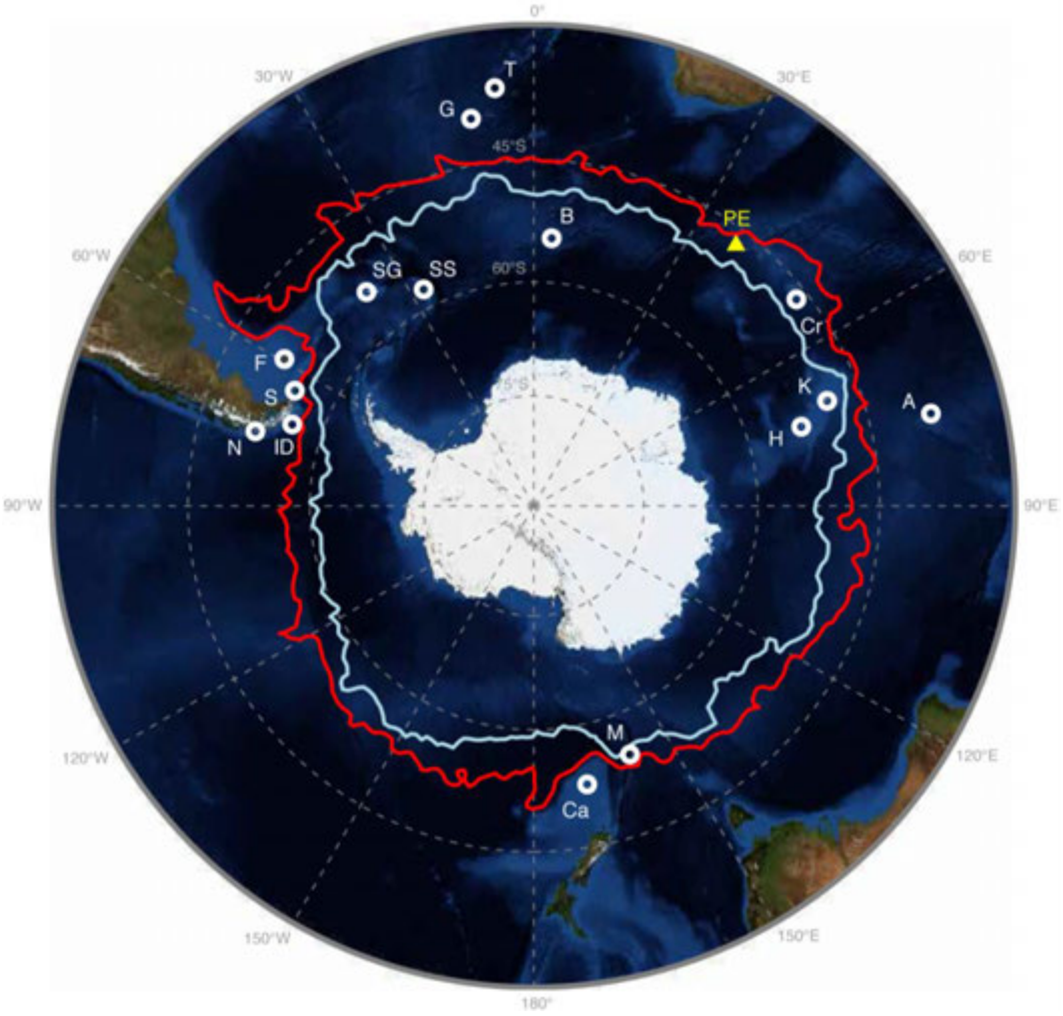


Figure 2.1. Map showing the position of the Prince Edward Islands (PE) in relation to the Sub-Antarctic Front (red line) and Antarctic Polar Front (blue line) defined by Swart et al. (2010). Locations of other major macaroni and rockhopper penguin breeding colonies are also shown: Crozet (Cr), Kerguelen (K), Heard (H), Amsterdam (A), Macquarie (M), Campbell (Ca), Noir (N), Ildefonse and Diego Ramirez (ID), Staten (S), Falklands (F), South Georgia (SG), South Sandwich (SS), Bouvetøya (B) and Gough (G) and Tristan da Cunha (T) islands.

Oceanographic setting of the Prince Edward Islands

The sub-Antarctic Prince Edward Island (PEI) archipelago is located in the Indian Ocean sector of the Southern Ocean (Fig. 2.1) and consists of Marion Island (290 km^2) and the smaller Prince Edward Island (45 km^2) 22 km to the northeast (Fig. 2.2). These islands are important breeding grounds for a large diversity of marine predators that rely on the surrounding waters for sustenance.

Figure 2.2. Satellite image of the larger Marion Island and the smaller Prince Edward Island on a clear day (courtesy of NASA Earth Observatory).

The first focused marine survey around the islands, the Marion Offshore Ecosystem Study was initiated in the late 1980s in order to investigate the links between land-based top predators, life in the water column and the physical oceanography (McQuaid and Froneman 2008). Subsequent research programmes, such as the Marion Islands Offshore Variability Study, the Marion Offshore Variability Study, and the Dynamics of Eddies Impact on Marion's Ecosystem (McQuaid and Froneman 2008), have also addressed the enigma of how a tiny archipelago can sustain such large populations of seals and seabirds in an ocean environment usually associated with low productivity.

The PEI archipelago lies directly in the path of the easterly flowing Antarctic Circumpolar Current (ACC), in a transition zone called the Antarctic Polar Frontal Zone (PFZ), which is bounded to the south by the Antarctic Polar Front (APF) and to the north by the sub-Antarctic Front (SAF). The open waters of the PFZ are subject to almost continuous deep mixing due to wind stress, resulting in relatively low phytoplankton biomass and production (McQuaid and Froneman 2008). Picophytoplankton (< 2.0 μm) dominate these waters due to their ability to tolerate the poor light environment and comparatively low macronutrient availability (Perisinotto et al. 1990). The transitional nature of the PFZ and its blend of species from sub-tropical, sub-Antarctic and Antarctic waters mean that it effectively acts as an ecotone. There are no clear trends in the spatial distribution of zooplankton communities in these waters due to the extreme spatial and inter-annual variability in species composition and community structure (Pakhomov and Froneman 1999; Hunt et al. 2001). This is largely attributed to the periodic intrusion of tongues of warmer sub-tropical surface waters from the north and colder Antarctic waters from the south, each introducing their own species assemblages into the PFZ (Pakhomov and Froneman 1999). Also, the interaction between the ACC and the South-West Indian Ridge (upstream of the PEIs) generates warm and cold core features that periodically move past the PEIs (Ansorge and Lutjeharms 2003). These eddies support higher densities of macrozooplankton (mainly euphausiids and amphipods) and micronekton than the surrounding waters (Pakhomov et al. 2003) and are important foraging grounds for some of the top predators breeding at the PEIs, such as grey-headed albatrosses *Thalassarche chrysostoma* (Nel et al. 2001).

At the frontal boundaries, where there is increased stratification of the water column, chlorophyll-a density increases and phytoplankton community structure changes, with nano- (2.0 - 20.0 μm) and microphytoplankton (> 20.0 μm) becoming the dominant size classes (Pakhomov and Froneman 1999). Larger size classes of phytoplankton are preferred by larger zooplankton and myctophid fish, which occur in greater densities at the frontal boundaries (Hulley 1990; Pakhomov et al. 1994). For many marine top predators, these areas act as foraging hot-spots due to the increased abundance of preferred prey species (Bost et al. 2009). The SAF and APF are usually located well away from the islands and are therefore only accessible to land-based marine predators during certain stages of their breeding cycle. For those with limited foraging ranges, such as breeding crested penguins, they must depend on resources in the vicinity of the islands. Unfortunately, the dynamics of inshore resources are not well understood during summer because most of the oceanographic work at the islands has been conducted during April/May.

Despite being located in the poorly productive waters of the PFZ, the shallow (< 300 m) shelf waters between Marion and Prince Edward Islands are particularly productive, especially during periods of high water retention over the island shelf (Perissinotto and Duncombe Rae 1990). Such conditions arise when the SAF and APF are far from the archipelago, weakening the local flow rates of the ACC and allowing frictional forces to trap eddies between the two islands (Ansorge and Lutjeharms 2002). This increases both water column stability and availability of nutrients that are conducive to phytoplankton blooms (Perissinotto et al. 1990). These large-scale processes are complemented by smaller scale enhancement of phytoplankton growth by extensive beds of the giant kelp *Macrocystis laevis* (Attwood et al. 1991). These kelp beds contribute to water column stability by subduing the effects of swells and retaining freshwater run-off from the islands (McQuaid and Froneman 2008), and provide an alternative source of organic matter for autochthonous primary production (Kaehler et al. 2000).

Increased phytoplankton production is usually synonymous with increased zooplankton biomass, as observed at the SAF and APF, but in the vicinity of the PEIs, total zooplankton biomass is generally lowest in the shallow shelf waters between the two islands, and highest offshore (Pakhomov and Froneman 1999; Pakhomov et al. 2000; McQuaid and Froneman 2008). The most likely explanation for this pattern relates to the interaction of the ACC with the islands. The PEIs are located on a shallow plateau that rises steeply from a depth of > 3000 m (Pakhomov and Froneman 1999). As this plateau obstructs the natural flow of the ACC, the current diverges and the bulk of the water accelerates around, rather than between the two islands (Pakhomov and Froneman 1999b). Zooplankton drifting past the islands therefore forms concentrated belts of elevated stocks close to the island shelf, creating important foraging grounds for the island's top predators (McQuaid and Froneman 2008).

This implies that the zooplankton and micronekton communities in the immediate vicinity of the PEIs must originate from farther upstream. Using stable isotope analyses, Kaehler et al. (2000) confirmed the allochthonous diet of the pelagic zooplankton community surrounding the PEIs, indicating that they fed on nano- and picophytoplankton associated with the open waters of the PFZ. In contrast, the inter-island and nearshore benthic communities derive their diet from autochthonous sources, indicating that they graze on microphytoplankton blooms and kelp-derived organic matter (Kaehler et al. 2000).

Despite the extreme temporal and spatial variability of the PFZ, there is a general consistency in the structure of the zooplankton community in the waters surrounding the PEIs. Mesozooplankton (200 - 2000 μm) dominate, with the smaller (200 - 1000 μm) copepods being the most abundant, and the larger (1000 - 2000 μm) chaetognaths (*Eukrohnia hamate* and *Sagitta gazellae*), amphipods (*Themisto gaudichaudi*) and euphausiids (*Thysanoessa* spp.) comprising the bulk of the total biomass (Hunt et al. 2001; Pakhomov et al. 2000). Macrozooplankton (> 2 cm) may also contribute substantially to total biomass (up to 45% of total zooplankton biomass; Pakhomov and Froneman 1999b), with the most important groups being euphausiids (*Euphausia vallentini* and *Nematoscelis megalopes*), chaetognaths (*Sagitta gazellae* and *S. maximum*) and tunicates (mainly *Salpa thompson*) (Pakhomov and Froneman 1999b; Pakhomov et al. 2000a; Gurney et al. 2002).

The offshore zooplankton community differs markedly from the inter-island shelf community (Pakhomov et al. 2000). In the inter-island shelf waters, euphausiids are less important, being replaced by benthic species, such as the benthic shrimp *Nauticaris marionis*, which are more abundant. Nekton communities in shelf waters are dominated by demersal fish, which form an important part of the diet of nearshore predators, such as gentoo penguins (Adams and Klages 1989). Despite the changes in species composition, total nekton abundance and biomass do not differ between the open waters of the PFZ and the shelf waters of the PEIs (Pakhomov et al. 2001).

Marine environments in the Southern Ocean are changing and it is imperative that research efforts are increased to better understand the implications of such changes. Mean annual sea surface temperatures at Marion Island have increased more than 1.4 °C since the 1950s (Melice et al. 2003). Long-term southward shifts in the positions of the Sub-Antarctic and Sub-Tropical Fronts have been recorded (Hunt et al. 2001; Beal et al. 2011; Downes et al. 2011), meaning that intrusions of warmer, less-productive waters to the islands are becoming more common. Continued monitoring, coupled with the establishment of baseline information regarding the at-sea foraging behaviour of marine top predators, such as the crested penguins, can offer valuable insights into changes in the marine environment.

The macaroni penguin

Macaroni penguins (Fig. 2.3) are the most abundant penguin species with a total breeding population of 6.3 million pairs (Crossin et al. 2013). They are the largest avian consumers of marine resources in the Southern Ocean (Brooke 2004) and have a wide distribution, ranging from the Southeast Pacific to the South Indian Ocean (Fig. 2.4; Birdlife International 2017a). The sub-Antarctic islands where they breed include (but are not restricted to) South Georgia, Bouvetøya, Marion, Crozet, Kerguelen and Heard Islands (Fig. 2.1).

Figure 2.3. A pair of macaroni penguins; *Eudyptes chrysolophus* means 'good diver with a golden crest'

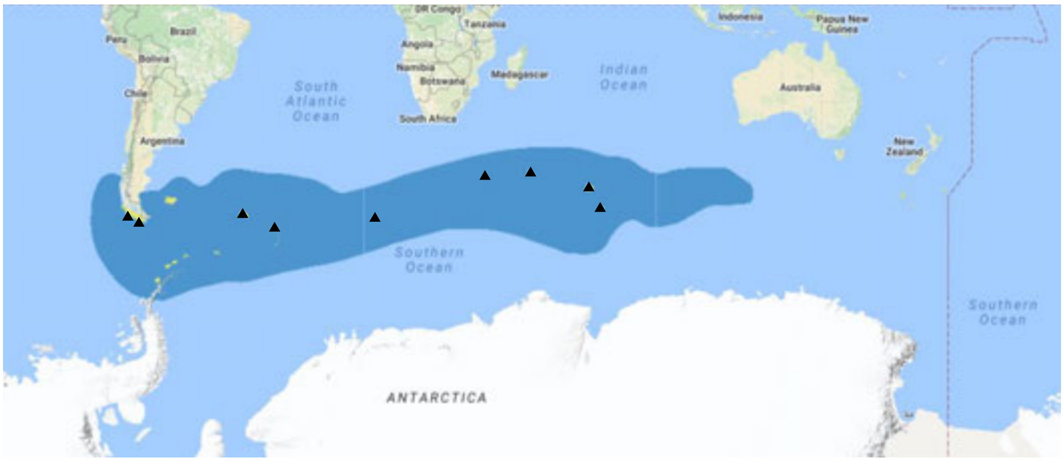


Figure 2.4. Global distribution of macaroni penguins (Birdlife International 2017a).

Breeding biology

The annual calendar of a macaroni penguin can be separated into breeding and non-breeding phases (Fig. 2.5). The non-breeding phase consists of the pre-moult, moult and winter periods. During winter, penguins spend six months at sea before returning to their breeding colonies for the austral summer. Males arrive several days earlier than females to establish territories and build nests. Dates of arrival fluctuate between years and localities but at Marion Island macaroni penguins generally arrive in early October (Crawford et al. 2006). After courtship and mating occurs, both sexes fast for 3 – 4 weeks before two eggs are laid and incubation begins (Strange 1982). The incubation period lasts for 34 – 40 d (Williams 1981), during which males and females take turns to incubate the eggs, with shifts lasting between 10 - 26 d (Green et al. 1998; Barlow and Croxall 2002a). The chick-rearing season is divided into two stages based on parental duties; brood-guard and crèche. During brood-guard, the female does all the provisioning whilst the male remains at the nest to brood or guard the chick, subsisting on his fat reserves. After 20 – 24 d the chick is large enough to thermoregulate by itself, allowing both parents to forage at sea simultaneously. During this stage, chicks gather in crèches, which increases their chances of survival against land-based predators, such as brown skuas *Stercorarius antarcticus* and giant petrels *Macronectes* spp. Once chicks are 60 to 70 d old, they lose their down feathers and fledge in mid-February. The parents, now with no chick-provisioning responsibilities, head to sea for several weeks on a pre-moult foraging trip to replenish lost body stores and fatten up for the annual moult. The pre-moult foraging trip ranges from 18 to 21 d at South Georgia (Croxall et al. 1988; Green et al. 2009) to over 50 d at the Crozet Islands (Thiebot et al. 2014). After returning from their pre-moult foraging trip, penguins spend 3 to 4 weeks fasting in the colony whilst old feathers are shed and replaced with new ones. This ensures that they are in good condition to survive the long winter at sea. Macaroni penguins leave Marion Island in mid-April, only returning in October.

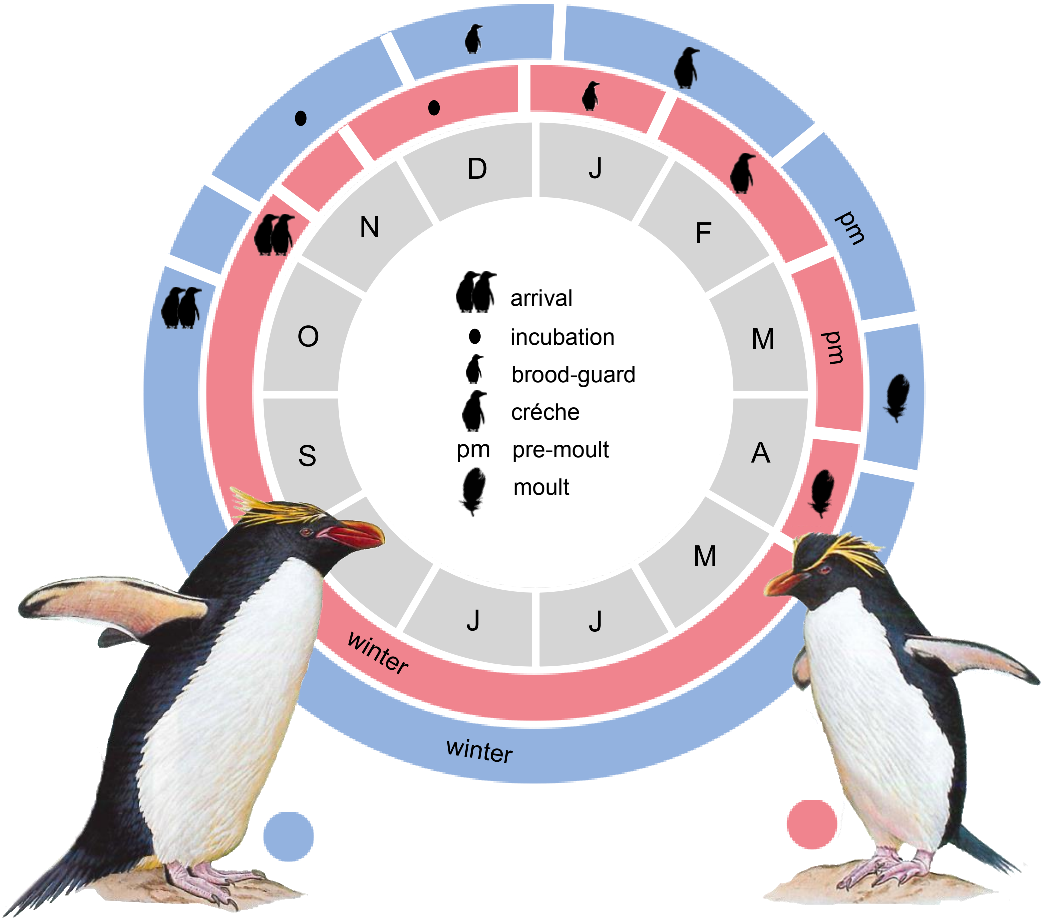


Figure 2.5. Annual cycles of macaroni (blue) and rockhopper (red) penguins at the Prince Edward Islands

Diet

Macaroni penguins generally prey on mesopelagic fish, cephalopods and swarming crustaceans (Brown and Klages 1987; Deagle et al. 2008; Waluda et al. 2010). The most common prey type across their geographic range is krill (Euphausiidae). At South Georgia and Bouvetøya they primarily feed on Antarctic krill *Euphausia superba* (Waluda et al. 2010; Blanchet et al. 2013) and at Marion, Crozet, Kerguelen and Heard Islands they feed on *E.*

vallentini and/or *Thysanoessa vicina/macrura* (Brown and Klages 1987; Deagle et al. 2008). Diet may, however, vary considerably within a single breeding season (Brown and Klages 1987; Green et al. 1998; Deagle et al. 2008) and between years (Brown and Klages 1987), with the contribution of fish, cephalopods or other crustaceans sometimes dominating the diet. For example, the proportion of euphausiids in the diet of macaroni penguins at Heard Island decreased by 93 % over a single breeding season, with myctophid fish *Krefftichthys anderssoni* becoming the dominant prey item (Green et al. 1998). Similarly, the proportion of crustaceans in the diet of macaroni penguins at Marion Island decreased and the proportions of fish and cephalopods increased as the breeding season progressed (Brown and Klages 1989). Contributions of prey items can also vary greatly between years, as benthic shrimp *Nauticaris marionis* dominated the diet at Marion Island in 1983/84 but was not recorded in 1984/85 (Brown and Klages 1987).

Diving behaviour

The diving behaviour of a penguin is largely influenced by the movement of its prey. Krill, the main prey of macaroni penguins, migrate vertically through the water column, being nearest to the surface at night and migrating deeper during the day (Wilson et al. 1993). Penguins rely heavily on their eyesight for feeding, which makes foraging at night difficult. It is therefore no surprise that macaroni penguins forage mostly during the day (Green et al. 1998; Green et al. 2005). When they do forage at night, diving is restricted to the upper 20 m of the water column and the duration of dives is much shorter (Croxall et al. 1988, 1993; Pichegru et al. 2011). During the day, macaroni penguins are capable of diving to 150 m (Pichegru et al. 2011).

During the chick-rearing period, the diving behaviour of macaroni penguins has been studied at South Georgia (Croxall et al. 1988, 1993; Mori and Boyd 2004), Heard Island (Green et al. 1998; Deagle et al. 2008), Bouvetøya (Blanchet et al. 2013), Crozet (Bon 2016), Kerguelen (Sato et al. 2004; Bon 2016) and Marion Island (Pichegru et al. 2011), and that of its sibling species, the royal penguin *Eudyptes schlegeli,* has been studied at Macquarie Island (Hull 2000). Additionally, the diving behaviour of macaroni penguins from South Georgia has been recorded during both breeding and non-breeding stages using implanted data loggers (Green et al. 2005). Macaroni penguins at all localities dive most frequently to depths < 10 m but these are thought to be related to travelling (Deagle et al. 2008). The depths at which penguins primarily forage varies between localities, sexes, breeding stages and seasons but are usually distinguished by a second peak in the dive depth distribution. At Marion and Bouvetøya Islands, penguins target a deep layer between 50 and 80 m (Pichegru et al. 2011; Blanchet et al. 2013). At Heard Island, most foraging dives are between 10 and 60 m and are concentrated around dawn and dusk, but this behaviour changes throughout the breeding season (Green et al. 1998). Seasonal change in diving behaviour is most likely associated with a temporal change in the type and/or behaviour of the prey targeted. For example, at Heard Island, macaroni penguins that fed on a larger proportion of fish performed deeper dives than those that fed on euphausiids, indicating prey-specific diving behaviours (Deagle et al. 2008). Only two studies have documented the diving behaviour of macaroni penguins outside the breeding season, both of which have been at South Georgia. Croxall et al. (1988) recorded diving depths during the pre-moult foraging trip that were similar to those during the breeding season. Green et al. (2005) recorded diving behaviour throughout the year and found that penguins dived deeper, for longer and more efficiently during winter than in the summer breeding season. Male macaroni penguins, which are larger than females, dive deeper and for longer than females (Green et al. 1998; Green et al. 2005).

Foraging range

The distance an adult penguin travels and the time spent at sea are constrained by their parental duties while breeding. These constraints are dependent on the energy demands of offspring and partner (during incubation), and as these change, so do the limitations on the extent a penguin is able to travel to find prey. During winter, when penguins only feed for themselves, they are free to travel great distances from their colonies. Macaroni penguins from the Crozet Islands travel at least 1200 km away from their colonies during this period, whereas those from Kerguelen reach up to 2400 km (Bost et al. 2009; Thiebot et al. 2011). Macaroni penguins at both localities spend most of the winter period in the vicinity of the Antarctic Polar Front, similar to conspecifics at South Georgia (Ratcliffe et al. 2014).

For macaroni penguins, adults typically undertake longer and farther foraging trips during incubation compared to the short and close foraging trips observed during the brood-guard stage of chick-rearing. For example, foraging ranges during incubation at South Georgia are mostly between 300 and 700 km (Barlow and Croxall 2002a; Green et al. 2009), whereas chick-rearing penguins remain within 60 km of their colonies (Trathan et al. 1998; Barlow and Croxall 2002a). Similarly, at the Crozet Islands, most macaroni penguins were observed about 50 km offshore during the chick-rearing period (Stahl et al. 1985). Foraging ranges do, however, change as the energy demands of chicks change. At Heard Island, foraging trips averaged 47 km during brood-guard, whereas those during crèche ranged from 53 – 347 km (Deagle et al. 2008). At Bouvetøya, foraging trips during the late brood-guard/early crèche stage ranged from 2 – 248 km with a mean of 48 km (Blanchet et al. 2013). At Marion Island, foraging ranges of 59 – 303 km were estimated for macaroni penguins rearing large chicks (26 – 62 d old; Brown 1987a). It appears common that foraging range increases as chicks get larger, most probably because the chicks can withstand increasingly prolonged periods between meals and because provisioning duties are shared between males and females (Williams 1982).

Several studies have investigated the foraging ranges of macaroni penguins during the pre-moult foraging trip. Estimates of 711 and 1180 km were obtained for two penguins at Marion Island using speed-meters (Brown 1987a). At South Georgia, mean foraging ranges of 634 and 697 km were recorded in 2002 and 2003, respectively (Green et al. 2009; Waluda et al. 2010), when penguins headed north to the Sub-Antarctic and Antarctic Polar Fronts (Green et al. 2009). At Crozet and Kerguelen Islands macaroni penguins travelled > 800 km south to the Antarctic Polar Front (Thiebot et al. 2014). At Bouvetøya penguins travelled > 400 km north to the Antarctic Polar Front (Lowther et al. 2014).

Population dynamics

Populations of macaroni penguins have declined throughout their circumpolar range in recent decades, resulting in them being listed as Vulnerable by the International Union for Conservation of Nature (BirdLife International 2017a). The Prince Edward Islands support approximately 302,000 pairs of macaroni penguins, comprising 4% of global population, with ~85 % breeding at two colonies on the south-east coast (Fig. 2.5; Crawford et al. 2009). Approximately 12,000 pairs breed at Prince Edward Island and 290,000 pairs breed at Marion Island (Crawford et al. 2009). In 2008/09, population numbers at Marion Island were 30 % less than they were in 1994/95 (Crawford et al. 2009). Declines have been attributed to inadequate breeding success, as pairs fledged an average of 0.46 chicks per year between 1994/95 and 2002/03 (Crawford et al. 2003a). The macaroni penguin population at the Prince Edward Islands is at the northern limit of the species' range and is therefore expected to be more affected by a changing climate than populations at other localities (Pichegru et al. 2011).

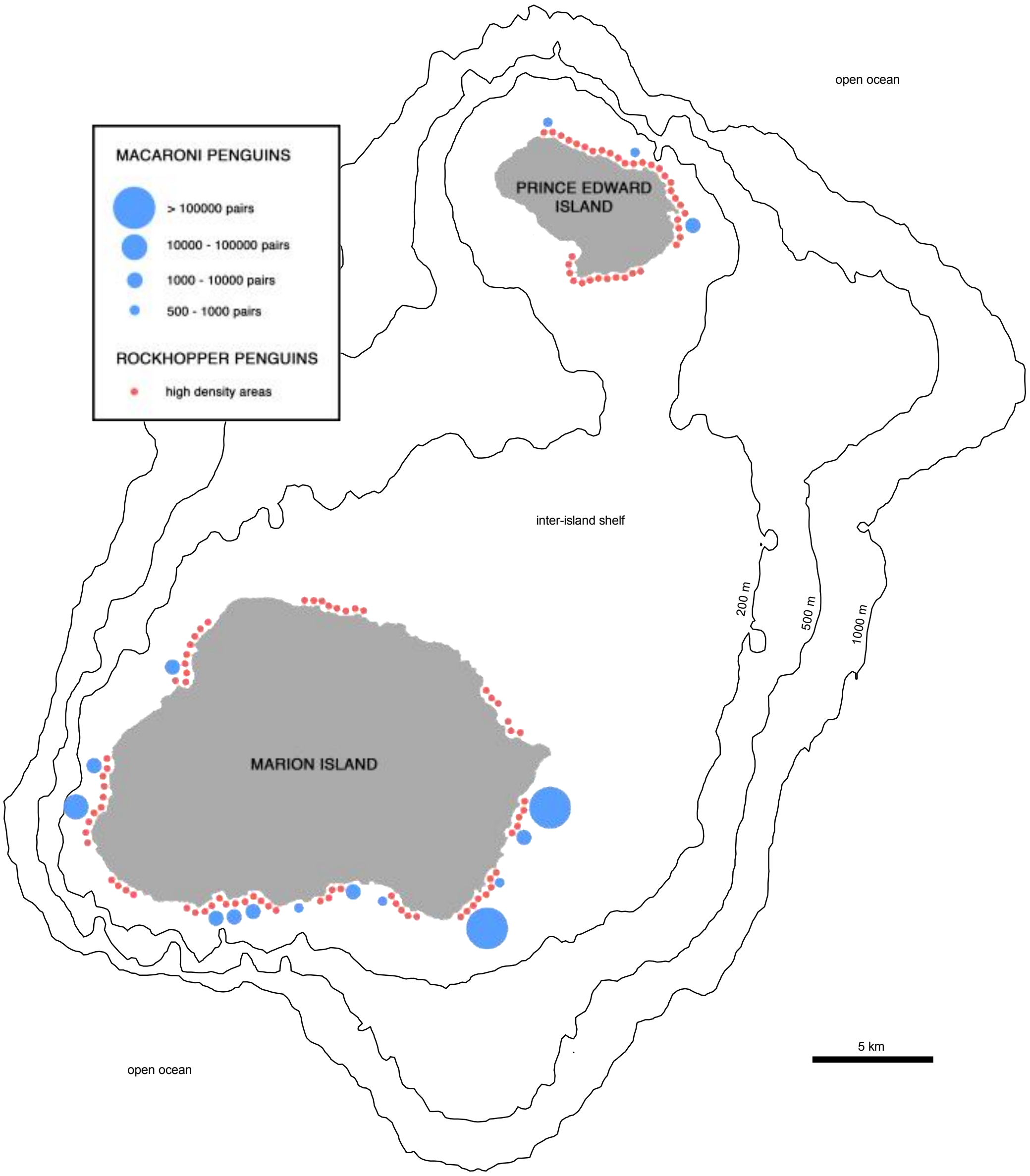


Figure 2.5. The major breeding distribution of macaroni and rockhopper penguins at Marion and Prince Edward Islands in relation to local bathymetry (200 m, 500 m and 1000 m isobaths). Small colonies of macaroni (< 500 pairs) and rockhopper penguins (< 100 pairs) are not shown

The rockhopper penguin

The rockhopper penguin was recently split into two species – northern *E. moseleyi* and southern *E. chrysocome* – based on genetic and morphological differences (Jouventin et al. 2006). Northern rockhopper penguins breed at temperate islands, such as Gough, Tristan da Cunha, Amsterdam and St Paul Islands, whereas southern rockhopper penguins inhabit sub-Antarctic islands. Within the southern rockhopper penguins, two subspecies are recognised – the southern *E. c. chrysocome* and eastern *E. c. filholi* (Fig. 2.6; Banks et al. 2006; de Dinchin et al. 2009). The southern subspecies occurs around southern South America and the Falklands, whereas the eastern subspecies is found at islands in the southwest Indian and southwest Pacific Oceans (Fig. 2.7; Birdlife International 2017b). Eastern rockhopper penguins (hereafter referred to as rockhopper penguins) are the most widespread of the eudyptids and inhabit (but are not restricted to) the Prince Edwards, Crozet, Kerguelen, Heard, Macquarie, Antipodes, Auckland and Campbell Islands.

Figure 2.6. An eastern rockhopper penguin *Eudyptes chrysocome filholi*, meaning 'good diver with golden hair'

Figure 2.7. Global distribution of southern rockhopper penguins *Eudyptes chrysocome* (Birdlife International 2017b). Eastern subspecies occurs in the Indian Ocean and New Zealand island groups.

Breeding biology

The breeding biology of rockhopper penguins is almost identical to macaroni penguins (Fig. 2.5). Dates of arrival vary slightly between years and localities but at Marion Island rockhopper penguins generally arrive in early November (Crawford et al. 2006). The incubation period lasts 28 – 32 d (Williams 1981) and brood-guard is ~ 20 – 24 d (Williams 1982). Chicks generally fledge in early March, 60 – 70 d after hatching, after adults have departed for the pre-moult foraging trip. Adults return to moult ~ 1 month later and leave the island in early May, returning only in November.

Diet

Like macaroni penguins, rockhopper penguins predominantly feed on krill (Euphausiidae), although mesopelagic fish, cephalopods and other swarming crustaceans often contribute considerably to the diet (Brown and Klages 1987). At the Crozet and Kerguelen Archipelagos, they primarily feed on *E. vallentini* (Tremblay and Cherel 2003) but at Kerguelen, benthic prey (a few fish and the mysid *Mysidetes morbihanensis*) also forms an important part of the diet in some years (Tremblay and Cherel 2000). At Macquarie Island, the diet is dominated by euphausiids and myctophid fish, particularly *E. vallentini* and *K. anderssoni* (Hull 1999). At Campbell Island, the diet is dominated by *E. vallentini* but they feed on the southern blue whiting *Micromesisteus australis* in years of low krill availability (Morrison et al. 2014). At Staten Island, *E. vallentini* dominates the diet numerically but cephalopods contribute more in terms of mass (Schiavini and Rey 2004). At Marion Island, *E. vallentini* and *T. vicina* generally dominate the diet (Brown and Klages 1987; Adams and Brown 1990) but there is large temporal variation in the diet. Brown and Klages (1987) recorded a considerably change in the diet across a single breeding season, with myctophid fish and cephalopods becoming more common as chicks got older (Brown and Klages 1987). Inter-annual variation in the diet has also been recorded at Marion Island, with the benthic shrimp *N. marionis* dominating the diet in 1983/84 but not recorded the following year, mirroring the pattern observed in macaroni penguins (Brown and Klages 1987).

Diving behaviour

The diving behaviour of rockhopper penguins during the breeding season has been studied at Crozet (Wilson et al. 1997; Tremblay and Cherel 2003), Kerguelen (Tremblay and Cherel 1999, 2000, 2003), Macquarie (Hull 2000), Falklands (Putz et al. 2006), Staten (Schiavini and Rey 2004; Putz et al. 2006) and Noir Islands (Raya Rey et al. 2009). Additionally, the diving behaviour of northern rockhopper penguins has been studied at Amsterdam Island (Cherel et al. 1999; Tremblay and Cherel 2003) and Tristan da Cunha (Booth 2011).

Most studies during the chick-rearing period report mean dive depths of < 30 m (Wilson et al. 1997; Cherel et al. 1999; Hull 2000; Tremblay and Cherel 2003; Schiavini and Rey 2004) and mean dive durations of 57 – 79 s (Cherel et al. 1999; Schiavini and Rey 2004), although they are capable of diving to 109 m and for as long as 168 s (Cherel et al. 1999). Tremblay and Cherel (2000) distinguished two types of dives at the Kerguelen archipelago – pelagic and benthic. Pelagic dives are the typical dives described for most penguins, whereas benthic dives are characterised by ‘series of consecutive square-wave dives reaching similar maximum depths, with no deeper dives within the series’ (Tremblay and Cherel 2000, p 257). At Kerguelen Island, the mass of food brought ashore and the proportion of benthic dives during daily trips were positively related, indicating the importance of feeding on pelagic prey trapped at or near the sea floor during the day (Tremblay and Cherel 2000). Northern rockhopper penguins at Amsterdam Island exhibited shallower dives with shorter durations and bottom times than those of rockhopper penguins at Kerguelen and Crozet (Tremblay and Cherel 2003), which highlights the influence that different marine environments have on diving behaviour. Diving behaviour also varies throughout the breeding season. At Macquarie Island, rockhopper penguins spent more time pursuing prey at the bottom of dives while provisioning chicks than during incubation (Hull 2000). At Amsterdam Island, the number of dives per foraging trip increased and the mean dive depth decreased as chicks got older (Cherel et al. 1999).

Foraging range

During winter, mean maximum ranges of ~2500 km and ~950 km have been recorded for rockhopper penguins from the Kerguelen and Crozet Archipelagos, respectively (Thiebot et al. 2012), where penguins at both localities spend most of their time in the Sub-Antarctic and Polar Frontal Zones (Thiebot et al. 2012). Southern rockhopper penguins at Beauchêne Island (south Falklands) also spend winter in the Sub-Antarctic and Polar Frontal Zones (Ratcliffe et al. 2014). However, southern rockhopper penguins from Steeple Jason Island (north

Falkands) spend winter in sub-tropical waters over the Patagonian shelf (Pütz et al. 2002; Ratcliffe et al. 2014). This indicates that winter habitat preferences vary between populations.

During incubation, rockhopper penguins tend to embark on extended trips far from the colony (up to 500 km). Southern rockhopper penguins breeding at a colony on the west coast of the Falklands showed sex-specific differences in foraging strategies and ranges during incubation (Ludynia et al. 2013). Most males performed long trips, farther away from the colony, whereas most females performed day trips near the colony (Ludynia et al. 2013). The long trips conducted by males ranged between 191 and 432 km, and the few longs trips conducted by females ranged between 84 and 195 km (Ludynia et al. 2013). These penguins travelled west of the island to the productive waters of the Patagonian Shelf. At a colony on the north coast of the Falklands, males also undertook long trips during incubation, ranging from 136 and 466 km away from the colony (Pütz et al. 2003). These penguins foraged near the edge of the Patagonian shelf north of the island, as well as in the deeper waters beyond (Putz et al. 2003).

During the chick-rearing period rockhopper penguins are essentially inshore feeders, foraging either in shelf waters and/or in waters of a close shelf-break and slope (Schiavini and Rey 2004). Foraging ranges of rockhopper penguins during the chick-rearing period have been studied at Marion (Brown 1987a), Macquarie (Hull 1999), Antipodes (Sagar et al. 2007) and Falkland Islands (Masello et al. 2010). Foraging ranges have also been estimated from dive data at Staten (Schiavini and Rey 2004), Noir (Rey et al. 2009), Crozet and Kerguelen Islands (Tremblay and Cherel 2003).

A maximum foraging range of 20 km was estimated for southern rockhopper penguins rearing chicks at Staten Island (Schiavini and Rey 2004). At Antipodes Island, foraging trips during brood-guard ranged between 22 and 54 km, and immediately following the brood-guard two penguins embarked on trips as far as 104 and 109 km away from the colony (Sagar et al. 2005). Similarly, rockhopper penguins at Marion Island ranged from 5 to 50 km whilst rearing small chicks, and following this period a penguin travelled > 150 km from the colony on a four-day foraging trip (Brown 1987a). These longer trips occur during a transition phase between brood-guard and crèche, when rockhopper penguins take longer trips, perhaps to exploit more productive waters offshore and replenish lost body stores lost during the brood-guard phase (Tremblay and Cherel 2005). Foraging ranges and trip duration are often strongly correlated (Deagle et al. 2008). At Crozet Island, penguins embarked on longer foraging trips during crèche compared to brood-guard (Tremblay and Cherel 2005), and at Marion Island, chick-feeding rates were lower during crèche than during brood-guard (Williams 1982), suggesting that penguins travel farther offshore during the crèche stage. No studies have investigated the foraging ranges of rockhopper penguins during the pre-moult foraging trip.

Population dynamics

In recent decades, populations of rockhopper penguins have declined throughout their circumpolar range, resulting in them being listed as Vulnerable (BirdLife International 2017b), however, the Falkland Island population has increased in recent years (Baylis et al.

2013). The Prince Edward Islands support approximately 80,000 pairs of rockhopper penguins, comprising 7 % of global population (Crawford et al. 2009): c. 38,000 pairs breed at Prince Edward Island and 42,000 pairs at Marion Island (Crawford et al. 2009). In 2008/09, the population at Marion Island was 70 % less than in 1994/95 (Crawford et al. 2009). This decline has been attributed to inadequate breeding success (0.54 – 0.66 chicks per pair per year), which is correlated with a ~20 % decrease in the mass of adults returning to breed (Crawford et al. 2008).

Methods

Fieldwork and study colonies

Data collection took place over three breeding seasons (2011/12 to 2013/14). I spent a year based at the research station on Marion Island (Fig. 2.8) from April 2011 to May 2012; sampling in other years was conducted by field assistants (Table 2.2). Given the large proportions of both species located along the southeast coast, Funk Bay was chosen as the main study colony (Figs. 2.9, 2.10). During my time on the island I deployed GPS and TDR loggers (see description below) during guard, creché and pre-moult periods. Deployments were also carried out at Funk Bay during guard and pre-moult periods in 2012/13 and 2013/14 (macaroni penguins only). A considerable number of macaroni penguins also breed on the southwest coast (Fig. 2.9), and so deployments in 2012/13 were carried out at Swartkops during the guard phase (Fig. 2.11). In 2013/14, deployments on rockhopper penguins were carried out at Ship's Cove located on the northeast coast opposite the inter-island shelf. GLS loggers (see description below) were deployed in April 2013 and 2014 (Table. 2.2). Blood samples were collected in 2011/12 and feather samples were collected in 2012, 2013 and 2015 (Table. 2.2). Where applicable, adult body mass was measured using an electronic scale (±10 g) and culmen length and depth taken with Vernier calipers (±0.1 mm) to determine sex (inferred from bill measurements given by Williams and Croxall 1991, Poisbleau et al. 2010). All procedures performed during the course of this research were in accordance with the ethical standards of the Faculty of Science Animal Ethics Committee, University of Cape Town (2013/V5/NEW).

Figure 2.8. Research station (base) at Marion Island

Table 2.2. Summary of data collection

Year	Data	Stage	Collected by
2007, 2008, 2012	PTT	winter	Bruce Dyer
2011/12	GPS + TDR	guard, créche, pre-moult	Thomas Whitehead, Maëlle Connan
2011/12	Blood	winter, summer	Thomas Whitehead, Marguerite Schoeman
2012	Feathers	pre-moult	Thomas Whitehead
2012/13	GPS + TDR	guard, pre-moult	Ben Dilley, Delia Davies
2013	feathers	pre-moult	Thomas Whitehead
2013	GLS	winter	Thomas Whitehead, Pierre Pistorious
2013/14	GPS + TDR	guard, pre-moult	Stefan Schoombie, Kim Stevens, Alexis Osborne, Vonica Perold
2014	GLS	winter	Maëlle Connan
2015	feathers	pre-moult	Maëlle Connan

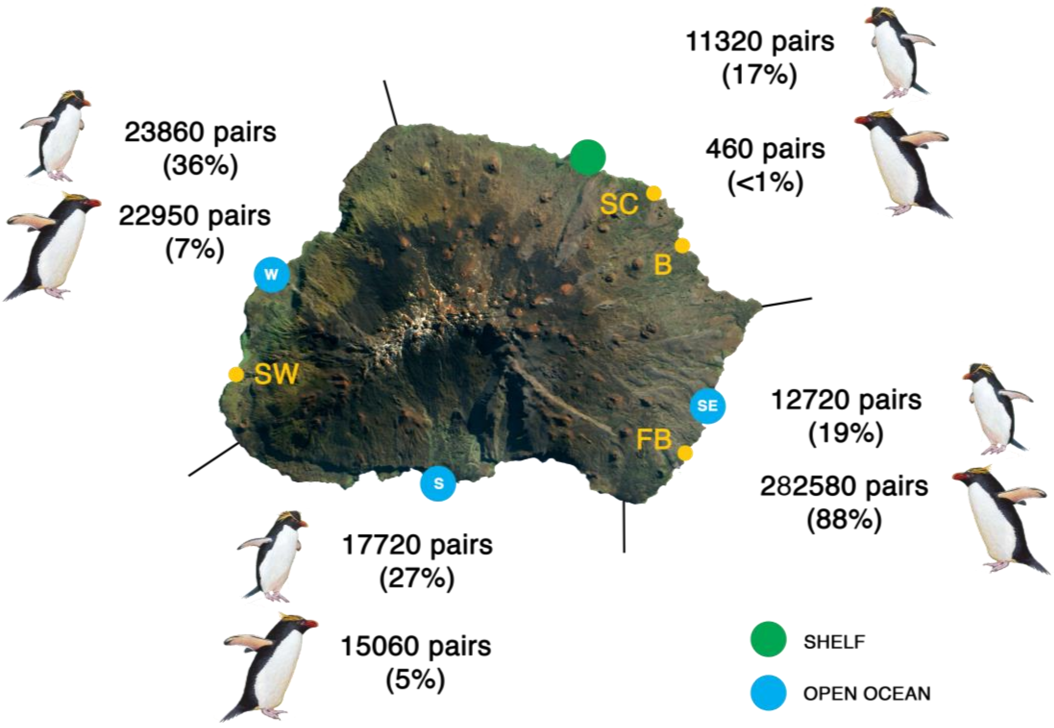


Figure 2.9. Distribution of macaroni and rockhopper penguins at Marion Island (based on 2011/12 census data, DEA). Coastline is divided into shelf (green) and open ocean (blue) habitats and percentages of the population in each sector are shown (W = west, S = south, SE = southeast). Locations of Funk Bay (FB), Swartkops (SW), Ship's Cove (SC) and the base (B) are shown

Figure 2.10. Funk Bay, Marion Island

Figure 2.11. Macaroni penguins at the Amphitheatre at Swartkops, Marion Island

GPS loggers and time-depth recorders

GPS loggers and time-depth recorders (TDRs) were used to investigate horizontal and vertical habitat use during chick-rearing (Chapter 3) and pre-moult periods (Chapter 4). CatTraQ™ GPS loggers (16 Mb memory, 230 mA lithium-ion battery, Mr Lee Technologies, 45.7 × 30.5 × 12.7 mm, 25 g, accuracy < 10 m) were customised at the IPHC-DEPE (Strasbourg, France) by removing the original packaging, replacing the main switch with a reed switch, and moulding in resin. Each GPS was programmed using @trip PC (version 2.0) to sample position at one to 90-minute intervals depending on breeding stage. TDRs (2 Mb memory, G5, CEFAS Technology Ltd., UK, 35.5 × 11.5 mm, 2.7 g) were programmed using G5 Host (version 4.0) to sample depth (12-bit resolution with an accuracy of ±1 m) and temperature (12-bit resolution with an accuracy of ±0.1 °C) at up to 1 s resolution. GPS loggers were sealed in black heat-shrink tubing and TDRs attached to the rear of the GPS unit (Fig. 2.12). Following Wilson et al. (1997), each unit (< 2 % of total body mass) was attached to feathers on the dorsal midline of the penguin's lower back using waterproof Tesa tape (Beiersdorf AG, Germany) and the tape edges sealed with cyanoacrylate glue (Loctite 401, Henkel). Birds were marked with a temporary, biological dye (Porcimark, Jørgen Kruuse A/S, Denmark) for easy identification and returned to their nest within 15 min of capture. Data were stored in the memory of each logger while it was attached, and downloaded after the logger was recovered.

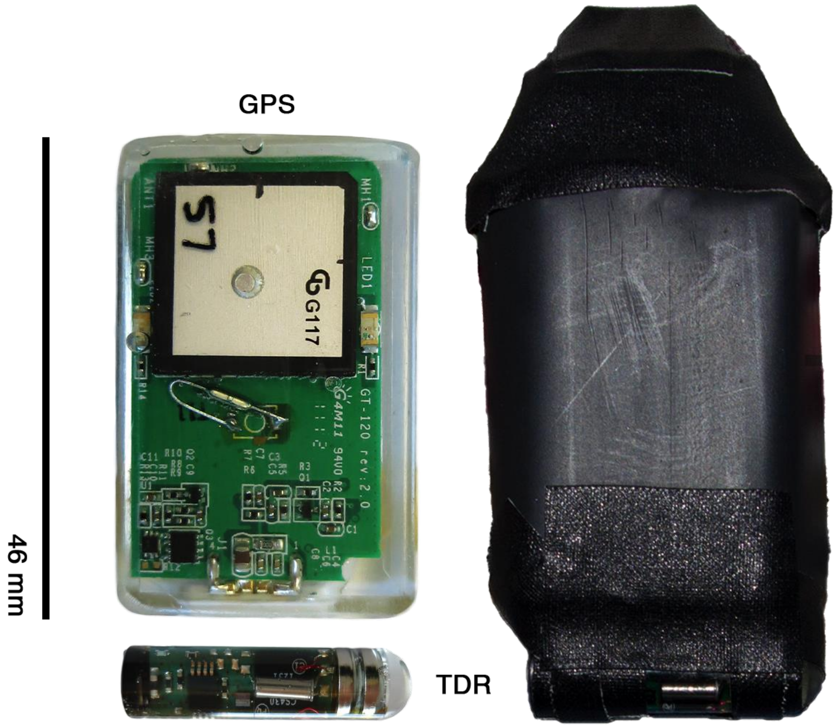


Figure 2.12. GPS logger, time-depth recorder (TDR) and GPS-TDR unit in heat-shrink tubing

Figure 2.13. GPS-TDR unit attached to a macaroni penguin (credit: Ben Dilley)

Figure 2.14. Geolocation logger (GLS) mounted to the leg of a rockhopper penguins at Ship's Cove, Marion Island

Geolocation

Due to the limited battery capacity of GPS loggers, they could not be used to track penguins during the long winter period. I therefore used light-based geolocation positioning loggers (GLS; 11x15x9 mm; 2.5 g; BioTrack, Dorset, UK) that are smaller and more energy efficient. GLS loggers record ambient light level and time, and allow the estimation of latitude and longitude twice a day (Thiebot et al. 2010). GLS loggers also record ambient sea temperature once during every 20-minute period of continuous immersion, with a resolution of ±0.05 °C and an accuracy of ±0.2 °C. GLSs were leg-mounted to penguins using specially designed bands (cable ties and heat-shrink tubing; Fig. 2.14; Ratcliffe et al. 2012) and removed when penguins returned to the island.

Figure 2.15. Satellite tags attached to a pair of macaroni penguins (credit: Peter Ryan)

Satellite tracking

ARGOS Platform Terminal Transmitters (PTTs, 30-45 g, Sirtrack, New Zealand) were used to track penguins during winter (Chapter 6) and were attached to feathers on the lower middle the back using cyanoacrylate glue (Loctite 401) and plastic cable ties (Fig. 2.15). Devices were duty-cycled to transmit for 8 hours (60 s transmission rate) and switch off for the next 16 hours. PTTs have a much higher spatial resolution than GLSs (< 10 km vs ~ 180 km, respectively; Phillips et al. 2004) and provide information on fine-scale at-sea distribution during long foraging trips when the use of GPSs are not possible.

Remote-sensing

The advent of satellites and the rapid advancement in imaging techniques and communications have made it possible to remotely measure the Earth's properties from space. This allows researchers to investigate the movement of animals in relation to environmental features and properties without *in situ* sampling of the environment.

In the marine environment, sea surface temperature (SST) and chlorophyll-a concentrations are often used to describe the at-sea distribution of marine predators. Marine predators may target specific temperature ranges (Trathan et al. 2009) and/or more productive areas (Cotté et al. 2015). As oceanographic fronts are important foraging areas for many marine predators (Bost et al. 2009), mean positions of the Sub-Tropical Front (STF), Sub-Antarctic Front (SAF), Antarctic Polar Front (APF), Southern Antarctic Circumpolar Current Front (SACCF) and Southern Boundary (SBdy; Fig. 2.16) were defined by sea surface height (SSH) contours of 0.35 m, 0.03 m, -0.48 m, -0.94 m and -1.24 m, respectively (following Swart et al. 2010). The southern extent of the APF (APF-S) was also included and defined as -0.63 m (Swart et al. 2010). These fronts were used to delineate major water masses: Sub-Antarctic Zone (SAZ) = waters between the STF and SAF, Polar Frontal Zone (PFZ) = between the SAF and APF, Antarctic Zone (AZ) = between the APF and SACCF, and Southern Zone (SZ) = between the SACCF and SBdy. Sea level anomaly (SLA), eddy kinetic energy (EKE) and geostrophic currents provide information on how marine predators interact with the mesoscale environment, including eddies. Submesoscale filaments were identified using finite-size Lyapunov exponent (FSLE), which is a measure of local stirring by mesoscale currents and a threshold of > 0.1 FSLE.day^{-1} (see d'Ovidio et al. 2004 for details). Table 2.3 shows the full list of environmental variables, abbreviations and sources included in this thesis. All environmental variables were spatially and temporally matched with locations using the function 'extract' in the R package 'raster'. A buffer of 2 km around each location was used and if more than one grid cell was included the arithmetic mean was taken.

Table 2.3. Environmental variables and sources

Variable	**Abbreviation**	**Source**
Chlorophyll-a concentration (mg.m^{-3})	-	Aqua MODIS, NPP, L3SMI[a]
Eddy kinetic energy (m^{2}.s^{-2})	EKE	Aviso[b,c]
Finite Size Lyapunov Exponent (d^{-1})	FSLE	Aviso[b]; LOcean[d]; CTOH[e]
Geostrophic currents (m.s^{-1})	-	Aviso[b]
Sea level anomaly (m)	SLA	Aviso[b]
Sea surface height (m)	SSH	Aviso[b]
Sea surface temperature (°C)	SST	GHRSST Level 4 AVHRR_OI Global Blended Sea Surface Temperature Analysis[f], Reynolds[f]
Sea surface temperature anomaly (°C)	SSTA	GHRSST Level 4 AVHRR_OI Global Blended Sea Surface Temperature Analysis[f]

[a] NASA Goddard Space Flight Center OceanColor Group (http://oceancolor.gsfc.nasa.gov/)

[b] Produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (www.aviso.altimetry.fr/duacs/)

[c] Downloaded as geostrophic velocities (U and V components) and computed as EKE = 0.5 x ($U^2 + V^2$)

[d] Laboratory of Oceanography and Climate: Experiments and Digital Approaches (www.locean-ipsl.upmc.fr)

[e] Center for Topographic studies of the Ocean and Hydrosphere (http://ctoh.legos.obs-mip.fr/)

[f] NASA Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center (http://podaac.jpl.nasa.gov/)

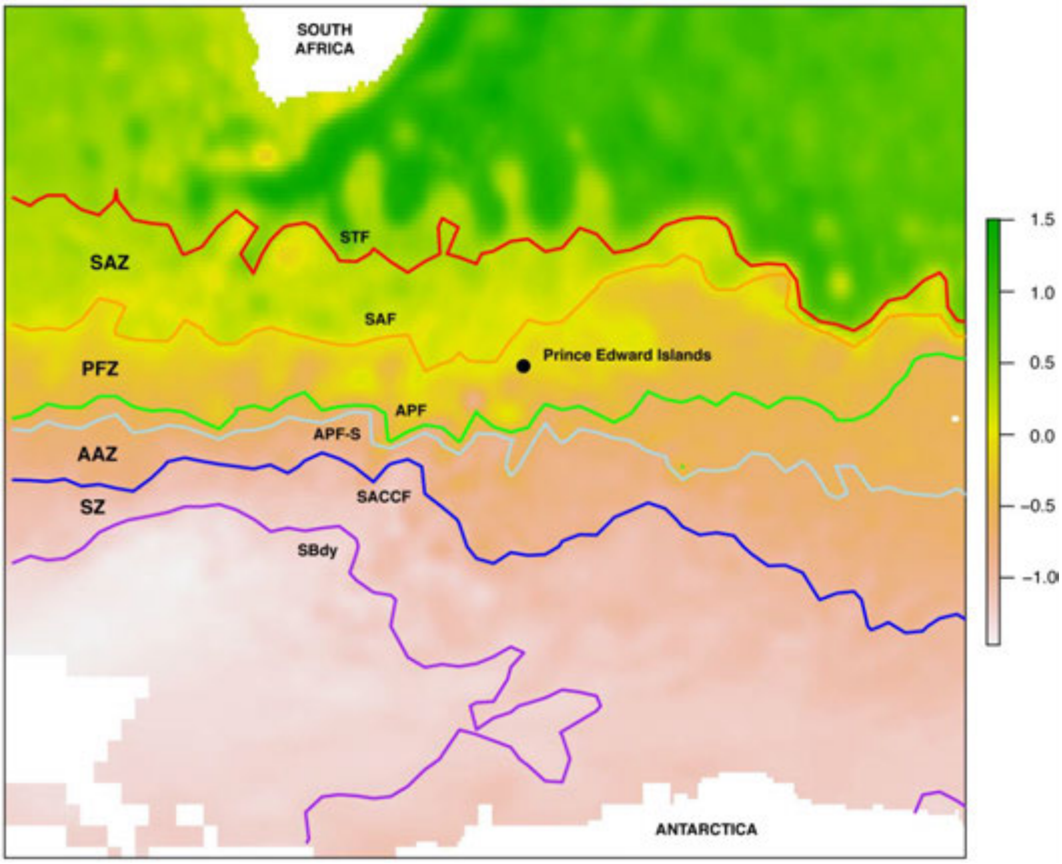


Figure 2.16. Map of sea surface height (SSH; m) showing the mean location of the sub-Tropical Front (STF), sub-Antarctic Front (SAF), Antarctic Polar Front (APF, APF-S), Southern Antarctic Circumpolar Current Front (SACCF) and Southern Boundary (SBdy). Frontal zones are also shown; Sub-Antarctic Zone (SAZ), Polar Frontal Zone (PFZ), Antarctic Zone (AAZ), Southern Boundary Zone (SZ)

Stable isotopes

Atoms of an element consist of the same number of electrons and protons, while the number of neutrons can differ. Variants of an element with different numbers of neutrons are called isotopes. Due to the higher atomic mass of isotopes with more neutrons, physiological processes within organisms lead to a differential uptake and retention of certain isotopes (Fry 2006). The ratio of heavy to the light isotope is usually reported relative to an international standard and expressed in parts per thousand, or per mil (‰):

$$\delta\,\mathrm{X} = \left(\frac{\mathrm{Rsample}}{\mathrm{Rstandard}} - 1\right) \times 1000$$

where X is the heavy isotope of an element and R is the ratio of heavy to light isotopes.

The use of stable isotopes as natural tracers allows us to reconstruct the diet and quantify the isotopic niche of animals (Cherel and Hobson 2007; Newsome et al. 2007). In marine food webs, the two most commonly used isotopic markers are carbon and nitrogen, which provide information on prey origin and trophic level, respectively (Cherel and Hobson 2007). The ratio of carbon-13 to carbon-12 (δ^{13}C) varies according to inshore versus offshore, benthic versus pelagic and, in the Southern Ocean, low-latitude versus high-latitude food webs, thus providing information on the broad-scale foraging areas of predators (Cherel and Hobson 2007). Δ^{13}C is also an indicator of ecosystem productivity due to phytoplankton-driven changes in baseline δ^{13}C of the food web (Hilton et al. 2006, Jaeger and Cherel 2011). The ratio of nitrogen-15 to nitrogen-14 (δ^{15}N) varies according to trophic level, with higher-order consumers having higher $\delta^{15}N$ than lower-order consumers within a given geographic area due to differential retention of the heaver ^{15}N isotope (Cherel and Hobson 2007).

The tissues analysed in this thesis were erythroctyes (red blood cells) and feathers. Erythrocytes were isolated from plasma using a centrifuge (10,000 rpm for one minute), then stored in an Eppendorf vial with 70% ethanol, which does not alter the isotopic composition of tissues (Cherel et al. 2007), before being frozen until further analysis. The turnover rate of isotopic markers in erythrocytes is ~ 2 months, whereas feathers remain chemically inert once grown (Cherel and Hobson 2007). Given that feathers start developing while penguins are at sea (Cherel et al. 2005), they provide useful information on diet during the pre-moult foraging trip (Chapter 5). Erythrocytes were used to investigate diet during late winter and summer (Chapter 6).

All preparations and analyses were conducted at the Stable Light Isotope Unit, University of Cape Town, South Africa. Prior to isotopic analysis, erythrocytes were dried at 50°C for 48 hours and ground into powder using a mortar and pestle. To remove impurities before drying, each feather was washed in a glass tube containing a 2:1 solution of chloroform:methanol in an ultrasonic bath for 5 min to remove any surface lipids and impurities. The feather was further rinsed in methanol and distilled water, then placed in an oven to dry (40°C for 48 h). As isotopic values in the distal half of each feather represent the diet of each penguin while at sea (Bearhop et al. 2002), only the distal half of each feather was cut and homogenised using scissors. Sub-samples (~0.4 mg) of erythrocytes/feathers were weighed in tin cups on a microbalance to the nearest microgram. The relative abundance of stable carbon and nitrogen isotopes were determined by combusting samples in a Flash 2000 organic elemental analyzer and passing gasses through a Delta V Plus isotope ratio mass spectrometer via a Conflo IV gas control unit (Thermo Scientific). Replicate measurements of internal laboratory standards (Merck gel, valine, seal bone) were used to ensure that there were minimal standard deviations of $\delta^{13}C$ and $\delta^{15}N$ measurements. All internal standards were calibrated against International Atomic Energy Agency standards. Carbon is expressed in terms of its value relative to Vienna PeeDee Belemnite, while nitrogen is expressed in terms of its value relative to atmospheric nitrogen.

More specific methodological details are included in relevant chapters.

CHAPTER 3

Habitat use and diving behaviour of sympatric crested penguins during the breeding season

‘One cannot think of penguins apart from the sea. I imagine that they must regard coming to the island not so much as a [surfing] *holiday, to be enjoyed, as in the light of a painful necessity, to be endured.’*

Cherry Kearton, *The Island of Penguins*, 1930

Abstract

During the breeding season, central place foragers may have to contend with distant or limited resources, enhancing potential competition with ecologically similar species. To minimise competition, species should segregate in space, time and/or diet. To investigate potential mechanisms of segregation that allow large numbers of macaroni and eastern rockhopper penguins to breed sympatrically at the Prince Edward Islands, habitat use and diving behaviour were studied over three successive breeding seasons (2011/12 – 2013/14) using GPS loggers and time-depth recorders. Data from 70 macaroni and 67 rockhopper penguins were collected at three colonies during guard and crèche. Most penguins foraged in deeper waters (> 3000 m) beyond the island shelf, except for rockhopper penguins at Ship's Cove (at the inter-island shelf) that foraged in waters < 200 m deep. Foraging trip duration and range were highly correlated for both macaroni and rockhopper penguins ($r^2 = 0.82$ and 0.94, respectively), indicating that the longer a penguin spent at sea, the farther it travelled. Trip duration and range of both species were similar at Funk Bay and Swartkops colonies, but rockhopper penguins at Ship's Cove foraged closer to the colony and spent less time at sea. During the guard phase, trip duration and range increased as chicks got older for both species. At sites where both species were tracked, macaroni penguins spent 7 ± 3 h longer at sea and travelled 12 ± 5 km farther than rockhopper penguins (trip duration: 29 ± 17 h vs 27 ± 15 h, range: 49 ± 22 km vs 37 ± 21 km, respectively). During crèche, most foraging trips of macaroni and rockhopper penguins were completed within one day (48 and 89 %, respectively), but penguins also performed several longer self-provisioning trips (5 – 14 d; 18 and 10 %, respectively) to the Antarctic Polar Front. Vertical habitat use was similar between

species (most foraging dives occurred between 40 and 60 m) but macaroni penguins performed fewer travelling dives (< 10 m) and more deep dives (> 80 m). On average, macaroni penguins dived for longer (143 ± 14 s vs 113 ± 16 s), spent more time at the bottom of dives, where feeding is considered to take place (70 ± 14 s vs 42 ± 10 s), and had higher bottom time dive efficiencies (0.38 ± 0.08 vs 0.28 ± 0.06) than rockhopper penguins. In 2012/13 when cooler sea surface temperatures persisted and local geostrophic flow was reduced, both species performed deeper, less efficient dives associated with the pursuit of fish. Overall, the three-week difference in the breeding cycle of macaroni and rockhopper penguins appears to be the most important mechanism reducing spatiotemporal overlap during the initial and latter weeks of the breeding season. However, overlap is likely to be high from January to mid-February (macaroni penguins – crèche, rockhopper penguins – guard/crèche). During periods of high prey availability in the upper water column (40 to 60 m), competition may be negligible, but when environmental changes reduce prey availability, competition is inevitable. In such circumstances, the larger macaroni penguins, better equipped at diving deeper, for longer, and more efficiently, should outperform rockhopper penguins. Additionally, their ability to dive deeper may provide macaroni penguins with access to more energy-rich myctophid fish. The contrasting pressures associated with reduced prey availability may explain the faster population declines of rockhopper penguins (70 %) relative to macaroni penguins (30 %) since 1994/95. More detailed studies linking at-sea foraging behaviour with diet and measures of breeding success are required to better elucidate how climate-driven changes near the Prince Edward Islands will affect crested penguins.

Introduction

During the breeding season seabirds are constrained by the need to regularly provision offspring. Swimming seabirds, such as penguins, are particularly constrained, as travelling is slower and more costly than for flying seabirds and the distance they can travel to find resources is limited (Schmidt-Nielsen 1987). This makes penguins highly dependent on local prey availability and sensitive to environmental changes. The gregarious nature of penguins also exacerbates foraging constraints through density-dependent inter- and intraspecific competition for resources (Birt et al. 1987; Lewis et al. 2001; Ballance et al. 2009). Knowledge of how penguin parents acquire sufficient resources to feed chicks within such constraints, whilst maintaining body condition, is fundamental to understanding their ecology.

At the Prince Edward Islands, approximately 302,000 pairs of macaroni and 80,000 pairs of eastern rockhopper penguins breed sympatrically (Crawford et al. 2009). This is the closest to parity in population size of any location where two eudyptids breed together (Table 1.1). These closely related species have similar breeding cycles, but rockhopper penguins commence breeding three weeks later than macaroni penguins (Brown 1987a). Both species feed primarily on swarming crustaceans (e.g. euphausiids *E. vallentini* and *T. vicina*), myctophid fish (e.g. *K. anderssoni*) and small cephalopods (Brown and Klages 1987; Crawford et al. 2003a, b), but there is high seasonal and inter-annual variability in diet composition (Brown and Klages 1987). A previous investigation of foraging ranges using speed-meters estimated that macaroni penguins foraged farther offshore than rockhopper penguins (59 – 303 km versus 4 – 157 km, respectively; Brown 1987a), however, chicks were of different ages (26 – 62 d and 7 – 30 d, respectively), precluding assessments of inherent differences in habitat use. Knowledge on the diving behaviour of macaroni penguins at Marion Island is limited to a single study during the guard period (Pichegru et al. 2011) and no studies have focused on the diving behaviour of rockhopper penguins.

In the context of the principle of competitive exclusion (Gause 1934), it is predicted that if resources are limited, these two closely related species should segregate aspects of their ecology, or one species will exclude the other. Given the recent population declines of macaroni and rockhopper penguins (30 and 70 % in since 1994/95, respectively; Crawford et al. 2009), and that breeding success of both species is below that expected to maintain a stable population (Crawford et al. 2003a, b), resources may be limited. To better understand potential mechanisms of segregation between these two species during the breeding season, more detailed information about their foraging strategies are needed.

In this chapter, GPS loggers and TDRs were used to investigate the habitat use and diving behaviour of macaroni and rockhopper penguins during three consecutive breeding seasons (2011/12 – 2013/14). The primary focus was to compare the horizontal and vertical habitat use between species to determine whether they partition resources. Additionally, seasonal and inter-annual variation in foraging behaviour were investigated in relation to oceanographic conditions to gain a better understanding of how penguins might respond to climate-driven ecosystem changes.

Methods

Study site and animals

The Prince Edward Islands consist of the smaller Prince Edward Island and the larger Marion Island (Fig. 3.1a). At-sea data were collected from adult macaroni and rockhopper penguins at three sites at Marion Island (Fig. 3.1a). Rockhopper penguins breed in small colonies scattered around the coastline, whereas macaroni penguins breed in larger colonies, with ~ 85 % of the population occurring in two colonies on the southeast coast (Crawford et al. 2009). Given that potential interspecific competition is likely to be highest along this stretch of coast, Funk Bay was chosen as the primary focus for deployments (Fig. 3.1a). A large proportion of the remaining population of macaroni penguins breeds on the west coast (Fig 2.9), and so deployments were also carried out at Swartkops during guard in 2012/13 (Fig. 3.1a). The bathymetry immediately offshore of these two colonies drops rapidly to > 3000 m (Figs. 3.1b, c). To complement investigations of spatial variation in the foraging strategies of rockhopper penguins, deployments were also carried out at Ship's Cove in 2013/14, which is located at the inter-island shelf (Fig. 3.1d). Dates of peak hatching in the 2011/12 breeding season (10 and 30 December, respectively) were used to delineate three chick-rearing stages based on chick age; early guard (< 13 d), late guard (14 – 22 d) and crèche (> 30 d). Only females provision chicks during the guard phase, whereas both sexes provision chicks during crèche.

Logger deployments

GPS loggers were deployed in all three years to sample position at 1-minute intervals. TDRs were programmed to sample depth and temperature at 1 s (2012/13 and 2013/14) and 3 s (2011/12). Penguins were captured in the late afternoon or evening, prior to their departure the following day. After one to six trips to sea, penguins were recaptured at their nest, reweighed and the logger removed. See Chapter 2 for more details on GPS and TDR deployments.

GPS data analysis

Many GPS loggers recorded insufficient locations to be used in analyses. This was likely due to the high dive rate of penguins and the low positioning of the unit on the penguins' back to reduce hydrodynamic drag, which did not allow sufficient time out of the water to regularly acquire locations (following Bannasch et al. 1994). Data from useable tracks were analysed using R (version 3.1.0; R Development Core Team 2015) and the 'Spatial Analysis' tool of Ethographer (Sakamoto et al. 2009) in Igor Pro (WaveMetrics Inc., USA, version 6.2.2.2). Duplicated and on-land locations were removed in Igor Pro. Maximum foraging range was defined as the distance between the colony and the furthest point of the trip. Tracks were linearly rediscretised at 1-minute intervals uising the function 'redisltraj' in the R package 'adehabitatLT'. Kernel density utilization distrbutions were made for each species at each colony and the overlaps computed using the function 'kerneloverlaphr' and the 'Bhattacharyya's affinity' (BA) method (Fieberg and Kochanny 2005).

Dive data analysis

Temperature and dive data were analysed in Igor Pro. Temperature data were used to infer the start and end of each trip based on a rapid decrease and increase in temperature, respectively. Mean sea surface temperature was calculated for each trip. To account for the delayed response time of the temperature sensor to detect changes (28 s to reach 66 % of the step from 5 to 30 °C) and avoid the influence of air temperature, sea surface temperature was considered as the first temperature reading after 15 s of continual submersion. Depth data were corrected for a drifting surface interval using a purpose-written macro (WaterSurface_D2GT; Sakamoto et al. 2009). A dive was considered when depth >3 m (Tremblay and Cherel 2003). The following parameters were extracted for each dive; maximum depth, duration, descent rate, ascent rate, bottom time, and post-dive interval. Bottom time was defined as the time elapsed from the first and last time the depth change rate was < 0.25 $m.s^{-1}$ (Kato et al. 2006) and was considered to be related to the time spent feeding (Ropert-Coudert et al. 2000; Charrassin et al. 2001). Dive efficiency, defined as bottom time/(dive duration + post-dive interval) was also calculated for dives where post-dive interval < 180 s (Ydenberg and Clark 1989; Tremblay and Cherel 2003). As shallow dives are often associated with travelling, only dives >10 m were considered as foraging dives following a distinct mode in dive depth distributions (see ‘Results’). Civil twilight was used to define sunrise and sunset. For each trip, the number of dives performed (total, >10 m and >80 m), the proportion of trip spent underwater and the vertical travel distance (VTD; sum of maximum dive depths) were calculated.

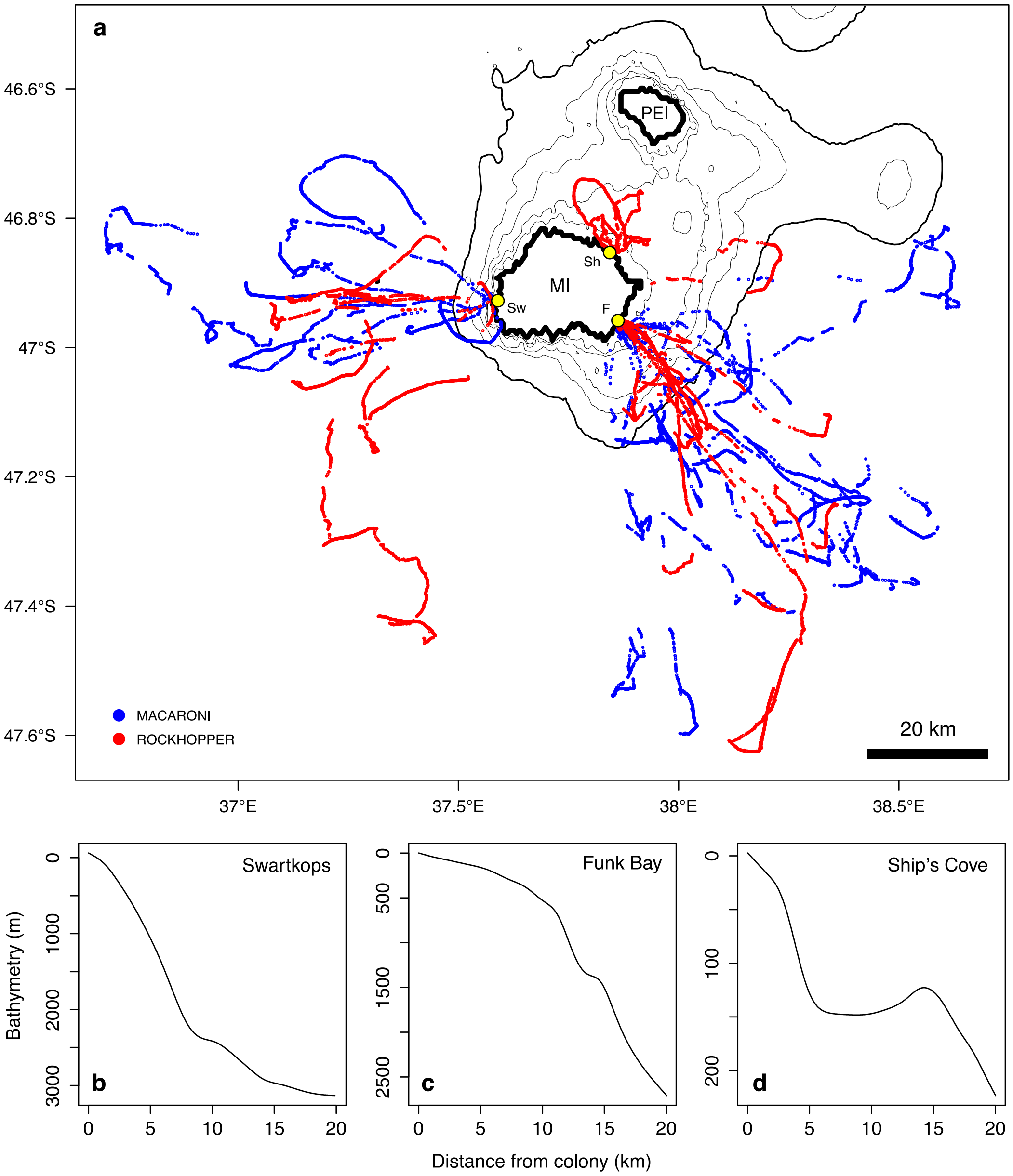


Figure 3.1. Map of Marion (MI) and Prince Edward (PEI) islands (a) showing the location of Swartkops (Sw), Funk Bay (F) and Ship's Cove (Sh) and GPS tracks of macaroni (blue) and rockhopper (red) penguins. Depth contours are also shown; 100, 200, 500, 1000 and 2000 m (bold). Slopes of perpendicular transects to each colony are shown in panels b, c and d (note: scale of y-axis differs)

Stable isotope analysis

See Chapter 2 for details on the application of stable isotopes to studying the trophic ecology of marine predators. To investigate the penguins' summer trophic ecology, 23 macaroni (12 male, 11 female) and 23 rockhopper penguins (11 male, 12 female) at Funk Bay at the end of the crèche stage in February and March 2012, respectively, and blood was collected via venipuncture in the medial metatarsal vein using a sterile slightly heparinized syringe with a 25G needle. Samples represent the guard and crèche stages of chick-rearing when both parent share rearing duties (Tremblay and Cherel 2005). Replicate measurements of internal laboratory standards indicated minimal standard deviations of δ^{13}C and δ^{15}N (Merck gel: δ^{13}C = 0.2 ‰, δ^{15}N < 0.1 ‰; valine: δ^{13}C = 0.1 ‰, δ^{15}N < 0.1 ‰; seal bone: δ^{13}C = 0.2 ‰, δ^{15}N < 0.1 ‰).

Environmental data

SSTA and chlorophyll-a concentrations were downloaded as monthly composites and geostrophic currents and SSH as daily composites (see Chapter 2 for data sources). Daily mean geostrophic flow was calculated for a 0.4° area offshore of each colony. A composite map of the bathymetry of the Prince Edward Islands was computed by Dr Dave Hedding (UNISA, South Africa) using General Bathymetric Chart of the Oceans (http://www.gebco.net/) and South African Navy data.

Statistical analysis

All analyses were performed in R (version 3.1.0; R Development Core Team 2015). Linear models (LM) were used to examine differences in weight between stages (2011/12 only), years and sites, and ANOVAs used to report the overall effect of variables with multiple factors (i.e. year). The function 'glht' in the R package 'multcomp' was used to perform post-hoc Tukey HSD tests. Linear mixed-effect models (LMEs) were used to determine if trip duration and range differed between stages, sites, years and species, with individual identity included as a random effect to account for multiple trips for some individuals. Seasonal variation was assessed separately for each species at Funk Bay in 2011/12, comparing early guard, late guard and crèche phases. Sex was included as a fixed effect to account for potential sex-specific differences in behaviour during crèche. Inter-annual and spatial variation during guard was assessed separately for each species. The number of days since hatching (based on 2011/12) was included to account for potential temporal variation during guard. Interspecific comparisons of dive parameters were made with stage, year, site and sex included as fixed effects. LMs were used to determine whether masses of male and female penguins were influenced by δ^{13}C and δ^{15}N values. Further analyses of stable isotope data are performed and reported in Chapter 6. To determine the influence of environmental conditions on diving behaviour, mean dive depth was modeled in relation to mean geostrophic flow near the colony and SST encountered by penguins, with species and site included as fixed effects, and individual identity included as a random effect.

Table 3.1. Summary of data collected from macaroni and rockhopper penguins during the chick-rearing period at Marion Island

Species	Site	Season	Stage	# deployments	# trips	# TDR	# GPS
Macaroni penguin	Funk Bay	2011/12	guard	21	27	25	18
			crèche	8	23	21	11
	Funk Bay	2012/13	guard	9	11	11	7
	Funk Bay	2013/14	guard	24	28	22	15
	Swartkops	2012/13	guard	8	9	8	7
	Total			**70**	**98**	**87**	**61**
Rockhopper penguin	Funk Bay	2011/12	guard	19	21	21	13
			crèche	12	28	25	6
	Funk Bay	2012/13	guard	5	13	11	9
	Swartkops	2012/13	guard	7	9	8	7
	Ship's Cove	2013/14	guard	24	27	27	9
	Total			**67**	**98**	**92**	**44**

Results

Seventy macaroni and 67 rockhopper penguins were equipped with GPS and TDR loggers over three breeding seasons (Table 3.1). Dive data were available for 87 and 92 trips, respectively, but due to poor location acquisition of GPS loggers, maximum range could only be determined for 61 and 44 trips, respectively (Table 3.1). Given the bimodal distribution in trip durations (Fig. S3.2), trips were grouped into short (< 4 d) and long (> 5 – 14 d). Maximum range and trip duration of short trips (< 4 d) were highly correlated for both species (r_{mac} = 0.82 and r_{rock} = 0.94), indicating that trip duration is a good proxy for maximum range for crested penguins breeding at Marion Island (Fig. 3.2). In 2011/12, mean dates of hatching and the start of crèche were 10 Dec and 4 Jan, respectively, for macaroni penguins, and 30 Dec and 24 Jan, respectively, for rockhopper penguins. Overall, mean body masses of macaroni and rockhopper penguins weighed before their foraging trips were 4.3 ± 0.4 kg and 2.5 ± 0.3 kg, respectively, with macaroni penguins ~ 70 % heavier than rockhopper penguins. In 2011/12, there were no significant differences in the mass of penguins between guard and crèche (LM_{mac}, $t_1 = 2.0$, $P = 0.05$ and LM_{rock}, $t_1 = 0.0$, $P = 0.98$). During guard, macaroni penguins at Swartkops were 0.5 ± 0.2 kg lighter than those at Funk Bay (LM, $t_3 = -2.8$, $P < 0.01$). Similarly, rockhopper penguins at Swartkops were 0.3 ± 0.1 kg lighter than those at Funk Bay and Ship's Cove (Tukey HSD, $P < 0.01$ in both cases). At Funk Bay, mass of female macaroni and rockhopper penguins during guard did not differ between years ($ANOVA_{mac}$, $F_2 = 0.4$, $P = 0.70$ and $ANOVA_{rock}$, $F_1 = 0.3$, $P = 0.62$).

Table 3.2. Maximum range and trip duration of macaroni and rockhopper penguins at Marion Island. [a]early guard only; [b]not including Ship's Cove

				Macaroni penguin			Rockhopper penguin		
	Stage	Site	Year	Mean ± SD	Range	N (*n*)	Mean ± SD	Range	N (*n*)
Trip duration (h)	Guard	Funk Bay	2011/12	34 ± 18	4 - 64	21 (25)	25 ± 15	9 - 52	21 (21)
		Funk Bay	2012/13[a]	17 ± 9	5 - 35	9 (11)	18 ± 10	8 - 30	5 (11)
		Funk Bay	2013/14	30 ± 18	6 - 61	19 (22)	-	-	-
		Swartkops	2012/13	30 ± 8	15 - 39	7 (8)	38 ± 14	27 - 67	7 (8)
		Ship's Cove	2013/14	-	-	-	12 ± 4	6 - 26	24 (27)
				29 ± 17			**27 ± 15**[b]		
	Crèche (short)	Funk Bay	2011/12	16 ± 5	10 - 19	4 (15)	13 ± 5	1 - 17	10 (22)
	Crèche (long)			200 ± 52	120 - 277	6 (6)	301 ± 43	253 - 336	3 (3)
Maximum range (km)	Guard	Funk Bay	2011/12	50 ± 25	14 - 98	17 (18)	42 ± 25	12 - 78	13 (13)
		Funk Bay	2012/13[a]	36 ± 15	21 - 59	5 (7)	23 ± 11	11 - 41	5 (9)
		Funk Bay	2013/14	53 ± 21	16 - 87	14 (15)	-	-	-
		Swartkops	2012/13	48 ± 25	12 - 81	6 (7)	40 ± 11	30 - 61	6 (7)
		Ship's Cove	2013/14	-	-	-	11 ± 8	1 - 30	9 (9)
				49 ± 22			**37 ± 21**[b]		
	Crèche (short)	Funk Bay	2011/12	32 ± 10	22 - 43	4 (7)	11 ± 9	2 - 20	3 (3)
	Crèche (long)			323 ± 64	252 - 406	4 (4)	314 ± 114	194 - 420	3 (3)

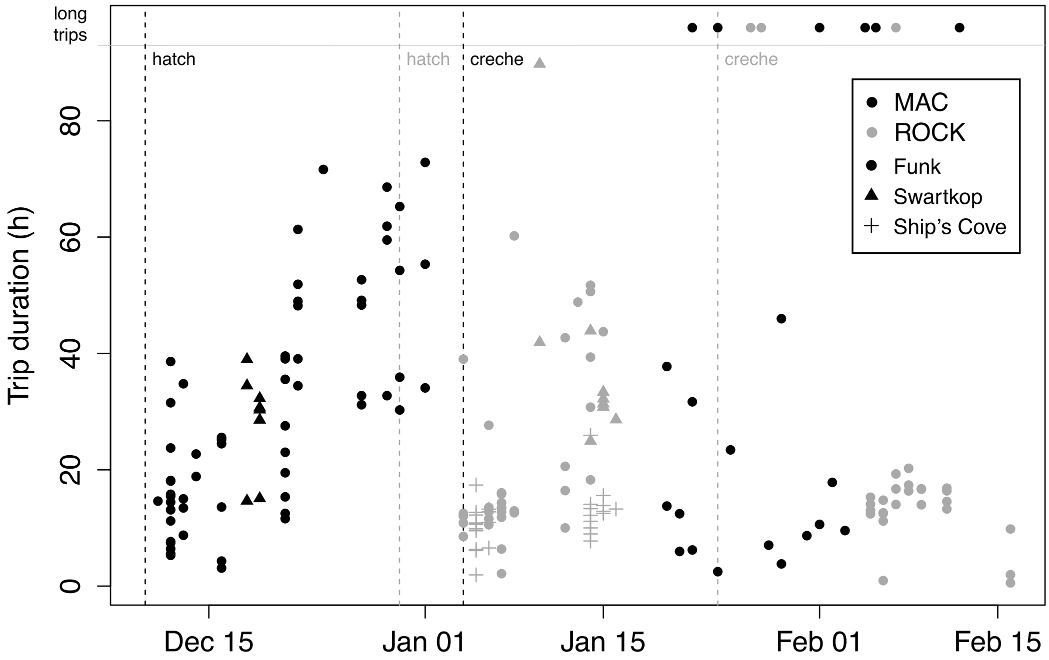


Figure 3.2. Seasonal variation in trip duration of macaroni (MAC) and rockhopper (ROCK) penguins at Marion Island (2011/12 – 2013/14). See Table 3.2 for duration of long trips (> 4 d)

Foraging strategies during guard

For **macaroni penguins,** all foraging trips during guard were < 4 d and < 100 km from the colony (Table 3.3). Median bathymetry exploited at Funk Bay and Swartkops was 3223 m and 3323 m, respectively. Trip duration increased with the number of days since hatching (LME, $F_{11} = 73.4$, $P < 0.001$), was similar between Funk Bay and Swartkops (LME, $F_{52} = 0.04$, $P = 0.84$) and differed between years (LME, $F_{52} = 5.1$, $P < 0.01$). Although mean trip durations reported in Table 3.2 indicate that trips were shorter in 2012/13, this was because deployments were only performed during early guard. Taking days since hatching into account, trip duration was 13 ± 6 h and 14 ± 4 h shorter in 2011/12 than in 2012/13 and

2013/14, respectively (LME, $t_{52} = 2.2$, $P < 0.05$ and $t_{52} = 3.2$, $P < 0.005$, respectively), but was similar between 2012/13 and 2013/14 (LME, $t_{52} = 0.2$, $P = 0.98$). Maximum range also increased with the number of days since hatching (LME, $F_4 = 12.6$, $P < 0.05$), was similar between Funk Bay and Swartkops (LME, $F_{38} = -0.3$, $P = 0.92$) and was similar between years (LME, $F_{38} = 2.7$, $P = 0.08$).

For **rockhopper penguins,** all foraging trips during guard were < 4 d and < 100 km from the colony (Table 3.3). Median bathymetry exploited at Funk Bay, Swartkops and Ship's Cove was 3042 m, 3307 m and 136 m, respectively. At Funk Bay, trip duration increased with the number of days since hatching (LME, $F_7 = 15.3$, $P < 0.01$) and did not differ between years (LME, $F_{24} = 0.07$, $P = 0.79$). At Ship's Cove and Swartkops, trip duration did not vary in relation to the number of days since hatching (LME, $t_{54} = 2.0$, $P = 0.18$ and $t_{54} = -3.0$, $P = 0.20$, respectively). Trip duration differed between sites (LME, $F_{54} = 12.7$, $P < 0.001$). Foraging trips at Ship's Cove were 12 ± 3 h shorter than at Funk Bay (LME, $t_{54} = -3.5$, $P < 0.005$) and 24 ± 5 h shorter than at Swartkops (LME, $t_{54} = 4.5$, $P < 0.001$). Trip duration at Swartkops was 12 ± 5 h longer than at Funk Bay, but this was only near significant (LME, $t_{54} = 2.2$, $P = 0.06$). At Funk Bay, maximum range was similar between 2011/12 and 2012/13 (LME, $t_{16} = -0.8$, $P = 0.44$). Maximum range did not vary in relation to the number of days since hatching at Funk Bay (LME, $t_3 = 2.8$, $P = 0.11$) or at Ship's Cove (LME, $t_7 = 1.9$, $P = 0.10$). Maximum range differed between sites (LME, $F_{30} = 6.2$, $P < 0.01$) Maximum range at Ship's Cove was 24 ± 7 km shorter than at Funk Bay (LME, $t_{30} = -3.5$, $P < 0.001$) and 19 ± 9 km shorter than at Swartkops, but this was not significant (LME, $t_{30} = 2.0$, $P = 0.11$). Penguins at Funk Bay and Swartkops had similar maximum ranges (LME, $t_{30} = -0.6$, $P = 0.54$).

For **interspecific comparisons**, macaroni penguins at Funk Bay and Swartkops spent an average of 7 ± 3 h longer at sea (LME, $t_{84} = -2.3$, $P < 0.05$) and foraged 12 ± 5 km farther offshore (LME, $t_{61} = -2.3$, $P < 0.05$) compared to rockhopper penguins. This took temporal variation during guard into account. Interspecific overlap of foraging areas at Funk Bay and at Swartkop was high (BA = 0.79 and 0.64, respectively). Rockhopper penguins at Ship's Cove showed little overlap with rockhopper and macaroni penguins at Funk Bay (BA = 0.05 and 0.08, respectively). There was no overlap between any other colonies (Fig. S3.3).

Foraging strategies during crèche

Trips were separated into day (< 1 d), short (1-4 d) and long trips (> 4 d, Fig. S3.1). For **macaroni penguins**, 48 % of foraging trips were completed on the same day. Six long trips were recorded (18 % of trips; 5 females, 1 male). All 5 tracked females performed a single long trip, whereas only 1 of the 4 tracked males did. For **rockhopper penguins**, most foraging trips were completed on the same day (89 % of trips). Three long trips were recorded (11 % of trips; 1 female, 2 males). The two long trips performed by males were at the beginning of crèche. For **interspecific comparisons**, short trips were of similar duration (LME, $t_1 = -0.9$, $P = 0.40$) and range (LME, $t_1 = -1.6$, $P = 0.18$) between species. Day trips of rockhopper penguins were 5 ± 2.6 h longer than macaroni penguins, but the difference was only near significant (LME, $t_1 = 1.9$, $P = 0.08$). Long trips of rockhopper penguins were 101 ± 35 h longer (LME, $t_1 = 2.9$, $P < 0.05$) than macaroni penguins, but maximum ranges were similar

(LME, t_1 = -0.1, P = 0.90). During long trips, both species targeted waters near the APF (Fig. 3.3).

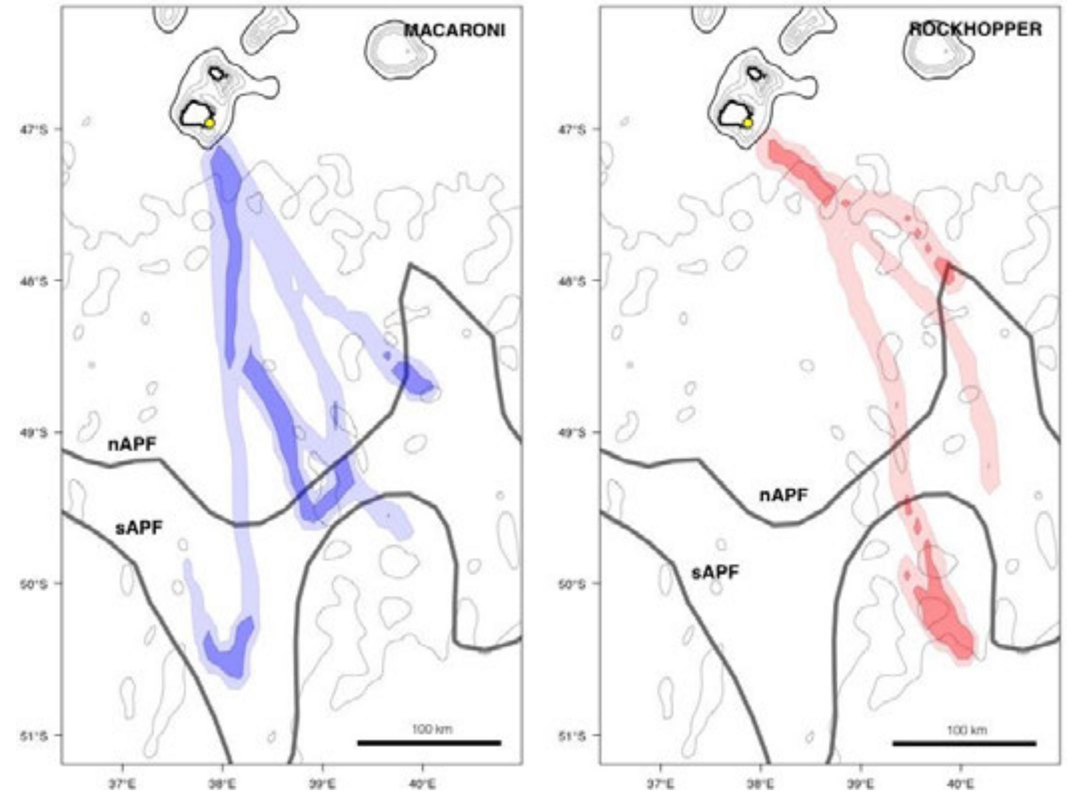


Figure 3.3. Long foraging trips performed by macaroni and rockhopper penguins during crèche phases. Kernel density estimates of 50% (dark) and 95% (light) contours were applied to locations. Mean positions of the north and south extent of the Antarctic Polar Front (nAPF and sAPF, respectively) during January and February are shown

Diving behaviour

For **macaroni penguins**, seasonal variation in diving behaviour was evident 2011/12, with penguins performing deeper, longer and fewer dives during crèche compared to early guard

(Table 3.3). Maximum depth of foraging dives at Funk Bay varied between years, with those in 2012/13 diving 24 ± 3 m deeper than in 2011/12 (LME, $t_2 = 7.8$, $P < 0.001$) and 16 ± 3 m deeper than in 2013/14 (LME, $t_2 = 7.8$, $P < 0.001$). Penguins in 2013/14 dived 7 ± 2 m deeper than in 2011/12 (LME, $t_2 = 3.0$, $P < 0.01$). Depths of foraging dives at Funk Bay in 2012/13 were 22 ± 6 m deeper than at Swartkops during the same year (LME, $t_{17} = 3.8$, $P < 0.005$). Mean depth of foraging dives was inversely related to trip duration (LME, $t_{76} = -2.6$, $P < 0.05$) and maximum range (LME, $t_{46} = -2.4$, $P < 0.05$), i.e. macaroni penguins dived shallower when performing longer trips, farther from the colony. Most dives were performed during the day (range between years: 85 % – 91 %). The distribution of dives in relation to time of day was similar between guard and crèche at Funk Bay in 2011/12, as well as during guard in 2013/14, but in 2012/13, dives were more variable, being most common in the morning (Fig. S3.2). Dives at Swartkops were concentrated in the mornings and evenings. Sex had no influence on dive depth and duration (LME, $t_1 = 0.9$, $P = 0.36$ and $t_1 = 0.1$, $P = 0.93$, respectively).

For **rockhopper penguins**, depth of foraging dives at Funk Bay in 2011/12 did not vary significantly throughout the season, but penguins performed longer dives during crèche compared to early guard (Table 3.3). At Funk Bay in 2012/13, dives were 12 ± 3 m deeper than in 2011/12 ($t_{30} = 3.4$, $P < 0.005$; Fig. 3.4), and 11 ± 5 m deeper than at Swartkops in the same year, but this was only near significant ($t_{18} = 2.0$, $P = 0.06$). At Ship's Cove in 2013/14, penguins performed fewer travelling dives than at other sites and dive depths were more evenly distributed (Fig. 3.4). Dive depth was not related to trip duration (LME, $t_{87} = -1.1$, $P = 0.26$) or maximum range (LME, $t_{36} = -0.5$, $P = 0.65$). Most dives were performed during the day (range between years: 89 – 96 %). The distribution of foraging dives in relation to time of day was similar during guard and crèche at Funk Bay in 2011/12 (Fig. S3.2). At Funk Bay in 2012/13, most dives were in the late morning, with noticeably fewer in the evening (Fig. S3.2). Contrastingly, at Swartkops in 2012/13, penguins exhibited a bimodal distribution, diving mainly in the morning and evening (Fig. S3.2). Penguins at Ship's Cove dived most commonly around midday (Fig. S3.2). Sex had no influence on dive depth and duration (LME, $t_1 = 0.04$, $P = 0.97$ and $t_1 = 1.2$, $P = 0.25$).

For **interspecific comparisons**, the overall distribution of dive depths was similar between species, with a peak in dives < 10 m and a second peak between 40 and 60 m (Fig. 3.5). Macaroni penguins performed fewer travelling dives (< 10 m) and dived less frequently (per hour) than rockhopper penguins (Table 3.1). Mean depth of foraging dives was 7 ± 2 m deeper for macaroni penguins compared to rockhopper penguins, owing to a greater proportion of dives > 80 m (Table 3.1). Peak dive durations differed between species (150 s and 120 s, respectively), with rockhopper penguins also performing considerably more short dives between 10 and 50 s (Fig. 3.5). Mean dive duration, post-dive interval and bottom time of macaroni penguins were longer than rockhopper penguins (Table 3.1). Macaroni penguins had higher dive efficiencies and spent less time underwater compared to rockhopper penguins (Table 3.1). Descent rates were similar between species, but macaroni penguins ascended faster (Table 3.1). In relation to depth, both species dived most efficiently between 20 and 50 m, and bottom times were longest at 40 to 60 m (Fig. 3.6). There were no notable interspecific differences in the distribution of foraging dives in relation to time of day (Fig. S3.2).

Table 3.3. Summary of the diving behaviour of macaroni and rockhopper penguins during three breeding seasons (2011/12 – 2013/14) at Funk Bay and Swartkops. Significance was assessed using linear mixed-effect models with site, year, sex and stage included as fixed effects, and individual identity included as a random effect (* < 0.05, ** < 0.01, *** < 0.001, ns = not significant)

	Macaroni penguin	**Rockhopper penguin**	**t-value**	***P***
Individuals (n)	68	42		
Trips (n)	81	64		
Dive rate (dives.h^{-1})	16.2 ± 3.7	26.1 ± 6.3	10.1	***
Dives > 10 m (%)	71.4 ± 15.3	61.5 ± 12.8	4.0	***
Dives > 80 m (%)	9.7 ± 13.9	3.0 ± 7.8	2.6	*
Time spent underwater (%)	49.3 ± 10.9	56.9 ± 11.7	2.8	**
Mean maximum depth (m)	54.8 ± 12.2	48.1 ± 10.2	3.5	***
Dive duration (s)	143.3 ± 14.2	113.2 ± 15.5	13.4	***
Post-dive interval (s)	46.9 ± 10.1	35.0 ± 6.1	7.9	***
Bottom time (s)	69.7 ± 13.7	41.6 ± 9.5	15.9	***
Dive efficiency	0.38 ± 0.08	0.28 ± 0.06	10.1	***
Descent rate (m.s^{-1})	1.43 ± 0.13	1.41 ± 0.16	1.8	ns
Ascent rate (m.s^{-1})	1.22 ± 0.18	1.05 ± 0.09	4.8	***

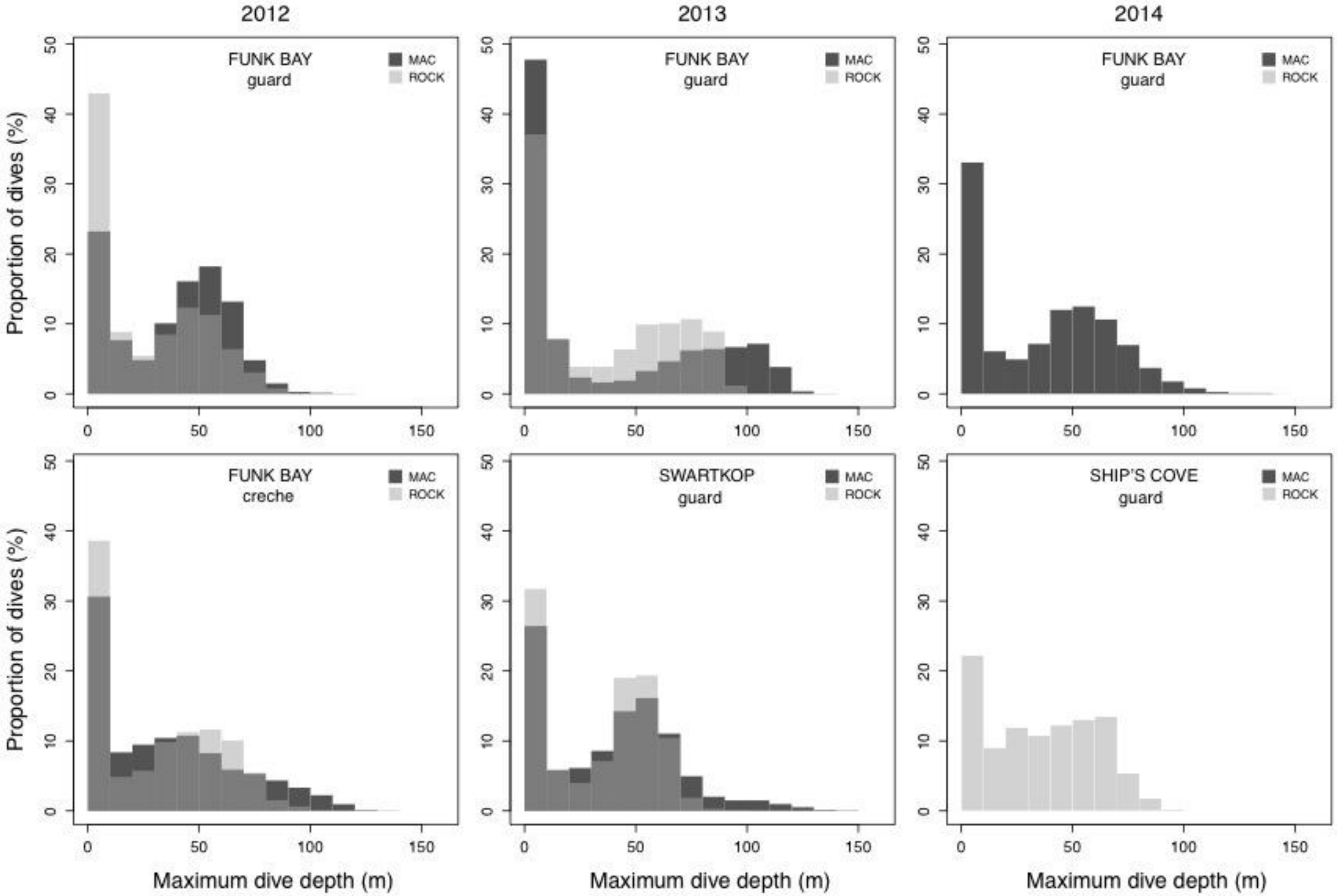


Figure 3.4. Distribution of maximum dive depths of macaroni and rockhopper penguins at individual sites during the breeding season at Marion Island

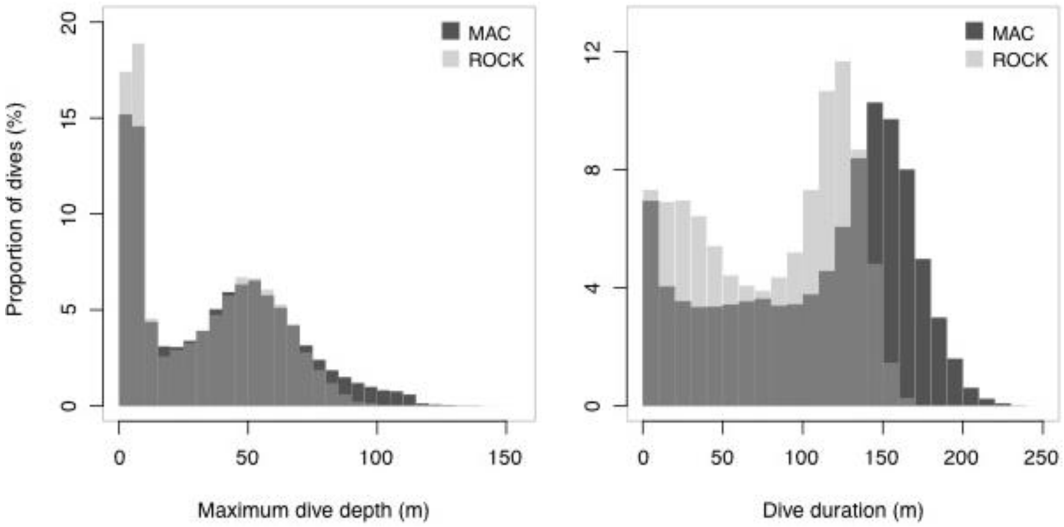


Figure 3.5. Distribution of maximum depth and duration of dives performed by macaroni (MAC) and rockhopper (ROCK) penguins during three breeding seasons (2011/12 – 2013/14) at Marion Island

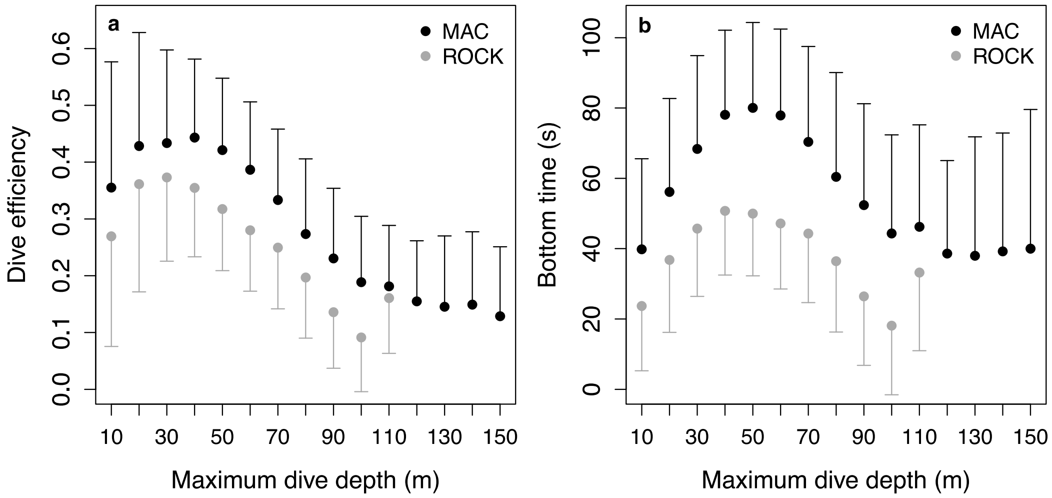


Figure 3.6. Dive efficiency (bottom time / dive duration + post-dive interval) (a) and bottom time (b) in relation to depth of dives performed by macaroni (MAC) and rockhopper (ROCK) penguins during three breeding seasons (2011/12 – 2013/14) at Marion Island

Table 3.4. Summary of dive parameters of macaroni penguins during guard

	Funk Bay			Swartkops
	2011/2	2012/13	2013/14	2012/13
Individuals (n)	19	9	18	7
Trips (n)	25	11	22	8
Dive rate (dives.h^{-1})	17.2 ± 2.2	17.7 ± 3.1	17.0 ± 3.3	13.2 ± 3
Dive > 10 m (%)	80 ± 9	55 ± 17	67 ± 13	76 ± 7
Dive > 80 m (%)	2 ± 2	29 ± 23	9.3 ± 8.5	5 ± 6
Time underwater (% trip)	56 ± 5	45 ± 9	49 ± 8	37 ± 10
VTD (km)	24 ± 14	12 ± 5	19 ± 13	15 ± 8
Maximum depth (m)	48 ± 5	71 ± 14	55 ± 8	49 ± 11
Dive duration (m)	141 ± 10	149 ± 16	141 ± 8	126 ± 15
Post-dive interval (s)	43 ± 9	53 ± 7	48 ± 11	49 ± 15
Bottom time (s)	74 ± 8	47 ± 5	79 ± 7	57 ± 7
Dive efficiency	0.39 ± 0.05	0.24 ± 0.03	0.43 ± 0.05	0.34 ± 0.04
Wiggles (n)	8 ± 1	5 ± 1	10 ± 2	6 ± 1
Descent rate (m.s^{-1})	1.44 ± 0.08	1.35 ± 0.12	1.52 ± 0.14	1.39 ± 0.10
Ascent rate (m.s^{-1})	1.15 ± 0.12	1.15 ± 0.12	1.39 ± 0.14	1.24 ± 0.10
Water temperature (°C)	6.6 ± 0.5	5.1 ± 0.1	5.6 ± 0.4	5.4 ± 0.1
Geostrophic flow (m.s^{-1})	0.24 ± 0.05	0.07 ± 0.00	0.19 ± 0.01	0.06 ± 0.00

Table 3.5. Summary of dive parameters of rockhopper penguins during guard

	Funk Bay		Swartkops	Ship's Cove
	2011/12	2012/13	2012/13	2013/14
Individuals (N)	19	4	6	24
Trips (n)	21	11	8	27
Dive rate (dives.h^{-1})	27.8 ± 4.0	20.9 ± 3.2	20.7 ± 3.2	23.7 ± 4.8
Dive > 10 m (%)	60 ± 11	62 ± 13	70 ± 6	80 ± 11
Dive > 80 m (%)	1 ± 2	12 ± 16	1 ± 1	2 ± 6
Time underwater (% trip)	57 ± 7	53 ± 13	53 ± 7	55 ± 7
VTD (km)	19 ± 10	14 ± 11	29 ± 15	10 ± 4
Maximum depth (m)	45 ± 5	56 ± 15	47 ± 3	44 ± 9
Dive duration (m)	106 ± 7	120 ± 17	116 ± 2	102 ± 14
Post-dive interval (s)	35 ± 5	40 ± 6	31 ± 5	36 ± 7
Bottom time (s)	39 ± 7	34 ± 8	44 ± 4	51 ± 6
Dive efficiency	0.29 ± 0.05	0.21 ± 0.05	0.30 ± 0.03	0.38 ± 0.04
Wiggles (n)	4 ± 1	4 ± 1	5 ± 0	6 ± 1
Descent rate (m.s^{-1})	1.42 ± 0.12	1.35 ± 0.13	1.36 ± 0.13	1.51 ± 0.10
Ascent rate (m.s^{-1})	1.04 ± 0.07	1.04 ± 0.10	1.08 ± 0.07	1.42 ± 0.06
Water temperature (°C)	6.4 ± 0.3	5.8 ± 0.2	5.9 ± 0.4	7.7 ± 0.1
Geostrophic flow (m.s^{-1})	0.31 ± 0.02	0.08 ± 0.00	0.20 ± 0.02	-

Drivers of variation in mass

Masses of female macaroni penguins were not influenced by $\delta^{13}C$ (LM, $t_{10} = -1.1$, $P = 0.30$) or $\delta^{15}N$ (LM, $t_{10} = -2.2$, $P = 0.05$), but masses of males were positively related to $\delta^{13}C$ (LM, $t_9 = 3.1$, $P < 0.05$, Fig. S3.4). There was no influence of $\delta^{15}N$ on the mass of males (LM, $t_9 = -1.0$, $P = 0.33$). Masses of male and female rockhopper penguins were not related to $\delta^{13}C$ (LM, $t_{10} =$

1.5, $P = 0.17$ and $t_9 = 2.1$, $P = 0.07$, respectively), but masses of females were negatively related to $\delta^{15}N$ (LM, $t_9 = -2.6$, $P < 0.05$, Fig. S3.4). There was no relationship between $\delta^{15}N$ and the mass of males (LM, $t_{10} = -0.4$, $P = 0.68$).

Environmental variation

Maps of geostrophic currents revealed that flow near the islands was reduced in 2012/13 compared to other years (Fig. 3.7). This was confirmed by mean values offshore of colonies during days that penguins went to sea (0.21 ± 0.08 $m.s^{-1}$, 0.10 ± 0.05 $m.s^{-1}$ and 0.19 ± 0.01 $m.s^{-1}$ in 2011/12, 2012/13 and 2013/14, respectively). When geostrophic flow offshore of colonies was reduced, dive depths of penguins were significantly deeper (LME, $t_{139} = 2.1$, $P < 0.05$; Fig. 3.8). The SAF showed little seasonal variation, but was ~ 150 km farther away from the islands in 2012/13 compared to other years (Fig. 3.9). The APF was ~ 80 km closer to the islands in 2013/14, and in January 2013 (Fig. 3.9). Maps of SSTA revealed a cool anomaly in 2012/13 associated with the more northerly location of the SAF, but warmer waters prevailed in 2011/12 and 2013/14 (Fig. 3.9; link to animation). Mean water temperatures encountered by penguins in 2011/12, 2012/13 and 2013/14 were 6.8 ± 0.7 °C, 5.6 ± 0.4 °C and 6.7 ± 1.1 °C, respectively. Cooler conditions in 2012/13 coincided with reduced productivity in December, but higher productivity in January, whereas productivity in 2011/12 and 2013/14 was highest in December (Fig. S3.5).

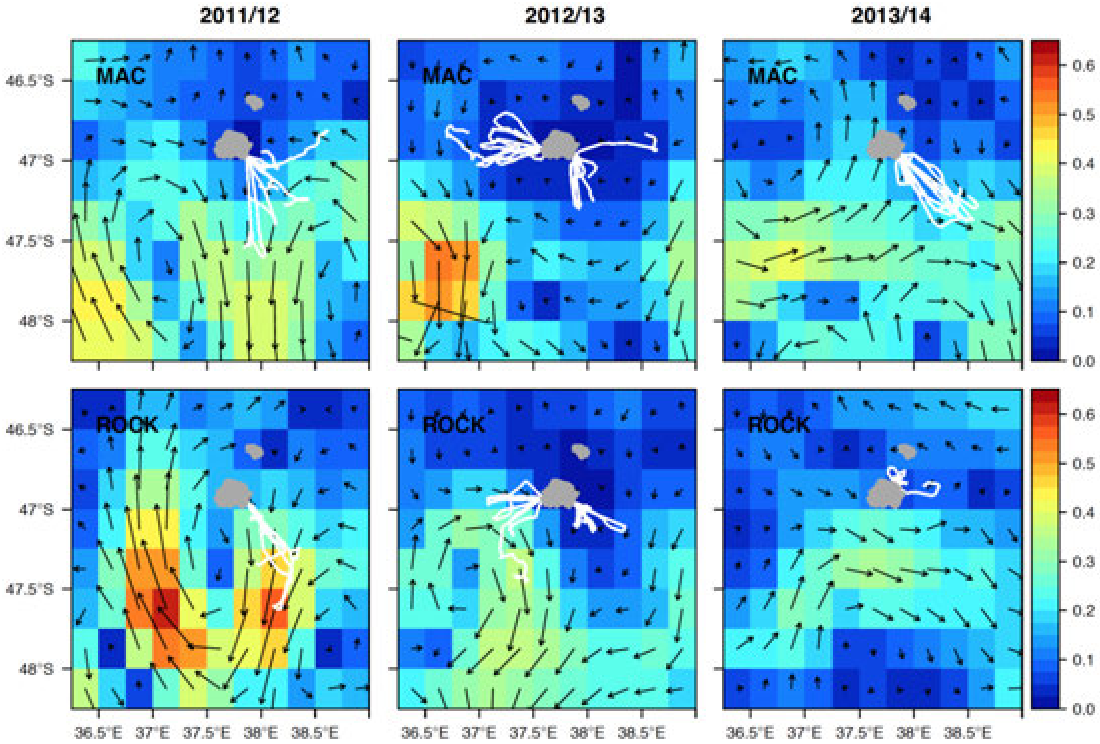


Figure 3.7 (previous page). Tracks of macaroni (MAC) and rockhopper (ROCK) penguins in relation to geostrophic currents (m.s^{-1}) near Marion Island during the guard period. Geostrophic currents are daily composites for 20 Dec and 15 Jan, respectively. Arrows show the direction and strength (length) of currents

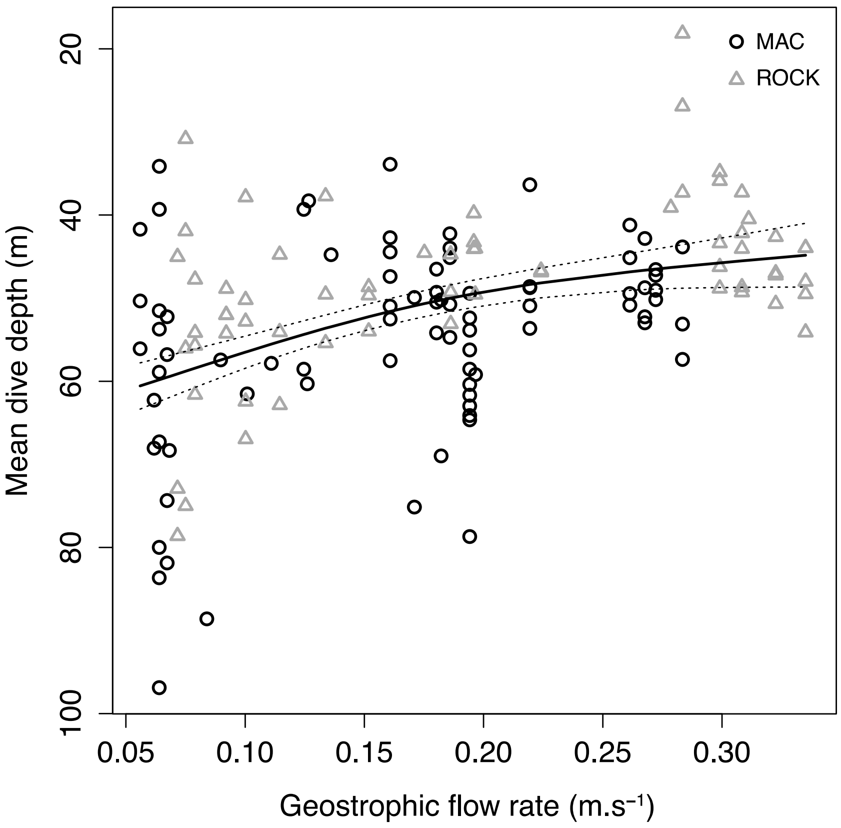


Figure 3.8. Mean dive depths of macaroni (open circles; MAC) and rockhopper (open triangles; ROCK) penguins in relation to geostrophic flow at foraging areas. Solid line represents predicted curve from generalized linear mixed-effects model, and dashed lines represent 95 % confidence intervals

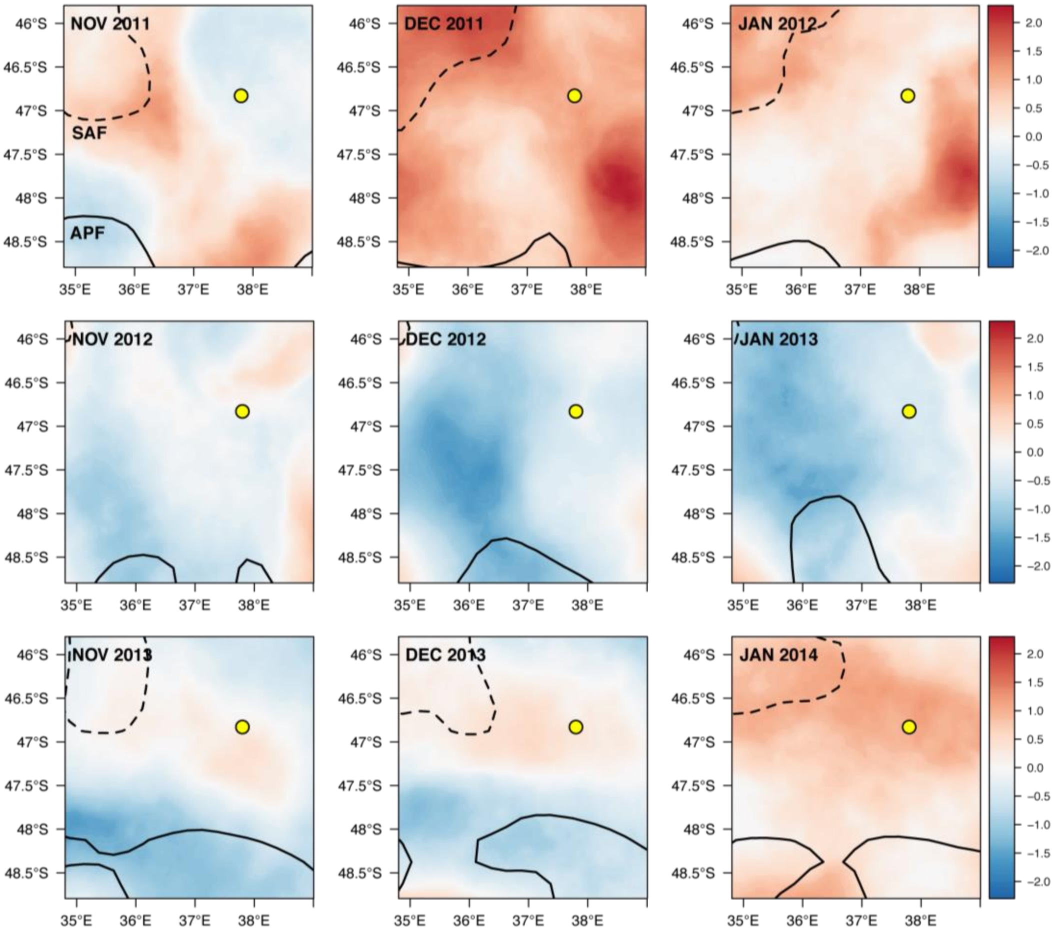


Figure 3.9. Monthly composites of satellite-derived sea surface temperature anomalies (°C) near Marion Island (yellow circle) over three successive breeding seasons (2011/12 – 2013/14). Positions of the Sub-Antarctic Front (dashed line) and Antarctic Polar Front (solid line) are shown

Discussion

Seasonal variation in the provisioning behaviour of macaroni and rockhopper penguins during the breeding season at Marion Island is described for the first time since the 1970s (Williams 1982) and more refined estimates of foraging ranges are presented (Brown 1987a). Rockhopper penguins exhibited spatial variation in foraging strategies. Evidence of seasonal and inter-annual variation in the diving behaviour of macaroni penguins expands on the work by Pichegru et al. (2011), and the diving behaviour of rockhopper penguins at Marion Island is described for the first time. Hatching dates of macaroni (10 Dec) and rockhopper (30 Dec) penguin eggs at Funk Bay in 2011/12 were similar to previously observed median hatching dates of 13 Dec (7 Dec – 20 Dec) and 1 Jan, respectively (Crawford et al. 2003a, b). Most macaroni and rockhopper penguin chicks had entered crèche by 4 Jan and 24 Jan, respectively; similar to previously observed median dates of 8 Jan (1 Jan – 18 Jan) and 24 Jan, respectively (Crawford et al. 2003a, b). Interestingly, the three-week difference in the breeding cycle of macaroni and rockhopper penguins corresponds to the duration of the guard period (~ 24 d). Furthermore, the onset of breeding for rockhopper penguins is three weeks later than predicted by local SST (Warham 1972). This appears to be a classic case of character displacement and likely evolved to reduce interspecific competition during guard, when foraging pressure near the colony is high (Brown 1987a). Allochrony has also been reported for royal and rockhopper penguins at Macquarie Island (Hull 1999), and Adélie and chinstrap penguins at King George Island (Trivelpiece et al. 1987).

Foraging strategies during guard

Foraging strategies of macaroni and rockhopper penguins at Funk Bay and Swartkops were similar, with both species targeting deep pelagic waters beyond the island plateau. It has been suggested that macrozooplankton concentrate around the plateau perimeter due to flow patterns arising from the interaction of the Antarctic Circumpolar Current with the island

(McQuaid and Froneman 2008). Pelagic foraging is typical of macaroni penguins at other localities (Barlow and Croxall 2002a; Deagle et al. 2008; Blanchet et al. 2013; Bon 2016), but they are also known to forage benthically (Deagle et al. 2008). Rockhopper penguins appear more flexible in their foraging strategies, exhibiting both pelagic and benthic foraging, depending on the marine environment near the colony (Tremblay and Cherel 2000, 2003; Schiavini and Raya Rey 2004). This flexibility is evident in the diversity of marine habitats used at Marion Island by rockhopper penguins; foraging offshore at Funk Bay and Swartkops, and over the inter-island shelf at Ship's Cove. Given that the bulk of both populations are located at colonies with close access to pelagic foraging areas (Fig 2.9), it would suggest that pelagic foraging areas are the most profitable for the two species. At Funk Bay, both species exhibited temporal variation in their foraging strategies, shifting from primarily day trips during early guard to overnight or multi-day trips during late guard (Fig. 3.2). This was also observed at colonies on the east coast of Marion Island in the 1970s (Williams 1982). The concurrent increase in trip duration and foraging range indicates that when penguins performed longer trips, they targeted prey patches farther from the colony. This supports previous observations where stomach contents became increasingly digested as chicks got older (Brown 1987a). When chicks are small, their need for regular meals constrains penguin parents to perform short foraging trips, near the colony. As chicks get larger, energy demands increase and they require larger meals, but can withstand longer periods without being fed. Theoretically, this allows penguin parents to spend more time at sea, but if sufficient resources are available near the colony, it is unlikely that a penguin would travel farther than necessary, especially given that more frequently fed chicks have a better chance of survival

(Morrison et al. 2016). Given the high density of penguins on the southeast coast, local depletion of prey resulting from high foraging pressure may force penguins to target more profitable prey patches farther offshore (i.e. Ashmole's halo effect; Birt et al. 1987). Indeed, trip duration and range of central place foragers are often linked to the density of inter- and intraspecific competitors (Lewis et al. 2001; Ballance et al. 2009). At Ship's Cove, where macaroni penguins are practically absent (< 500 pairs), rockhopper penguins showed no increase in trip duration or range. This may be due to lack of competition with macaroni penguins or reduced intraspecific competition, but may also be influenced by differences in prey availability in shelf versus pelagic environments (Pakhomov et al. 2000). A shift from day to overnights trips during guard has been reported at other localities for both macaroni (Crozet Island, Bon 2016; Heard Island, Deagle et al. 2008) and rockhopper penguins (Staten Island, Schiavini and Raya Rey 2004). However, rockhopper penguins at Crozet and Kerguelen Islands rarely performed overnight trips, but rather increased the duration of day trips as chicks got older (Tremblay and Cherel 2003, 2005). It is important to consider that environmentally driven changes in prey availability between years and localities may influence foraging strategies. At the Falkland Islands, southern rockhopper penguins performed longer trips, farther from the colony during warmer years when they fed on more squid and fish (Dehnhard et al. 2016). Similarly, rockhopper penguins at Campbell Island performed day trips during a year when krill dominated the diet, but switched from day to overnight trips when fish dominated the diet (Morrison et al. 2016). Despite the inter-annual variation in local SST and geostrophic flow in the present study, there were no apparent inter-annual differences in trip duration and range. A more thorough study involving more regular deployments (or a PIT tag system, see Horswill et al. 2014; Morrison et al. 2016) is needed to better investigate temporal variation in trip duration relative to environmental conditions and the changing energy demands of chicks.

Foraging strategies during crèche

As the energetic requirements of a penguin chick are the highest during crèche (Brown 1987b; Green et al. 2002), and males join females in chick provisioning, foraging pressure near the colony is at its highest during this stage of chick-rearing. Although both species predominantly performed day or overnights trips, similar to guard, the presence of long trips (> 4 d) potentially relieved some of the foraging pressure near the colony. Long trips during crèche are well documented in eudyptids (Tremblay and Cherel 2005; Deagle et al. 2008), and likely act as self-provisioning trips, allowing adults to replenish body stores lost due to fasting in males and intense foraging effort in females (Ropert-Coudert et al. 2004; Saraux et al. 2011). At other localities, long trips by males are typically performed during the transition period between guard and crèche (Barlow and Croxall 2002a; Deagle et al. 2008). This was observed for two of three male rockhopper penguins in this study, but no deployments were carried out for macaroni penguins during the transition phase. Female penguins at other localities performed long trips throughout crèche (Sagar et al. 2005; Raya Rey et al. 2007). This was evident for macaroni penguins in this study, but only one female rockhopper penguin performed a long trip. At Kerguelen and Crozet Islands, female rockhopper penguins performed 0 – 3 long trips lasting 5 – 29 days (Tremblay and Cherel 2005). At

Campbell Island, male rockhopper penguins undertook longer trips during a year of poor diet quality (Morrison et al. 2016), suggesting a greater investment in self-maintenance when resources are scarce. The duration of short trips performed during crèche appears highly variable between years and locations, and is likely dependent on local prey availability, such as during guard. For instance, the duration of crèche trips performed by macaroni penguins at South Georgia depends on the availability of Antarctic krill, with short day trips (5 ± 4 h) linked with high krill availability and overnight trips (24 ± 16 h) linked with low krill availability (Barlow and Croxall 2002a, b; Trathan et al. 2006). Macaroni penguins at Heard Island performed mostly overnight trips (Deagle et al. 2008). Rockhopper penguins at Crozet and Noir Islands performed mostly overnight trips (Tremblay and Cherel 2005; Raya Rey et al. 2009), but those at Kerguelen Island performed mostly day trips (Tremblay and Cherel 2005). Interestingly, Williams (1982) noted that during crèche, most (> 82 %) rockhopper penguin chicks at Marion Island fasted for 24 – 72 h – indicating very few day trips – whereas most trips in the present study were completed on the same day (89 %). This suggests that prey availability was particularly good during crèche in 2011/12 and/or that prey availability during Williams (1982) was comparatively poor.

Spatiotemporal overlap between species

The incubation period of macaroni and rockhopper penguins at Marion Island is approximately 3 Nov to 10 Dec and 25 Nov to 1 Jan, respectively (Crawford et al. 2003a, b). Although there are no data available for the at-sea distribution of macaroni and rockhopper penguins from Marion Island during this period, conspecifics travel large distances (>400 km) to forage in distant waters (Ludynia et al. 2013; Bon et al. 2015). Given that penguins at Marion Island likely adopt similar strategies, there should be no significant spatiotemporal overlap during the incubation period. After macaroni penguin eggs hatch (~ 10 Dec), adult females forage in waters <100 km from the colony, whilst rockhopper penguins undertake incubation foraging trips to distant waters. When rockhopper penguin eggs hatch (~ 30 Dec), adult females perform short, day trips near the colony, whilst macaroni penguins perform overnight trips farther offshore (end of guard). It is only when macaroni penguin chicks enter crèche that foraging areas overlap considerably, as both species perform day or overnight trips. Thus, it is likely that spatiotemporal overlap between species is high from January until mid-February, when macaroni penguins depart for the pre-moult foraging trip (Chapter 4). However, the larger proportion of overnight trips performed by macaroni penguins during crèche likely reduces spatiotemporal overlap to some extent. It is important to note that simultaneous deployments on macaroni and rockhopper penguins during the 2011/12 breeding season were not possible due to the limited number of loggers available, and therefore deployments alternated between species (Fig. 3.2). Future studies should quantify fine-scale spatiotemporal overlap between species by carrying out simultaneous deployments on macaroni and rockhopper penguins, particularly during early January to mid-February.

Variation in vertical habitat use

Macaroni and rockhopper penguins primarily foraged at 40 to 60 m, which likely reflects the vertical distribution of main prey species, euphausiids *E. vallentini* and *T. vicina* (Brown and Klages 1987; Crawford et al. 2003a, b). Although subtle, macaroni penguins dived to deeper depths (> 80 m) more often than rockhopper penguins. Such dives are typically associated with the pursuit of deeper-dwelling fishes (Green et al. 1998; Deagle et al. 2008). Both species feed on fish, but macaroni penguins generally consume greater proportions, more regularly (Cooper et al. 1990; Crawford et al. 2003a, b). The seasonal and inter-annual variation in vertical habitat use exhibited by penguins in this study mimics the high variability in diet (Brown and Klages 1987; Crawford et al. 2003a, b). As crested penguins at Marion Island are primarily reliant on allochthonous euphausiids during the breeding season (Kaehler et al. 2000), drivers of variation are likely linked to oceanographic processes that transport prey to the islands. At a broad scale, variability in the species composition and structure of zooplankton and micronekton communities near the islands has been attributed to fluctuations in the position of the SAF (Hunt et al. 2001; Hunt and Pakhomov 2003). For instance, periodic intrusions of warm water carrying sub-tropical and sub-Antarctic species, such as *E. vallentini*, are associated with the close proximity of the SAF, whereas intrusions of cooler water carrying Antarctic species occur when it is located farther north (Hunt et al. 2001; Hunt and Pakhomov 2003). In recent years, the average position of the SAF has shifted farther south, resulting in more frequent intrusions of warmer water to the Prince Edward Islands (Hunt et al. 2001). This has coincided with an increase in the importance of *E. vallentini* in the diet of gentoo penguins at Marion Island (Carpenter-Kling 2015). During the present study, two years (2011/12 and 2013/14) were characterised by warmer SSTs and a southward meander in the SAF upstream of the islands. During these years, penguins consistently dived to 40 – 60 m and diets were dominated by krill *E. vallentini* and *T. vicina* (DEA, unpubl. data; Table 3.6). Conversely, when cooler SSTs associated with the more northerly position of the SAF persisted in 2012/13, both species at Funk Bay dived considerably deeper and fed on a greater proportion of fish (DEA, unpubl. data; Table 3.6). However, penguins at Swartkops (on the west coast), one week after deployments at Funk Bay, did not dive deeper, suggesting high temporal variability or differences in prey distribution around the islands. The influence of geostrophic flow on vertical habitat use suggests that currents may structure the local distribution of prey. This may occur in two ways. Firstly, reduced flow may limit lateral advection of euphausiids and result in early depletion of existing stocks. In such circumstances, penguins may be forced to dive deeper to pursue fish, such as in 2012/13. Secondly, geostrophic flow may influence prey distribution through vertical stratification of the water column. Mixed layer depths are often shallower at the edges of fast flowing currents (Fox-Kemper and Ferrari 2008; Lévy et al. 2012), which may concentrate prey at depths where diving is more efficient. Conversely, when flow is reduced, increased mixing may push prey into deeper waters, resulting in more variable and deeper dives, as observed in 2012/13. Animations of geostrophic currents suggest that they are driven by meanders originating at the APF and/or eddies moving past the islands (Ansorge et al. 2009). It has been suggested that the eddy corridor that originates at the South-West Indian Ridge and passes immediately south of the Prince Edward Islands acts as a 'conveyor belt' of resources for top predators (Ansorge et al. 2009; Durgadoo et al. 2010). With so many potential drivers of variability in such a dynamic system, and the short temporal window in which the present study was conducted, it is difficult to identify specific drivers of variation in diving behaviour. Further investigations linking diving behaviour to oceanographic conditions are needed to better elucidate drivers of variability.

Table 3.6. Percentage of reconstituted mass of main prey items in the diet of macaroni and rockhopper penguins at colonies on the east coast of Marion Island (data supplied by Bruce Dyer, Oceans & Coasts, DEA)

	2011/12			2012/13			2013/14		
	Mac		Rock	Mac		Rock	Mac		Rock
	Dec	Jan	Jan	Dec	Jan	Jan	Dec	Jan	Jan
CRUSTACEANS	**87**	**72**	**98**	**50**	**63**	**82**	**97**	**80**	**85**
Euphausia vallentini	41	30	40	39	13	2	43	14	23
Thysanoessa vicina	46	42	58	11	48	76	53	66	62
FISH	**8**	**22**	**0**	**48**	**36**	**13**	**1**	**19**	**12**
Krefftichthys anderssoni		6		9	14		1	19	
Protomyctophum tenisoni	1	16		33	18				
Juvenile nototheniids						13			12
CEPHALOPODS	**4**	**0**	**0**	**2**	**0**	**5**	**1**	**0**	**2**
Other	1	6	2		1		1	1	1

Link between diet, diving behaviour and population dynamics

Recent population declines of macaroni and rockhopper penguins at Marion Island may be related to poor reproductive performance (Cooper et al. 1997; Crawford et al. 2003a, b;

Crawford et al. 2009). The nutritional stress hypothesis states that reduced reproductive performance may result from decreased prey abundance, quality and/or accessibility (Trites and Donely 2013). Reduced prey availability may increase energetic costs associated with foraging by forcing penguins to increase diving effort or to travel farther in search of suitable foraging areas. During guard at Funk Bay in 2011/12 and 2013/14, the relatively shallow, consistent and efficient dives performed by both species were associated with diets almost exclusively comprised of krill, particularly *E. vallentini* (DEA, unpubl. data; Table 3.6). Conversely, the deeper, more variable and less efficient dives performed in 2012/13 were associated with increased proportions of fish in the diet (DEA, unpubl. data; Table 3.6). Macaroni penguins targeted myctophids *Kreffichthys anderssoni* and *Protomyctophum tenisoni*, whereas rockhopper penguins fed on juvenile nototheniids (DEA, unpubl. data; Table 3.6), which are less energy-dense (Lenky et al. 2012). The lack of myctophids in the diet of rockhopper penguins may be due to their inability to reach the depths at which macaroni penguins were feeding. Although no measures of reproductive performance were available, previous studies at Marion Island revealed that macaroni penguins fledged heavier chicks when myctophids were more prevalent in the diet (Crawford et al. 2003b), but no trend was apparent for rockhopper penguins (Crawford et al. 2003a). This contrasts with studies at other localities where macaroni and rockhopper penguins fledged heavier chicks when euphausiids dominated the diet (Waluda et al. 2012; Morrison et al. 2014). The inverse relationship between prey diversity and prevalence of *E. superba* in the diet of macaroni penguins at South Georgia suggests that penguins only resort to feeding on alternative prey, such as fish and squid, when krill availability is insufficient (Waluda et al. 2012). It is hard to envisage penguins swimming past swarms of krill to feed on fish at deeper depths if krill swarms are sufficiently dense. The fact that bottom durations – linked to time spent feeding (Charrassin et al. 2001) – were longest at 40 to 60 m reinforces the notion that it is more profitable to feed on krill when sufficient stocks are available. However, when krill availability is reduced, the ability of macaroni penguins to dive deeper than rockhopper penguins may allow them access to more myctophids. The high energy density of myctophids may counteract the increased energetic costs associated with diving deeper, buffering them against fluctuations in krill availability. Conversely, rockhopper penguins may not cope as well as macaroni penguins during reduced krill availability, as evident in their pursuit of less energy-dense nototheniids. When rockhopper penguins at Campbell Island fed on less energy-dense southern blue whiting *Micromesisteus australis* they fledged lighter chicks (Morrison et al. 2014). If rockhopper penguins at Marion Island are similarly affected by switching to a fish-based diet, then breeding success in 2012/13 might have been negatively affected. The contrasting responses of macaroni and rockhopper penguins to reduced krill availability may explain contrasting rates of population decline (30 and 70 % in since 1994/95, respectively; Crawford et al. 2009). To test this hypothesis, future studies linking diet, diving behaviour and breeding success are needed.

Conclusions

At Funk Bay and Swartkops, both species foraged in pelagic waters off the island shelf (> 3000 m), with macaroni penguins foraging slightly farther away and spending more time at sea.

Vertical habitat use was similar between species, with most foraging dives between 40 and 60 m, but macaroni penguins dived to such depths more efficiently. Subtle differences in depth use were observed, with macaroni penguins performing fewer travelling dives (< 10 m) and more deep foraging dives (> 80 m). At Ship's Cove, rockhopper penguins foraged over the inter-island shelf, spent less time at sea and dived more efficiently than at other sites. This lower foraging effort was either attributed to the absence of macaroni penguins and/or differences in prey distribution between shelf and pelagic habitats. The overall similarity in foraging strategies at sites where both species co-exist in large numbers suggests that during periods of high spatiotemporal overlap, such as crèche, competition is inevitable. The partial allochrony – or temporal segregation of three weeks – appears to function as the most important mechanism in reducing interspecific competition during the initial (incubation/guard for macaroni penguins) and latter weeks of the breeding season. In years when the availability of prey in the upper water column is sufficient (such as 2011/12 and 2013/14), competition is unlikely to be significant, however, during years when prey availability is reduced and penguins are forced to pursue different prey deeper in the water column, the larger macaroni penguins, better equipped at diving deeper, for longer, and more efficiently, are likely to outperform rockhopper penguins. These subtle differences in diving behaviour indicate that niche differences exist between the two species. The apparent influence of geostrophic flow and/or SST on diving behaviour indicates that local currents influence prey availability. However, further studies of diving behaviour, coupled with diet analyses and measures of breeding success, over a wide range of environmental conditions are needed to better elucidate environmental drivers of prey availability and its influence on interspecific dynamics.

Supplementary material

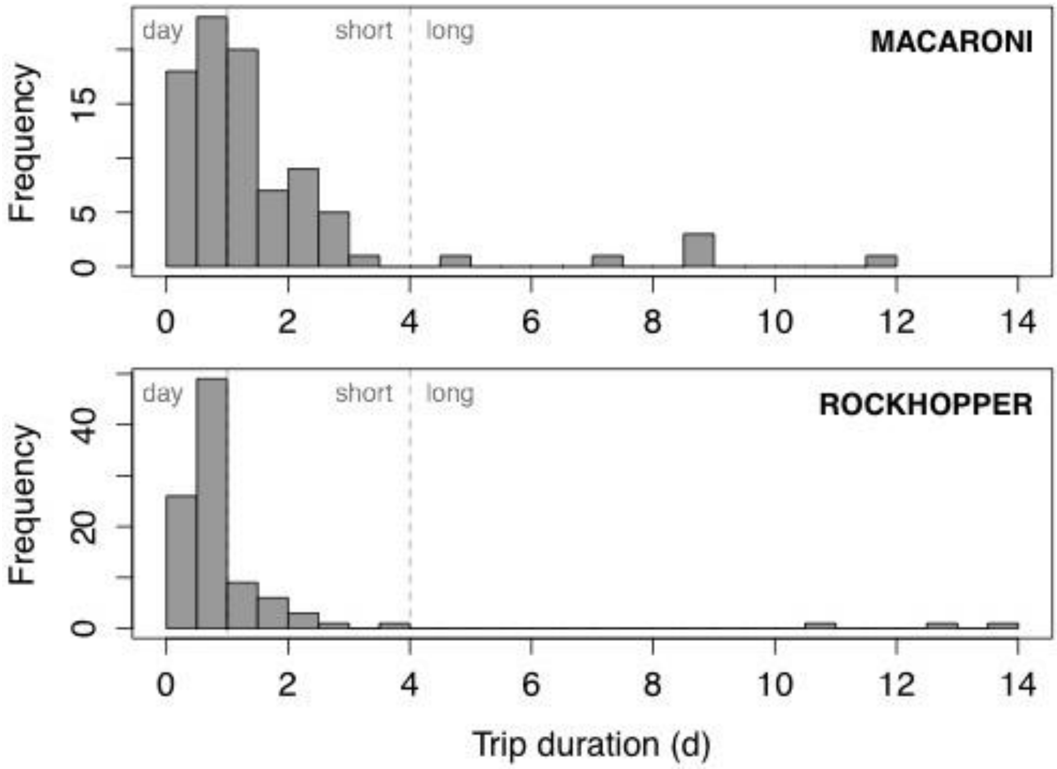


Figure S3.1. Distribution of trip durations of macaroni and rockhopper penguins during guard and crèche stages. Trips were grouped into day (< 1 d), short (< 4 d) and long trips (> 4 d)

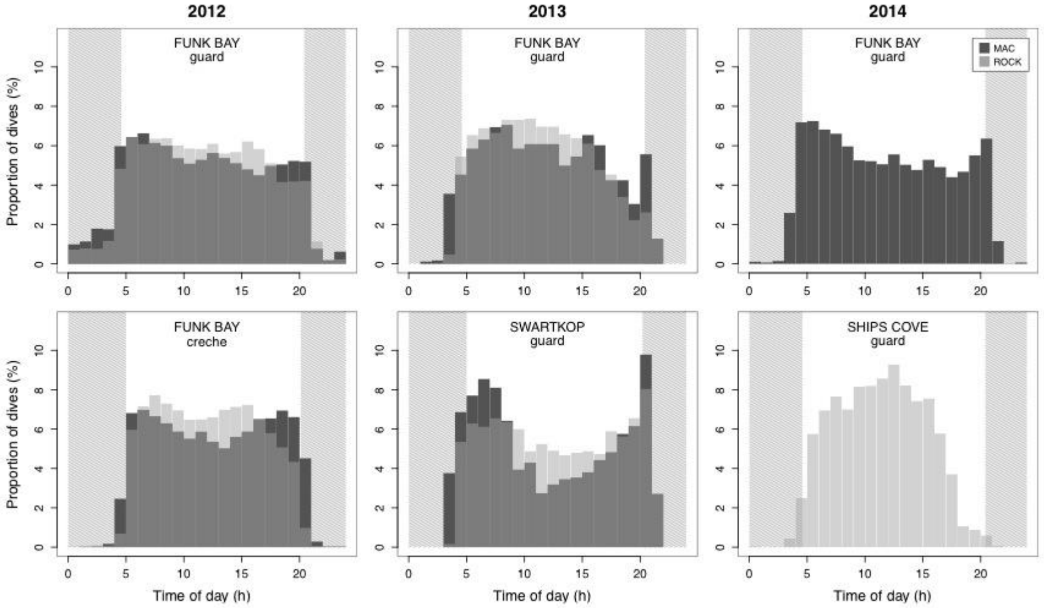


Figure S3.2. Distribution of foraging dives (> 10 m) performed by macaroni (MAC) and rockhopper (ROCK) penguins in relation to time of day (GMT+03:00). Shaded bars represent night hours defined by civil twilight (30 Dec for guard, and 20 Jan for crèche)

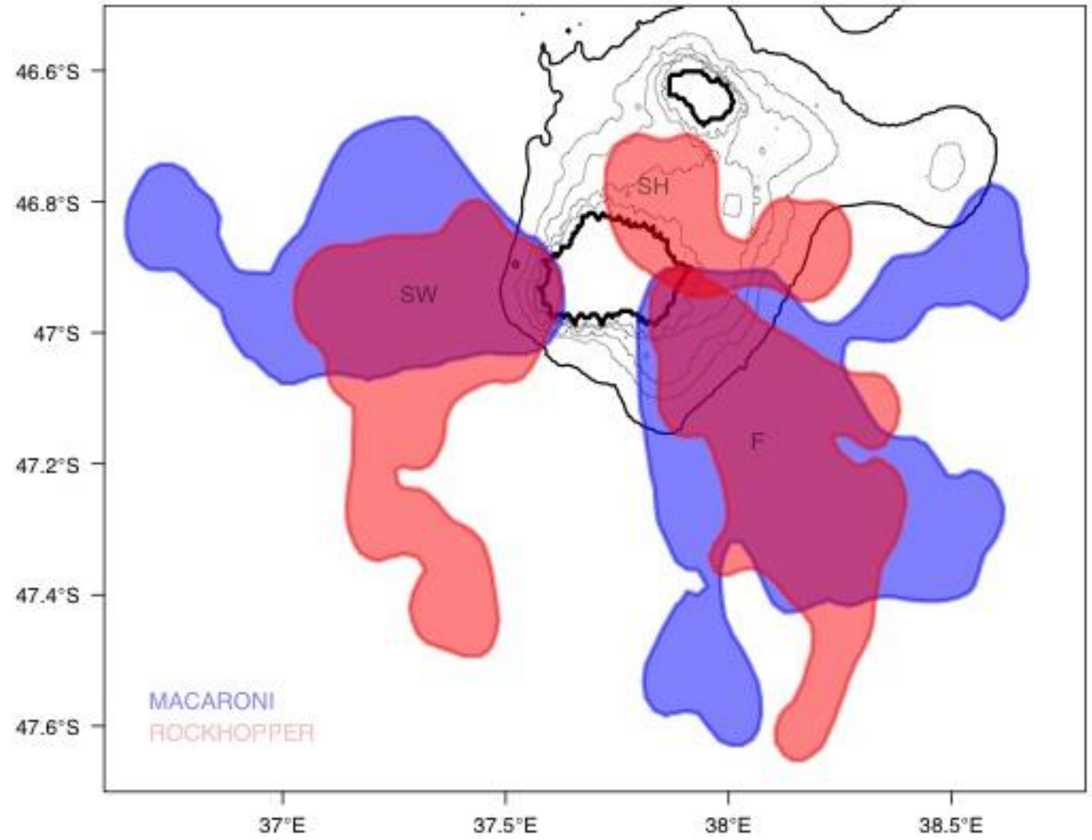


Figure. S3.3. Utilization distributions of macaroni (blue) and rockhopper (red) penguins at Funk Bay (F), Swartkop (SW) and Ship's Cove (SH) colonies on Marion Island during guard

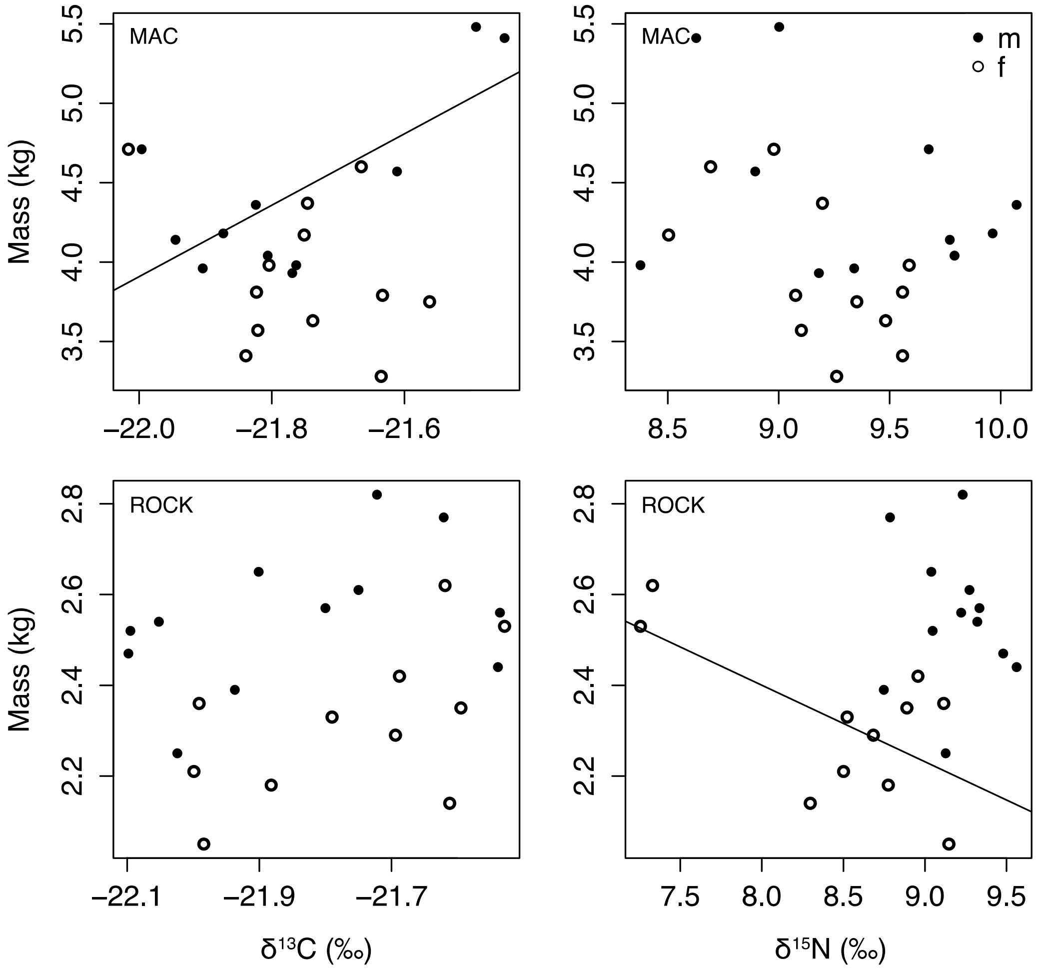


Figure S3.4. Mass of male (closed circles) and female (open circle) macaroni (MAC) and rockhopper (ROCK) penguins at the end of summer in relation to carbon and nitrogen stable isotopes in erythrocytes. The only significant relationship was with δ^{13}C of male macaroni penguins ($y = 2.25x + 53.30$, $R^2 = 0.46$, $P < 0.05$) and d δ^{15}N of female rockhopper penguins ($y = -0.17x + 3.75$, $R^2 = 0.36$, $P < 0.05$)

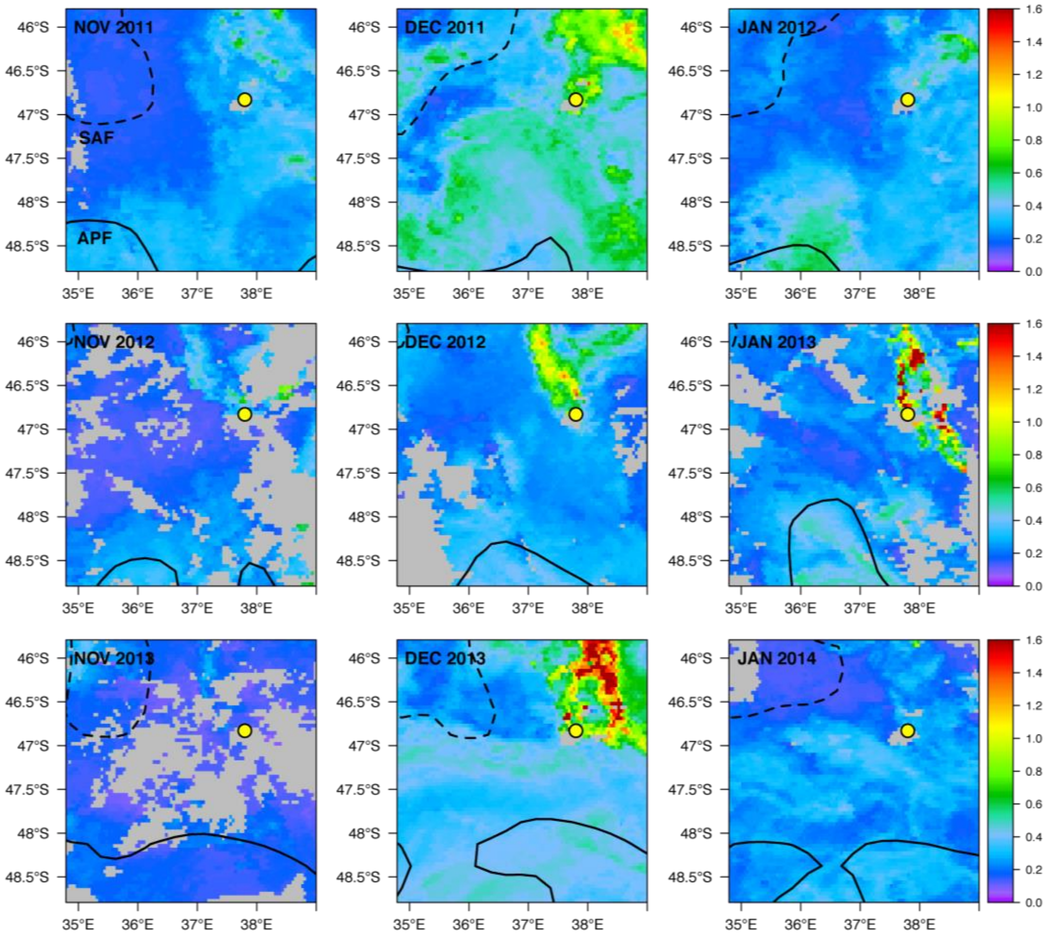


Figure S3.5. Monthly composites of satellite-derived chlorophyll-a concentrations (mg.m^{-3}) near Marion Island (yellow circle) over three successive breeding seasons (2011/12 – 2013/14). Positions of the sub-Antarctic Front (dashed line) and Antarctic Polar Front (solid line) are shown

Table S3.1. Seasonal variation in the foraging behaviour of macaroni penguins at Funk Bay during the 2011/12 breeding season. Significant differences (a, b) were assessed using linear mixed-effect models (* < 0.05, ** < 0.01, *** < 0.001, and ns = not significant)

	Early guard		Late guard		Crèche		
Individuals (n)	10		11		4		
Trips (n)	10		15		15		
Trip duration (h)	17.8 ± 11.3	a	50.2 ± 14.2	b	15.8 ± 13.2	a	***
Dive rate (dives.h^{-1})	18.0 ± 2.5	a	16.7 ± 1.9	ab	13.9 ± 4.9	b	*
Dives > 10 m (%)	83 ± 10		77 ± 9		75 ± 18		ns
Dives > 80 m (%)	1 ± 2	a	2 ± 2	a	11 ± 12	b	*
Time spent underwater (%)	59 ± 6		55 ± 4		48 ± 16		ns
VTD (km)	23.7 ± 14.3	a	64.7 ± 20.0	b	18.2 ± 12.9	a	***
Mean maximum depth (m)	45.8 ± 6.5	a	48.7 ± 4.4	ab	57.4 ± 13.2	b	*
Dive duration (s)	136.6 ± 9.4	a	143.1 ± 10.5	ab	155.7 ± 13.9	b	**
Post-dive interval (s)	43.7 ± 3.7	ab	39.5 ± 3.9	a	49.1 ± 12.1	b	*
Bottom time (s)	73.4 ± 6.7		73.7 ± 8.4		72.8 ± 12.6		ns
Dive efficiency	0.41 ± 0.04	b	0.40 ± 0.03	ab	0.37 ± 0.07	a	*
Descent rate (m.s^{-1})	1.44 ± 0.08	ab	1.44 ± 0.08	b	1.37 ± 0.15	a	*
Ascent rate (m.s^{-1})	1.12 ± 0.12		1.16 ± 0.12		1.13 ± 0.21		ns
Water temperature (°C)	6.9 ± 0.2		6.4 ± 0.6		7.1 ± 0.8		ns
Geostrophic flow (m.s^{-1})	0.19 ± 0.03	b	0.27 ± 0.01	c	0.14 ± 0.04	a	***

Table S3.2. Seasonal variation in the foraging behaviour of rockhopper penguins at Funk Bay during the 2011/12 breeding season. Significant differences (a, b) were assessed using linear mixed-effect models (* < 0.05, ** < 0.01, *** < 0.001, and ns = not significant)

	Early guard		Late guard		Crèche		
Individuals (n)	10		11		10		
Trips (n)	10		11		24		
Trip duration (h)	15.4 ± 8.6	a	33.9 ± 15.3	b	13.3 ± 5.3	a	***
Dive rate (dives.h^{-1})	28.8 ± 4.4		26.9 ± 3.4		28.7 ± 7.4		ns
Dives > 10 m (%)	64 ± 13		57 ± 10		59 ± 15		ns
Dives > 80 m (%)	1 ± 2		1 ± 1		1 ± 3		ns
Time spent underwater (%)	59 ± 9		55 ± 6		60.5 ± 14.3		ns
VTD (km)	26.1 ± 8.8	a	47.8 ± 20.6	b	23.9 ± 10.6	a	**
Mean maximum depth (m)	46.1 ± 4.7		43.3 ± 5.2		47.6 ± 11.0		ns
Dive duration (s)	103.4 ± 5.2	a	109.2 ± 7.8	ab	115.0 ± 20.2	b	*
Post-dive interval (s)	36.4 ± 5.4		34.5 ± 5.8		33.9 ± 5.4		ns
Bottom time (s)	33.8 ± 3.6	a	43.4 ± 5.2	b	46.6 ± 10.8	b	**
Dive efficiency	0.24 ± 0.02	a	0.30 ± 0.04	b	0.31 ± 0.05	b	***
Descent rate (m.s^{-1})	1.40 ± 0.10		1.44 ± 0.13		1.44 ± 0.19		ns
Ascent rate (m.s^{-1})	1.05 ± 0.06		1.04 ± 0.08		1.05 ± 0.11		ns
Water temperature (°C)	6.3 ± 0.3	a	6.5 ± 0.3	a	7.5 ± 0.5	b	***
Geostrophic flow (m.s^{-1})	0.32 ± 0.01	b	0.31 ± 0.01	b	0.15 ± 0.06	a	***

CHAPTER 4

Habitat use and diving behaviour of sympatric crested penguins during the pre-moult period

Abstract

After the breeding season penguins must replenish body condition and accumulate sufficient energy stores to survive their annual moult fast ashore; failure to do so will lead to starvation. Knowing where and how adult penguins find adequate resources during this energy intensive stage is vital to understanding their susceptibility to ecosystem changes. GPS and TDR loggers were used to track movements and record diving behaviour of macaroni and eastern rockhopper penguins from Marion Island (46°S, 37°E) during the pre-moult foraging trip in 2012, 2013 and 2014. Both species consistently travelled in a southerly direction to forage in cooler (~ 3.5 °C) Antarctic Zone waters south of the Antarctic Polar Front where they associated with mesoscale eddies and sub-mesoscale filaments. Dives were predominantly to depths of 30 to 60 m but macaroni penguins dived deeper more often. Mean trip durations of both species were similar (33 ± 6 d), but maximum foraging ranges of macaroni penguins (903 ± 165 km) were greater than rockhopper penguins (696 ± 152 km). Spatial overlap of core foraging areas between species was high, but a two to three-week difference in departure dates reduced potential interspecific competition at sea. Trip durations were longer in 2014 compared to 2013, when decreased productivity may have reduced prey availability, forcing penguins to remain longer at sea. Continued monitoring is vital to understand how crested penguins at Marion Island adapt to the predicted southward shift of major frontal boundaries.

Introduction

Knowing where and how predators find prey is vital to understanding their susceptibility to ecosystem changes. Marine environments are dynamic in space and time, with physical processes driving patchiness in primary production (Sokolov and Rintoul 2007) and prey distribution (Ansorge et al. 2009). Oceanographic features that retain and enhance predictable prey aggregations, such as fronts (Bost et al. 2009), shelf edges (Phillips et al. 2008), mesoscale eddies (Cotté et al. 2007) and sub-mesoscale filaments (Nordstrom et al. 2013; Cotté et al. 2015), act as important foraging areas for many pelagic mesopredators.

Penguins are key predators on a global scale, consuming more than 23 % of the estimated 70 million tonnes consumed by all seabirds annually (Brooke 2004). Perhaps the most energy demanding stage of a penguin's annual cycle is the period preceding the moult (Brown 1989; Adams and Brown 1990; Green et al. 2009a). Unlike most seabirds that stagger their moult, penguins replace their entire plumage in just two to five weeks (Adams and Brown 1990). Reduced waterproofing and insulation during this period forces penguins to remain on land, making them entirely dependent on endogenous fat and protein reserves for sustenance (Cherel et al. 1994). Penguins typically lose 40–50 % of their body mass during this time (Brown 1986). Such dependence on reserves requires penguins to commence the moult in excellent body condition, as failure to do so may result in starvation and impact survival (Keymer et al. 2001). For most penguins, which moult three to seven weeks after breeding (Williams 1995), finding adequate resources to accumulate sufficient energy stores is particularly challenging, as they must do so within a limited time period.

Among eudyptids, moult duration is similar across species (24–28 d; Adams and Brown 1990), but the duration of pre-moult foraging trips varies considerably; ranging from 13 d for macaroni penguins at South Georgia (Williams and Croxall 1991) to 70 d for Fiordland penguins *E. pachyrhynchus* in New Zealand (Warham 1974). Previous studies have reported large-scale dispersal (> 400 km) of macaroni penguins during pre-moult trips (Brown 1987; Waluda et al. 2010), but at most localities the foraging strategies of crested penguins during this crucial period remain poorly known.

GPS and TDR loggers were used to investigate the pre-moult habitat use and diving behaviour of macaroni penguins and the eastern race of the southern rockhopper penguin at the sub-Antarctic Prince Edward Islands. Approximately 302,000 and 80,000 pairs of macaroni and eastern rockhopper penguins breed at the islands, which together constitute 41 % of the total avian biomass (Ryan and Bester 2008; Crawford et al. 2009). Eudyptids breed sympatrically at many localities – usually involving the smaller rockhopper and the larger royal, erect-crested or macaroni penguins (Warham 1975) – but it is uncommon for large numbers of both species to co-exist, such as at the Prince Edward Islands. Macaroni and rockhopper penguins have similar breeding cycles at the islands, but a two to three-week difference in the onset of breeding means that macaroni penguins fledge in mid-February and rockhopper penguins in early March (Crawford et al. 2003a, b). Adult penguins typically depart just before chicks fledge, but previous studies have not recorded the timing of adult departures from the Prince Edward Islands.

Unlike breeding penguins that are constrained in terms of the distance they can travel by the need to provision offspring, pre-moult penguins are free to travel larger distances to potentially more profitable foraging areas. Thus, pre-moult penguins offer a good model to explore habitat preferences and may provide insights into fine-scale habitat preferences during the non-breeding season when high accuracy data are not available. In this chapter I 1) identify core foraging areas of each species, 2) determine whether foraging behaviour varies with environmental correlates, 3) quantify spatial and temporal overlap between species, and 4) identify potential drivers of inter-annual variation in foraging trip duration and range.

Methods

Study site

The Prince Edward Islands (46.9°S, 37.8°E) are located in the southwest Indian Ocean sector of the Southern Ocean. Among the pairs breeding at the islands, 96 % of macaroni penguins and 53 % of rockhopper penguins occur at the larger Marion Island (Crawford et al. 2009). At-sea data were collected from adult penguins breeding at Funk Bay, southeast Marion Island, during the pre-moult foraging trip in 2012 (macaroni penguins only), 2013 and 2014.

Logger deployments

GPS loggers were deployed in all three years to sample position at variable intervals between years (see Table S4.1). TDRs were deployed in 2012 and 2014 and were programmed to sample depth at variable intervals between years (Table S4.1). In 2014, TDRs also sampled temperature every 5 s. Birds were captured at the end of the breeding season prior to their expected departure for the pre-moult foraging trip. When birds returned to their nest site (at or near their nest) to moult they were recaptured, reweighed (2014 only) and the logger removed. See Chapter 2 for more details on GPS and TDR loggers and deployment techniques.

Trip characteristics

Data were analysed using R (Version 3.1.0; R Development Core Team 2015) and the 'Spatial Analysis' tool of Ethographer (Sakamoto et al. 2009) in Igor Pro (Wavemetrics Inc., USA, Version 6.2.2.2). Duplicated and on-land locations were removed in Igor Pro. Maximum foraging range was defined as the great circle distance between the colony and the furthest point of the trip. Bearing of the furthest point of the trip in relation to the colony was calculated using the function 'bearing' in the R package 'Circstats' and circular statistics (Kuiper's test) used to determine if travel direction of individuals within each species was random. Due to the low acquisition rates of locations during the daytime when penguins were predominantly diving (Fig. S1), as well as unequal sampling intervals between years (Table S4.1), tracks were linearly rediscretised at 6 hour intervals using the function 'redisltraj' in the R package 'adehabitatLT' (Calenge et al. 2009) to minimise inclusion of false locations. Travel speed was computed as a daily mean based on the total minimum distance travelled per day.

If GPS tracks were incomplete (Table S4.2) and temperature data were available from a TDR, landing date was determined by a rapid increase in ambient temperature when penguins left the water. When temperature data were not available, the change-point at which each bird started its journey back to the colony was determined using a non-parametric segmentation of daily travel speeds (Lavielle 2005). Mean travel speed of the return journey was calculated for complete tracks, averaged among all birds by species, and used to estimate the landing dates of incomplete tracks by calculating the time taken to travel the outstanding distance to the colony. Penguins typically maintain a constant speed travelling to and from the colony (Trathan et al. 2008), making the assumptions for such extrapolations reasonable.

Linear mixed-effect models (LMEs; R package ‘nlme’; Pinheiro et al. 2013) were used to determine whether trip parameters (duration and maximum foraging range) differed between years for each species. Potential differences between sexes were not considered due to small sample sizes, but sex was still included as a random effect. Post-hoc pairwise comparisons were performed using the function ‘glht’ in the R package ‘multcomp’. For interspecific and inter-annual comparisons, data were only considered for years when available for both species (2013 and 2014), and trip parameters modelled in relation to species and year, with sex included as a random effect.

Environmental data

Chlorophyll-a concentrations, EKE, FSLE, SLA, SSH and SST were used to characterise the marine environment used by penguins (see Table S4.3 for data resolution and sources). The core AAZ was considered as the SSH contour of -0.8 m (midpoint between APF and SACCF).

Habitat use

When prey is aggregated, optimal foraging theory predicts that predators should travel quickly through areas of low prey density to maximise time spent in high-density patches (Kareiva and Odell 1987; Weavers 1992). For diving marine predators, travel speed is a useful proxy for foraging behaviour (Bost et al. 1997; Cotté et al. 2007; Trathan et al. 2008), with slower speeds (reduced horizontal displacement) typically associated with increased foraging activity (Sato et al. 2004) and prey ingestion (Bost et al. 1997). Although restricting analyses to habitats penguins chose to travel through may underestimate habitat preferences by ignoring the habitats that penguins avoided, modelling travel speeds in relation to environmental covariates provides a relative index of preference for the habitat characteristics encountered. Due to the non-linearity between response variables and environmental covariates so common in species-habitat studies (Cotté et al. 2015), generalised additive models (GAMs) were used for their ability to automatically detect relationship shapes through flexible smoothers. GAMs were implemented using the function 'bam' in the R package 'mgcv' (Wood 2006) as this function allows for the inclusion of an autoregressive correlation structure (*rho* = 0.1) to account for the weak temporal autocorrelation present. To ensure normality of residuals, travel speeds were square-root transformed and models fitted with a Gaussian error distribution and identity link function. Prior to modelling environmental covariates were checked for collinearity, with a cut-off criterion of $r_s = 0.6$ for inclusion in the same model. SSH and SST were highly correlated in all years ($r_s = 0.93$ – 0.96). Due to potential inter-annual variation in environmental conditions and preferences, models were fitted separately for each year. Smoothers were applied to each environmental covariate and a separate smoother specified for each species. Smoothers were fitted using cubic regression splines with extra shrinkage, which avoids over-parameterisation by allowing variables to be penalised out of the model during fitting (Wood 2006). Interaction terms were specified with a tensor smooth and were fitted with a thin-plate regression spline. As travel speeds may differ between individuals, individual identity was included as a random effect. Smoothing parameters were estimated via restricted maximum likelihood (REML) and model selection performed using Akaike's information criterion (AIC).

Days where travel speed was less than the individual's mean were considered as core foraging phases (Fig S4.2; Cotté et al. 2007). Environmental characteristics of core foraging phases were compared between years for each species using LMEs, with individual identity included as a random effect. At-sea distributions of core foraging phases were broadly characterised for each species by computing 50 and 90 % utilisation distributions (UDs) of pooled locations from years when data were available for both species (2013 and 2014). This was performed using kernel analysis in the R package 'adehabitatHR' (Calenge 2006). Due to small sample sizes, population UDs for each species were broadly characterised by using a smoothing parameter of 1°. Spatial overlaps between the two species' 50 and 90 % UDs were computed using the 'VI' method in the function 'kerneloverlaphr' (Fieberg and Kochanny 2005). This method returns the volume of intersection as a proportion of the 100 % UD ranging from 0 (no overlap) to 1 (complete overlap). Daily utilisation distributions were also calculated for each species based on daily locations when ≥ 3 individuals of each species were at sea, and the daily overlap computed using the same method.

Dive data analysis

Depth data from 2012 were manually corrected for a drifting surface level (as temperature was not recorded) while 2014 data were corrected using Ethographer in Igor Pro (Sakamoto et al. 2009). To separate potential merged dives resulting from large sampling intervals (Table S4.1) all depth values < 1 m were replaced with zero. A dive was considered when depth > 3 m (Tremblay and Cherel 2003) and dive parameters (maximum depth, duration, descent rate and ascent rate) extracted for each dive. As shallow dives are typically associated with travelling, only dives > 10 m were considered as foraging dives following a distinct mode in dive depth distributions (Green et al. 2005). For each day at sea, the number of dives performed (total, > 10 m and > 80 m), the amount of time spent underwater and the vertical travel distance (VTD; sum of maximum dive depths) were also calculated. To account for the delayed response time of the temperature sensor to detect changes (28 s to reach 66 % of the step from 5 to 30 °C) and avoid the influence of air temperature, sea surface temperature ($T_{surface}$) was considered as the first temperature reading after 15 s of continual submersion. Additionally, the minimum temperature (T_{bottom}) of each dive was determined. For each dive, the difference between $T_{surface}$ and T_{bottom} (ΔT) was used to detect the presence of a thermocline, with a threshold of $\Delta T > 1$ °C used following temperature-depth changes associated with thermoclines in previous studies (Charrassin and Bost 2001). As positional data in 2014 were not available for entire trips, and daily means of satellite-derived sea surface temperatures and $T_{surface}$ (hereafter referred to as SST_{TDR}) were highly correlated ($r_s = 0.92$, $n = 304$ d), SST_{TDR} was used for further analyses. LMEs were used to compare daily means of dive parameters between species and water masses (< and > 4.5 °C SST_{TDR}), with individual identity nested within year included as a random effect. Kernel density plots were used to visualise the variation of maximum dive depths in relation to SST_{TDR}. LMEs were used to determine whether mean daily dive depths, durations, number of dives > 10 m and time spent underwater differed in relation to the presence/absence of sub-mesoscale filaments (only 2014), with individual identity included as a random effect.

Results

Trip characteristics

Twenty macaroni and 13 rockhopper penguins were tracked (Table 4.1). A large number of incomplete tracks resulted from insufficient battery life of GPS loggers (Table S4.2). For relatively complete trips (> 70 %) where the furthest point from the colony was confidently discernible, maximum ranges were reached at 58 ± 6 % (macaroni, $n = 12$) and 56 ± 8 % (rockhopper, $n = 5$) of the total trip duration. Thus, the inclusion of maximum ranges of incomplete trips in subsequent analyses was determined by criteria based on the lower confidence intervals of these means (i.e. 52 % of total trip duration for macaroni and 48 % for rockhopper penguins). Mean daily travel speeds of the return journey for trips where return dates were known were 3.8 ± 0.4 km.h^{-1} (n = 9) for macaroni and 3.5 ± 0.7 km.h^{-1} (n = 5) for rockhopper penguins. Travel direction was non-random (Kuiper's test $D_{macaroni}$ = 4.1 and $D_{rockhopper}$ = 3.4; $P < 0.01$); all individuals from both species travelled south (Fig. 4.1). For macaroni penguins, maximum foraging ranges were 232 ± 65 km further in 2012 compared to 2013 (LME, t_{13} = 3.6, P = 0.001), but were similar between other inter-annual comparisons ($LME_{2012\text{-}2014}$, t_{13} = 2.0, P = 0.12; $LME_{2013\text{-}2014}$, t_{13} = -1.7, P = 0.21).

Trip durations were 7 ± 3 days longer in 2014 compared to 2013 (LME, t_{13} = 2.4, P = 0.042), but were similar between other inter-annual comparisons ($LME_{2012\text{-}2013}$, t_{13} = 1.9, P = 0.15; $LME_{2012\text{-}2014}$, t_{13} = -0.5, P = 0.89). For rockhopper penguins, maximum foraging ranges were similar between years (LME, t_7 = 1.7, P = 0.14), but trip durations were 13 ± 3 days longer in 2014 (LME, t_8 = 4.4, P = 0.0022). For interspecific comparisons, maximum foraging ranges of macaroni penguins were slightly further (153 ± 76 km) than rockhopper penguins but this difference was only near significant (LME, t_{17} = -2.03, P = 0.058). Overall trip durations were similar between species (LME, t_{18} = -1.02, P = 0.32). For inter-annual comparisons, maximum foraging ranges were similar in 2013 and 2014 (LME, t_{17} = 1.4, P = 0.18), but trip durations were longer in 2014 compared to 2013 (LME, t_{18} = 2.2, P = 0.039). Mean body mass of macaroni penguins prior to departure (3.9 ± 0.4 g, n = 20) was 50% larger than rockhopper penguins (2.6 ± 0.2 g, n = 13). In 2014, mass gain during a trip as a proportion of individual body mass was 53 ± 21 % (n = 9) for macaroni penguins and 44 ± 16 % (n = 9) for rockhopper penguins. Mass gains of macaroni penguins (2.0 ± 0.7 kg, n = 9) were similar to those at Kerguelen (49.1 °S, 70.3 °E) instrumented with miniature GLS loggers (Thiebot et al. 2014), suggesting minimal impact of GPS loggers. Mass gains of rockhopper penguins in the present study averaged 1.1 ± 0.4 kg (*n* = 9).

Table 4.1. Trip characteristics (mean ± SD) of macaroni and rockhopper penguins during the pre-moult foraging period

Species	Year	Sex	Departure date	Trip duration (days)	Maximum foraging range (km)	Minimum total distance travelled (km)	Bearing at furthest point (°)
Macaroni penguin	2012	All (5)	19-Feb ± 1	35 ± 7	1018 ± 166	2349 ± 364	192 ± 9
		Male (2)	20-Feb ± 1	29 ± 3	932 ± 260	2094 ± 527	188 ± 8
		Female (3)	18-Feb ± 1	40 ± 6	1075 ± 95	2519 ± 130	195 ± 10
	2013	All (6)	16-Feb ± 2	29 ± 3	780 ± 60	1954 ± 230	180 ± 16
		Male (3)	17-Feb ± 1	27 ± 1	756 ± 78	1913 ± 226	189 ± 18
		Female (3)	16-Feb ± 2	30 ± 4	803 ± 35	1994 ± 276	170 ± 6
	2014[a]	All (9)	18-Feb ± 1	35 ± 6	873 ± 104	2164 ± 202	193 ± 9
		Male (5)	18-Feb ± 1	34 ± 6	841 ± 109	2141 ± 254	193 ± 11
		Female (4)	18-Feb ± 0	38 ± 8	938 ± 76	2211 ± 57	192 ± 8
Rockhopper penguin	2013	Male (4)	8-Mar ± 1	26 ± 3	626 ± 165	1640 ± 288	182 ± 12
	2014[b]	All (9)	4-Mar ± 1	37 ± 5	743 ± 137	1718 ± 250	182 ± 12
		Male (5)	4-Mar ± 1	34 ± 6	827 ± 138	1851 ± 242	183 ± 19
		Female (4)	4-Mar ± 2	40 ± 3	658 ± 79	1585 ± 212	181 ± 5

[a] maximum foraging range and trip duration calculated for 6 individuals (4 males, 2 females); [b] maximum foraging range calculated for 6 individuals (3 males, 3 females) and trip duration calculated for 7 individuals (4 males, 3 females)

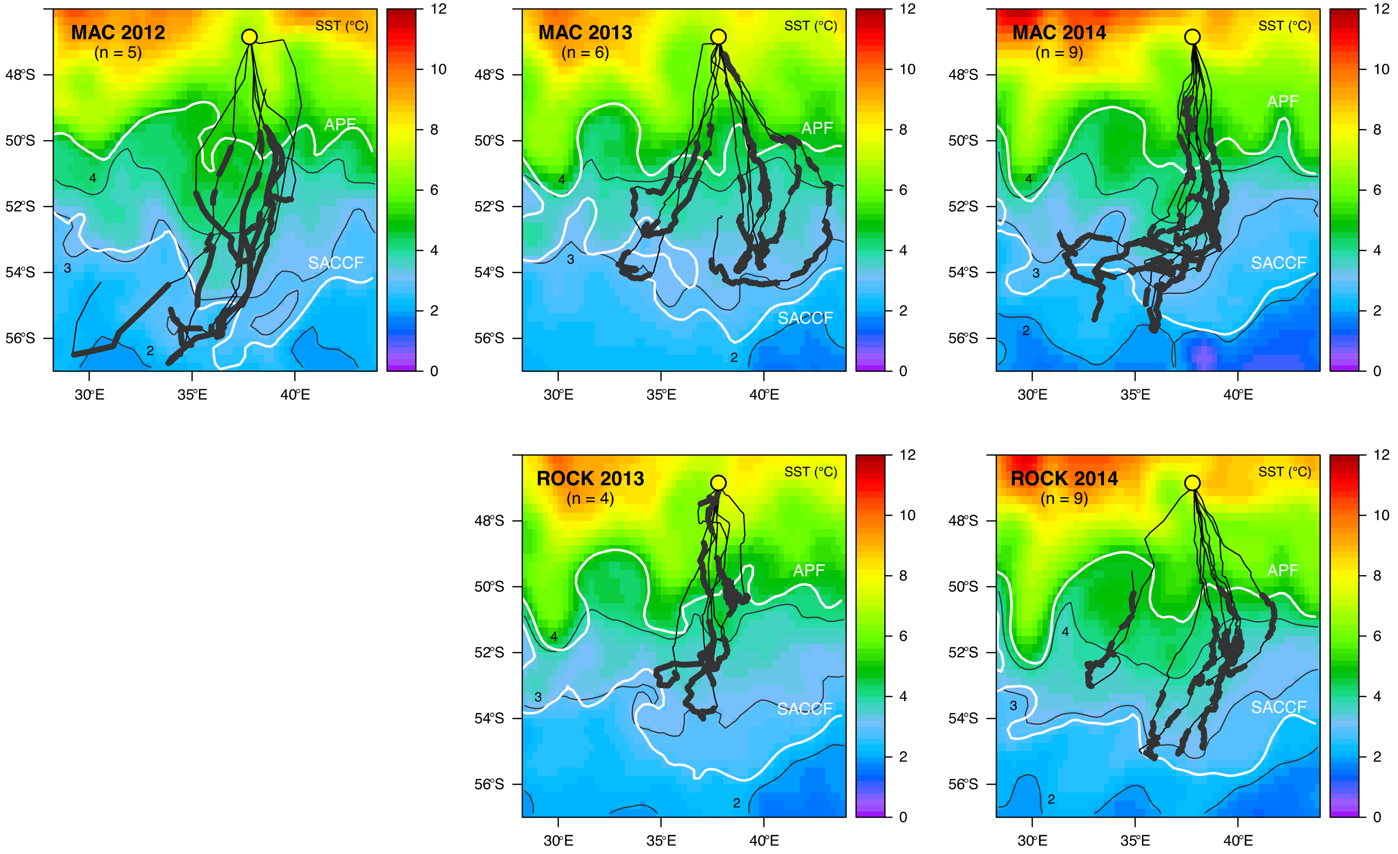


Figure 4.1. Tracks of macaroni (MAC) and rockhopper (ROCK) penguins during the pre-moult foraging trip from Marion Island. Thicker lines represent core foraging phases where daily travel speeds were less than each individual's mean. Maps depict sea surface temperature for the duration that penguins were at sea with 2, 3 and 4 °C isotherms shown as faint black lines (source: NASA), and white lines show the locations of the Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Current Front (SACCF) (source: Aviso). Rockhopper penguins departed two to three-weeks after macaroni penguins

Travel speed and marine habitat characteristics

Mean daily travel speeds of macaroni and rockhopper penguins were 2.6 ± 0.3 km.h^{-1} (*n* = 20) and 2.3 ± 0.4 km.h^{-1} (*n* = 13), respectively. Mean maximum travel speeds of raw locations for the two species were 6.1 ± 0.8 km.h^{-1} (*n* = 20, max = 7.6 km.h^{-1}) and 5.9 ± 0.7 km.h^{-1} (*n* = 13, max = 7.5 km.h^{-1}), respectively. The relationships of travel speed with SSH and SST were striking, with both species slowing down as they moved into cooler AAZ waters (Fig. 4.2). Change-points in the mean daily travel speed were detected at -0.65 m SSH and 5 °C SST for macaroni penguins and at -0.65 m SSH and 4.5 °C SST for rockhopper penguins. More than 90 % of locations within core foraging phases were in waters where SSH was < -0.65 m and SST was < 4.5 °C for both species.

Table 4.2 shows the summary of environmental characteristics within core foraging phases and Table 4.3 shows the GAM results. GAMs revealed an interaction between SST and EKE in 2012 and 2013, with both species travelling slower in cooler waters (< 4.5 °C SST) characterised by relatively low EKE (Fig. S4.3). Travel speed only varied in relation to SLA in 2014 when both species travelled slower in waters characterised by positive SLA (Fig. S4), but core foraging phases in all years were generally characterised by weak positive SLA (Table 4.2). Travel speeds only varied in relation to chlorophyll-a concentrations in 2013, when penguins travelled fast through the less productive waters (< 0.2 mg.m^{-3}) of the Polar Frontal Zone (PFZ) and slowed down in the more productive waters of the AAZ (Fig. S5). Additionally, rockhopper penguins travelled slower in marginally less productive waters in 2014 (Fig. S4). FSLE did not influence travel speeds and was thus excluded from the model selection process; however, the association of both species with sub-mesoscale filaments

(FSLE > 0.1 d^{-1}) was striking. Macaroni penguins associated with sub-mesoscale filaments (FSLE > 0.1 d^{-1}) during 57 ± 7 % (range 48–65 %, *n* = 5), 49 ± 11 % (range 38–69 %, *n* = 6) and 67 ± 8 % (range 59–83 %, *n* = 9) of trip locations (6 h intervals) in 2012, 2013 and 2014, respectively, and rockhopper penguins during 70 ± 4 % (range 65–74 %, *n* = 4) and 56 ± 19 % (range 36–93 %, *n* = 9) of trip locations in 2013 and 2014, respectively.

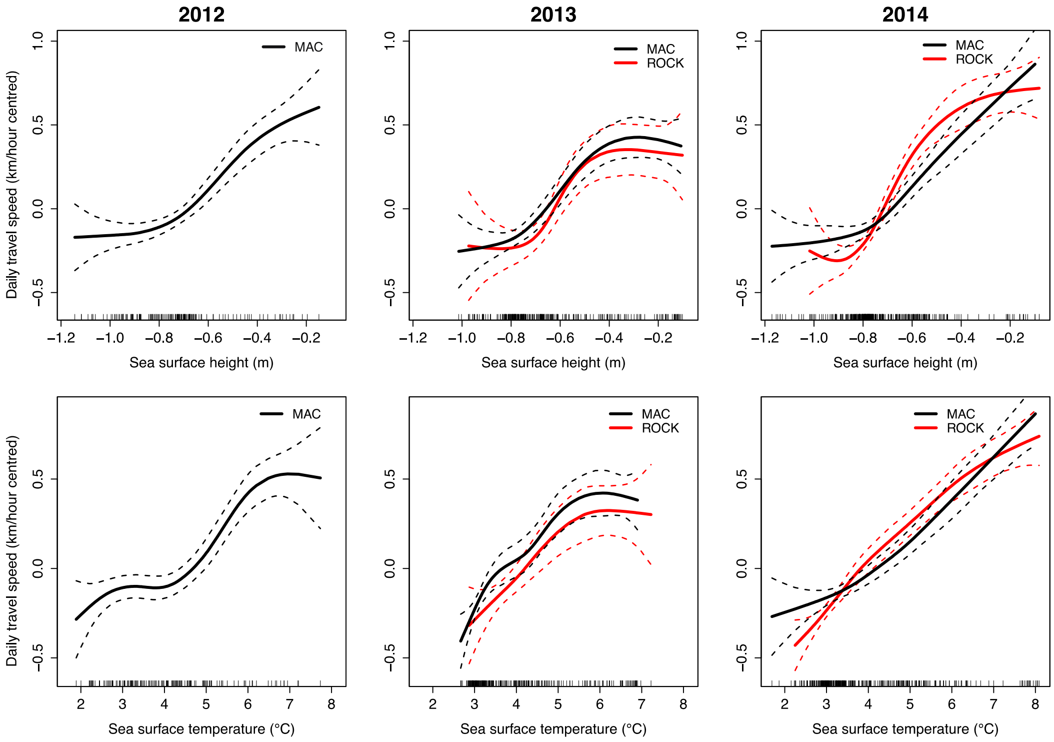


Figure 4.2. Daily travel speeds of macaroni (MAC) and rockhopper penguins (ROCK) in relation to sea surface height and sea surface temperature. Solid lines are predicted curves from generalised additive models and dashed lines represent 95% confidence intervals

Table 4.2. Summary of environmental covariates associated with core foraging phases (daily travel speeds less than the individual's mean) of macaroni and rockhopper penguins during the pre-moult foraging trip

	Macaroni				Rockhopper		
	2012	2013	2014	*P*-value	2013	2014	*P*-value
Chlorophyll-a concentration (mg.m^{-3})	0.27 ± 0.02^{a}	0.28 ± 0.02^{a}	0.15 ± 0.02^{b}	< 0.001	0.25 ± 0.03	0.12 ± 0.01	< 0.001
Eddy kinetic energy (cm^{2}.s^{-2})	169 ± 89	129 ± 97	157 ± 106	0.67	231 ± 166	142 ± 247	0.44
Finite-size Lyapunov exponent (d^{-1})	0.13 ± 0.01	0.12 ± 0.04	0.16 ± 0.5	0.21	0.19 ± 0.03	0.12 ± 0.05	0.02
Sea level anomaly (m)	0.10 ± 0.01^{a}	0.09 ± 0.04^{a}	0.06 ± 0.03^{b}	0.05	0.03 ± 0.01	0.07 ± 0.03	0.01
Sea surface height (m)	-0.81 ± 0.06	-0.76 ± 0.06	-0.79 ± 0.09	0.53	-0.68 ± 0.05	-0.80 ± 0.04	< 0.001
Sea surface temperature (°C)	3.6 ± 0.3	3.4 ± 0.2	3.5 ± 0.5	0.50	4.0 ± 0.3	3.2 ± 0.3	0.001

Mean chlorophyll-a concentrations in the region of interest (48–56 °S and 28–42 °E) during January to March were 0.23 ± 0.10 mg.m^{-3} in 2012, 0.22 ± 0.09 mg.m^{-3} in 2013 and 0.12 ± 0.06 mg.m^{-3} in 2014. Along-track chlorophyll-a concentrations within core foraging phases confirmed that the productivity of waters exploited by penguins in 2014 was significantly lower than in 2012 and 2013 (Table 4.2). The mean distance from the colony to the core AAZ south of the islands (33–41 °E) whilst macaroni penguins were at sea was 724 ± 119 km in 2012, 677 ± 107 km in 2013 and 734 ± 123 km in 2014, and 680 ± 106 km in 2013 and 722 ± 115 km in 2014 whilst rockhopper penguins were at sea. Mean SSTs within core foraging phases were ~ 3.5 °C (Table 4.2). The mean distance from the colony to the 3.5 °C isotherm south of the islands (33–41 °E) whilst macaroni penguins were at sea was 657 ± 102 km in 2012, 606 ± 54 km in 2013 and 681 ± 83 km in 2014, and 679 ± 47 km in 2013 and 632 ± 94 km in 2014 whilst rockhopper penguins were at sea. Positions of the APF and SACCF, and cooler isotherms (2–4 °C), during the pre-moult foraging trip varied marginally between years (Fig. 4.1; see also Fig. S6). Interestingly, a negative SST anomaly occurred south of the SACCF (~ 57 °S, 38 °E) at the end of February 2014 and temporarily pushed the 2 °C isotherm farther north (Fig. 4.1).

Spatial and temporal overlap between species

At-sea distributions of core foraging phases were similar between species with an overlap index of 0.32 (64 %) and 0.69 (77 %) for 50 and 90 % utilisation distributions, respectively (Fig. 4.3). Despite this large spatial overlap, spatiotemporal overlap was minimal because macaroni penguins started their pre-moult trip two to three weeks earlier than rockhopper penguins (Table 4.1; Fig. 4.4). In 2013, the peak daily spatiotemporal overlap (0.66) occurred when macaroni penguins were travelling back to the island and rockhopper penguins were on their outbound journey. In 2014, the two species were at sea together for a longer period (23 d) than in 2013 (8 d; Fig. 4.4), but unfortunately the expected increase in spatiotemporal overlap could not be computed due to the early failure of GPS logger batteries.

Table 4.3. Summary of selected generalised additive models explaining variance in the daily travel speed of macaroni (mac) and rockhopper (rock) penguins in relation to environmental covariates during the pre-moult foraging trip (see Table S4.4 for model rankings)

Year	Model	Term	edf	F	*P*-value	Dev. expl. (%)
2012	SST*EKE	SST*EKE	11.8	9.5	< 0.001	61
	SSH + CHLA + SLA	SSH	2.6	30.7	< 0.001	55
		CHLA	3.8	2.5	0.04	
		SLA	0.9	1.7	0.18	
2013	SST*EKE + SLA	SST*EKE:mac	6.6	13.2	< 0.001	55
		SST*EKE:rock	12.1	6.3	< 0.001	
		SLA:mac	0	0.3	1	
		SLA:rock	2.79	2.2	0.08	
	SSH*CHLA + EKE + SLA	SSH*CHLA:mac	5.7	15	< 0.001	51
		SSH*CHLA:rock	7.4	5.9	< 0.001	
		EKE:mac	0	0	1	
		EKE:rock	2.2	4.7	0.006	
		SLA:mac	1.1	2.8	0.07	
		SLA:rock	0	0.1	1	
2014	SST	SST:mac	2.4	55.8	< 0.001	63
		SST:rock	2.5	78.9	< 0.001	
	SSH*EKE + CHLA + SLA	SSH*EKE:mac	3	3	< 0.001	63
		SSH*EKE:rock	6.5	7.3	< 0.001	
		CHLA:mac	0	1.2	1	
		CHLA:rock	2.1	2.6	0.02	
		SLA:mac	1.2	1.4	0.001	
		SLA:rock	9.8	1.2	0.01	

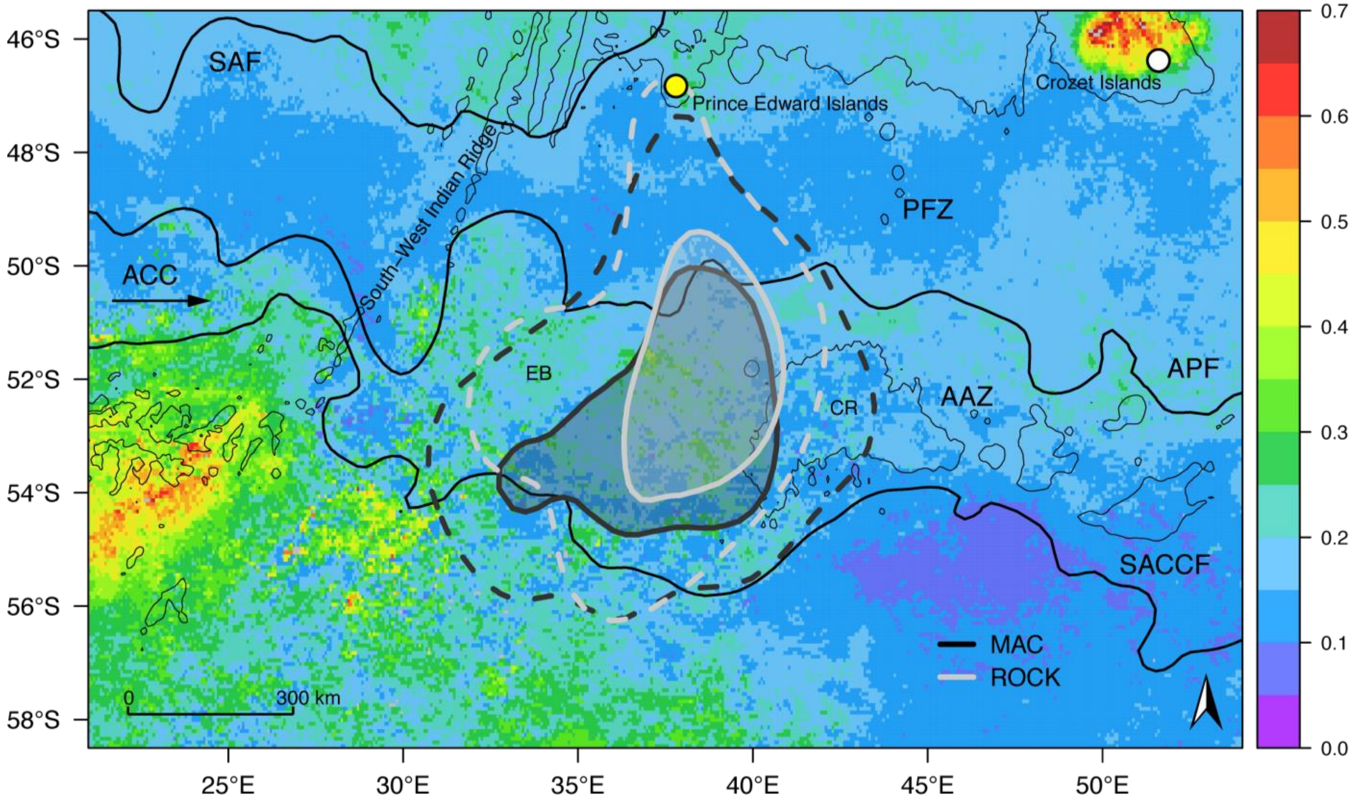


Figure 4.3. Kernel utilisation distributions of macaroni (MAC) and rockhopper (ROCK) penguins during 2013 and 2014 pre-moult foraging trips in relation to a composite map of satellite-derived chlorophyll-a concentrations (mg.m^{-3}) during January to March 2013 and 2014 (data source: Aqua Modis). Solid and dotted lines represent 50 and 90 % kernel density contours, respectively, of locations where travel speeds were less than the individual's mean. Positions of the Sub-Antarctic Front (SAF), Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Current Front (SACCF) are shown following Swart et al. (2010). PFZ = Polar Frontal Zone, ACC = Antarctic Circumpolar Current, AAZ = Antarctic Zone, EB = Enderby Basin, CR = Conrad Rise, thin black line = 3000 m isobath

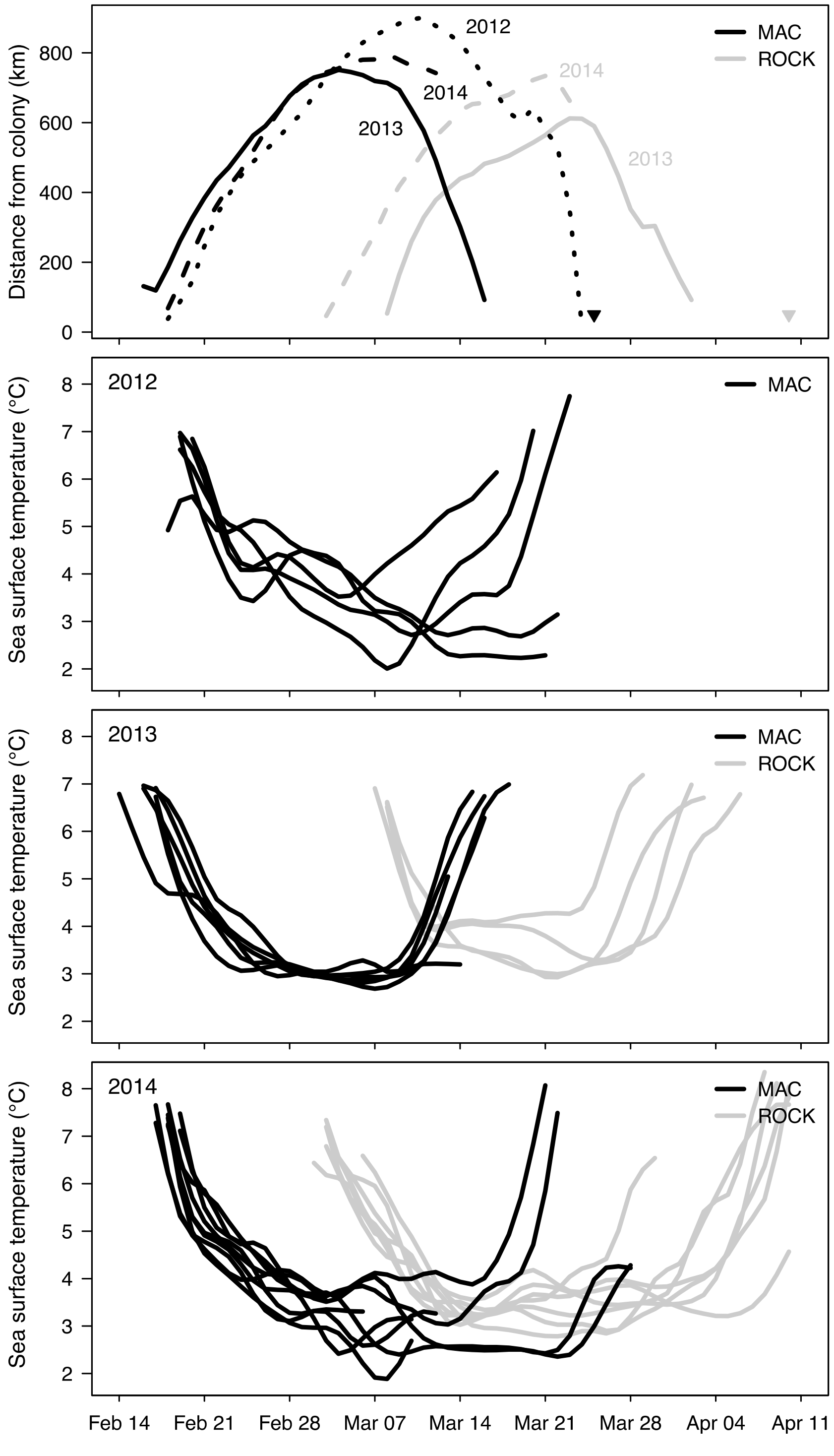


Figure 4.4. The evolution of distance from the colony (top panel) and sea surface temperatures of macaroni (MAC) and rockhopper (ROCK) penguins during the pre-moult foraging trip. Locations were only included when ≥ 3 individuals were at sea. Triangles denote mean return dates of trips in 2014 when GPS tracks were incomplete

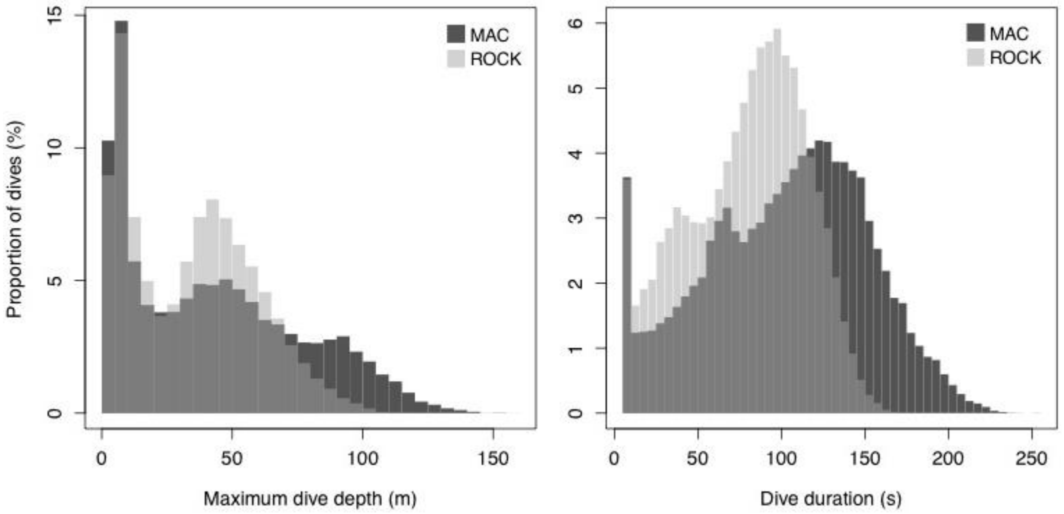


Figure 4.5. Distribution of maximum dive depths (a) and dive durations (b) of macaroni (MAC) and rockhopper (ROCK) penguins during the pre-moult foraging trip in 2014

Diving behaviour

Absolute maximum dive depths and durations were 156.3 m and 255 s for macaroni penguins and 122.3 m and 205 s for rockhopper penguins. Both species most frequently dived to depths < 10 m, but the distribution of deeper dives differed between species, with rockhopper penguins exhibiting a distinct mode between 30 and 60 m and macaroni penguins exploiting depths > 80 m more often (Table 4.4; Fig. 4.5). Dive durations differed markedly between species, with most (~ 50 %) dives of macaroni penguins and rockhopper penguins lasting 110 to 150 s and 70 to 120 s, respectively (Fig. 4.5). Table 4.4 shows the summary of daily diving behaviour of both species. Comparisons of daily diving behaviour of macaroni penguins in 2012 and 2014 revealed no significant differences, and thus data were pooled. However, the distribution of dive depths in relation to SST_{TDR} differed between years (Fig. 4.6). In both years, dive depths of macaroni penguins south of the SACCF were predominantly to depths of 30 to 60 m, but within AAZ waters dives in 2014 were more homogenously distributed within the water column (Fig. 4.6). rockhopper penguins concentrated diving activity in AAZ waters (3–4 °C) and dived predominantly to depths of 30 to 70 m (Fig. 4.6). Diurnal diving activity differed between water masses (Fig. 4.7), with penguins performing more night dives and diving more consistently throughout the day in warmer waters (> 4.5 °C). Macaroni and rockhopper penguins encountered a thermocline during an estimated 6.7 % (*n* = 29330) and 0.6 % (*n* = 68186) of dives > 10 m, respectively (Fig. 4.8). The presence of sub-mesoscale filaments did not influence the diving behaviour of macaroni penguins ($\mathrm{LME}_{\mathrm{dives>10m}}$, $t_{81} = -1.0$, $P = 0.3$; $\mathrm{LME}_{\mathrm{depth}}$, $t_{81} = 0.3$, $P = 0.8$; $\mathrm{LME}_{\mathrm{duration}}$, $t_{81} = -1.6$, $P = 0.1$; $\mathrm{LME}_{\mathrm{underwater}}$, $t_{81} = -0.3$, $P = 0.8$), but during days when filaments were present rockhopper penguins performed 26 ± 13 (10 %) more foraging dives (> 10 m; LME, $t_{136} = 1.2$, $P = 0.048$) at an average of 4.3 ± 1.9 m shallower (LME, $t_{136} = -2.3$, $P = 0.03$) and spent 1.3 ± 0.4 h (18 %) more time underwater (LME, $t_{136} = 3.1$, $P = 0.002$). Dive durations of rockhopper penguins, however, did not differ significantly in relation to filaments (LME, $t_{136} = 1.7$, $P = 0.1$).

Table 4.4. Summary of daily diving behaviour of macaroni and rockhopper penguins during the pre-moult foraging trip from Marion Island. Significances of linear mixed-effect model results comparing dive parameters between water masses (< and > 4.5 °C SST$_{\mathrm{TDR}}$) and species with individual identity nested within year are shown: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant

	Macaroni (n = 7)				Rockhopper (n = 7)					
	> 4.5 °C	< 4.5 °C		ALL	> 4.5 °C	< 4.5 °C		ALL	P_{ALL}	$P_{< 4.5}$
Days (n)	54	163		217	80	175		255		
Dive rate (dives.d^{-1})	292 ± 77	260 ± 31	**	269 ± 38	452 ± 69	300 ± 47	***	351 ± 54	**	ns
Dives > 10 m (%)	70 ± 11	86 ± 6	***	82 ± 6	68 ± 7	87 ± 5	***	81 ± 6	ns	ns
Dives > 80 m (%)	16 ± 9	25 ± 10	*	22 ± 8	2 ± 3	4 ± 3	ns	4 ± 2	**	**
Time underwater (h.d^{-1})	8.3 ± 1.7	8.3 ± 0.9	ns	8.3 ± 0.7	9.3 ± 1.2	7.1 ± 0.8	***	7.9 ± 0.8	ns	ns
VTD (km.d^{-1})	10.6 ± 1.7	12.6 ± 1.6	*	12.1 ± 1.1	11.2 ± 1.8	12.5 ± 1.4	*	12.2 ± 1.1	ns	ns
Maximum depth (m)[a]	39 ± 9	51 ± 8	**	48 ± 7	27 ± 3	43 ± 4	***	38 ± 3	***	**
Dive duration (s)[a]	127 ± 13	130 ± 12	ns	130 ± 11	95 ± 5	95 ± 7	ns	95 ± 5	***	***
Descent rate (m.s^{-1})[a]	1.08 ± 0.1	1.17 ± 0.07	**	1.15 ± 0.06	1.0 ± 0.07	1.12 ± 0.07	***	1.08 ± 0.06	ns	ns
Ascent rate (m.s^{-1})[a]	1.0 ± 0.12	1.13 ± 0.05	***	1.10 ± 0.05	0.88 ± 0.07	1.15 ± 0.07	***	1.07 ± 0.04	ns	ns

[a] for dives > 10 m; VTD = vertical travel distance

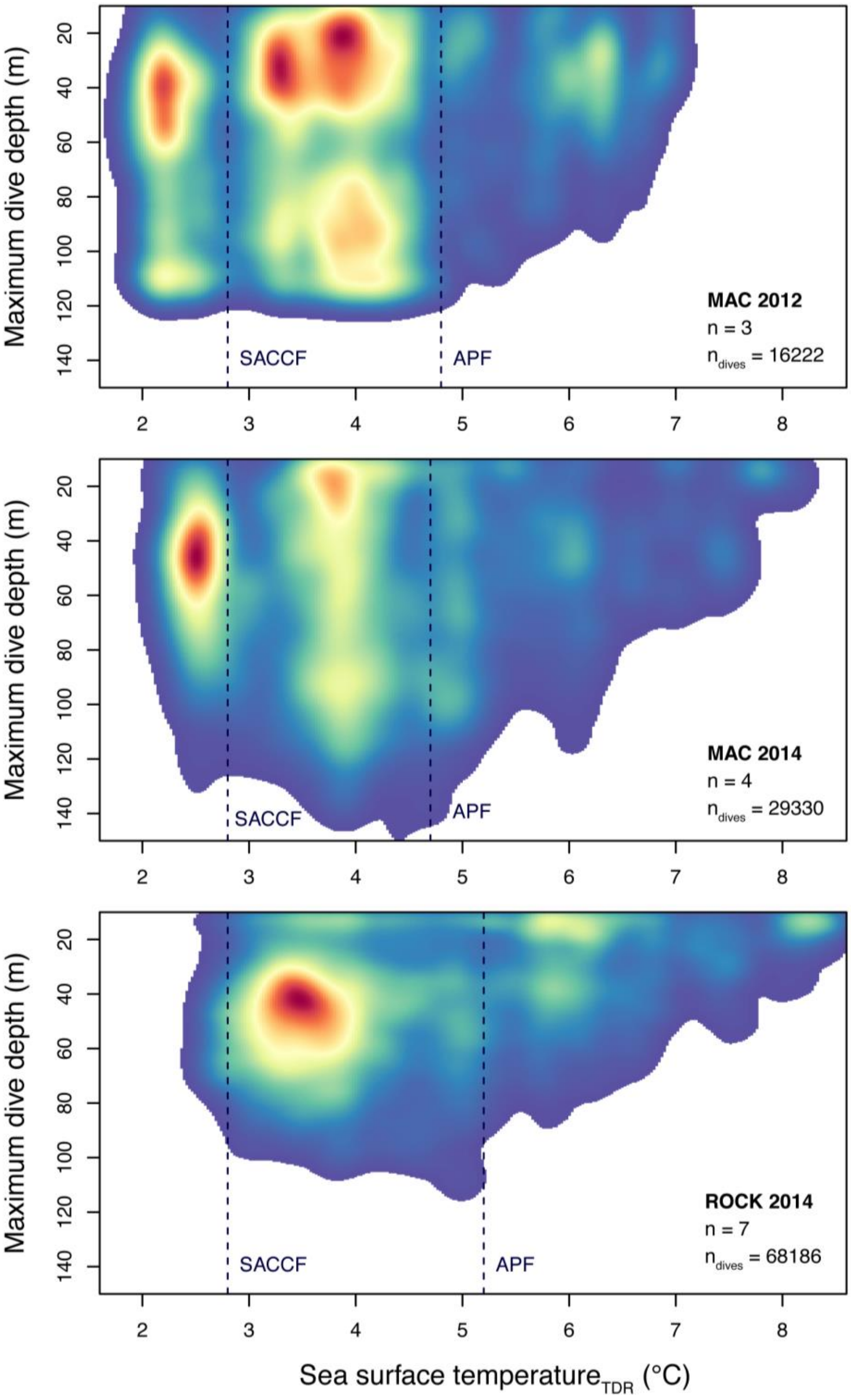


Figure 4.6. Kernel density estimates (99 %) of maximum dive depths (> 10 m) of macaroni (MAC) and rockhopper (ROCK) penguins in relation to sea surface temperature (SST_{TDR}) during the pre-moult foraging trip. Approximate positions of the Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Front (SACCF) are shown based on the mean SST encountered by penguins at -0.63 m SSH and -0.943 m SSH, respectively (Swart et al. 2010)

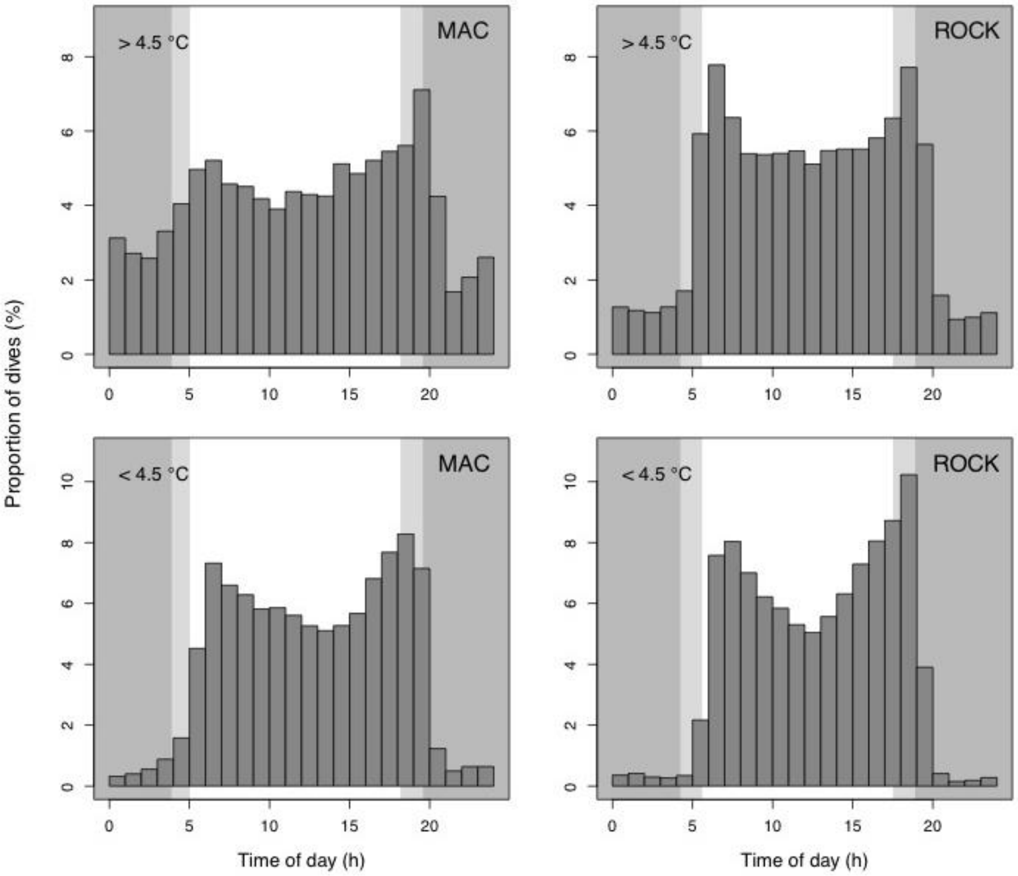


Figure 4.7. Proportion of dives (%) performed by macaroni (MAC) and rockhopper (ROCK) penguins in relation to time of day and sea surface temperature (> and < 4.5 °C) during the 2014 pre-moult foraging trip. Dark and light shaded bars represent night-time and nautical twilight periods, respectively, determined for the mean location of core foraging areas at the midpoint of the trip

Discussion

The consistent movement of both macaroni and rockhopper penguins to distant foraging areas south of the Prince Edward Islands during the pre-moult foraging trip is in accordance with ship-based observations made south of the islands in April 2008 where a peak abundance of crested penguin sightings (mostly macaroni penguins) was noted at 50–52 °S

(Ryan 2009). The long-distance dispersal of macaroni penguins *Eudyptes chrysolophus* during the pre-moult period was first, and rather accurately, inferred by Brown (1987) who used speed meters to estimate that two individuals travelled 700 – 1200 km from Marion Island. Such large-scale dispersal of macaroni penguins during the pre-moult period has since been reported at South Georgia (54.0 °S, 38.03 °W; Green et al. 2009b; Waluda et al. 2010; Horswill 2015), the Crozet (46.4 °S, 51.8 °E) and Kerguelen Archipelagos (Thiebot et al. 2014), and Bouvetøya (54.4 °S, 3.8 °E; Lowther et al. 2014) (Table 4.5). However, this chapter documents the pre-moult dispersal of rockhopper penguins for the first time.

Marine habitats and association with sub- and mesoscale features

Given that both species in this study travelled such large distances to forage in cooler waters (~ 3.5 °C) south of the APF, and assuming that penguins adopt foraging strategies that maximise net energy gain (MacArthur and Pianka 1966), it is likely that prey must be more available (or at least predictable) and/or more energy-rich than in PFZ waters nearer the Prince Edward Islands. Satellite-derived surface chlorophyll-a concentrations revealed the higher productivity of Antarctic Zone (AAZ) waters relative to Polar Frontal Zone (PFZ) waters typically observed during the austral summer (Sokolov and Rintoul 2007). As blooms are known to extend for hundreds of kilometres downstream of topographical features (Sokolov and Rintoul 2007), elevated primary productivity at the South-West Indian Ridge (SWIR; Fig. 4.3) may considerably enrich AAZ waters south of the islands. Total macrozooplankton and fish biomass is generally higher south of the APF compared to PFZ waters (Pakhomov et al. 1994; Pakhomov and Froneman 2000; Bernard and Froneman 2006). As macaroni and rockhopper penguins feed primarily on euphausiids during breeding (Crawford et al. 2003a, b), and isotope data from other localities suggest a primarily crustacean-based diet for both species during the pre-moult period (Jaeger and Cherel 2011; Thiebot et al. 2014), differences in PFZ and AAZ euphausiid communities may be a factor causing penguins to travel such large distances to AAZ waters. Euphausiid communities in PFZ waters are generally dominated by sub-Antarctic species (*Euphausia vallentini*, *E. longirostris, Nematoscelis megalops, Thysanoessa* spp.) whereas those in AAZ waters are typically Antarctic species (*E. triacantha*, *E. frigida*) (Pakhomov et al. 1994; Pakhomov and Froneman 2000; Ansorge et al. 2009); however, eddies are known to entrain species across the APF (Bernard et al. 2007; Ansorge et al. 2009). Penguins were unlikely targeting Antarctic krill *E. superba* as this species rarely occurs north of 60° in this region of the Southern Ocean (Atkinson et al. 2008). Additionally, the increased abundance of myctophids in AAZ waters may provide penguins with an energy-rich supplement to euphausiids, as suggested by studies of the diet of post-breeding crested penguins in the southern Indian Ocean (Cherel et al. 2007; Thiebot et al. 2012, 2014).

The region immediately upstream of the penguins' core foraging areas is characterised by extremely high mesoscale activity associated with the persistent generation of eddies over the SWIR (Durgadoo et al. 2011; Frenger 2013). These eddies typically move east, passing south of the Prince Edward Islands, or move south/south-east and dissipate over the Enderby Basin (Durgadoo et al. 2011; Ansorge et al. 2015). Eddies and associated filaments are important foraging areas for many top predators throughout the Southern Ocean (Nel et al. 2001; Cotté et al. 2007; Bost et al. 2009; Cotté et al. 2015; Massie et al. 2015) as they support elevated aggregations of macrozooplankton and micronekton (Ansorge et al. 2009). Maps of SLA and FSLE revealed a consistent eddy field in the lee of the SWIR during the study period (Fig. S7–S11), supporting the concept of an concentration of eddies in this region (Ansorge and Lutjeharms 2005). Movements of penguins appeared to be influenced by the structure of the mesoscale environment, with penguins avoiding extreme eddies (> 0.3 m) and waters characterised by high EKE. Such avoidance may benefit penguins by reducing the energetic cost of swimming against currents (Bon et al. 2015). Association of penguins with well-defined eddies was only apparent for a few individuals, but most penguins targeted waters characterised by weak positive SLA and relatively low EKE downstream of and/or within convergence zones between eddies (Fig. 4.9; Fig. S7–S11). Importantly, all penguins exhibited strong associations with sub-mesoscale filaments (Table 4.4; Fig. 4.9) that are often associated with eddy edges (Lapeyre and Klein 2006). Recent evidence highlights the importance of such features for macaroni penguins during the pre-moult period at Bouvetøya (Lowther et al. 2014) and the incubation period at the Crozet Islands (Bon et al. 2015). The edges of warm eddies have shallower thermoclines and mixed layers than the core (Ansorge et al. 2009), and sub-mesoscale filaments are associated with reduced vertical mixing and increased water column stability (Lévy et al. 2012), which may force prey into surface waters more accessible to penguins. It is possible that the dissipation of eddies over the Enderby Basin acts as an important mechanism for the lateral advection of prey into the region which are then retained along sub-mesoscale filaments and in neighbouring waters characterised by relatively lower EKE. Indeed, it is suggested that krill abundance is highest in waters of moderate EKE where upwelling is maintained but krill are less likely to be advected (Santora et al. 2012). If this is the case, macaroni and rockhopper penguins would be able to forage more efficiently in such areas that aggregate preferred prey and/or make them more accessible. Further investigations into these fine-scale foraging strategies are, however, needed to elucidate such mechanisms.

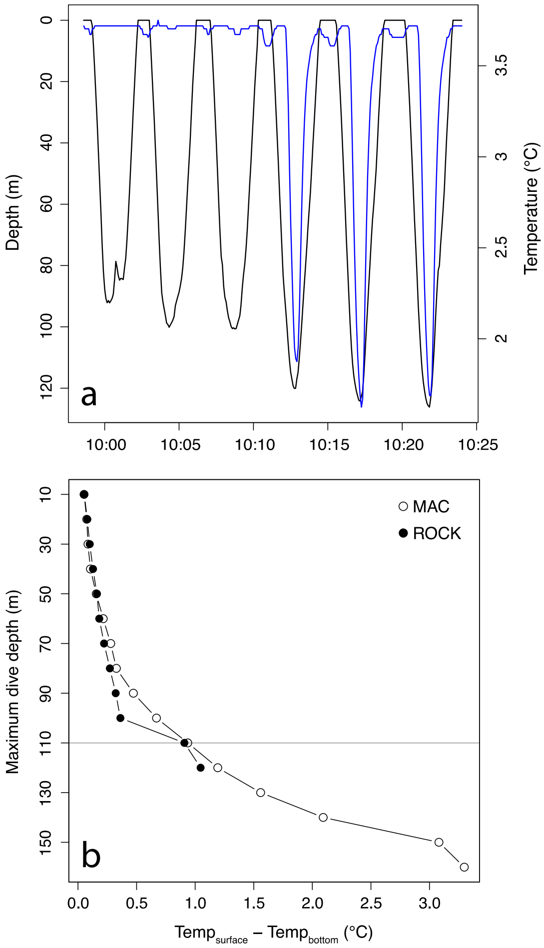


Figure 4.8. Depth profiles (black line) of a macaroni penguin during the pre-moult trip showing the sharp decline in water temperature (blue line) when the thermocline was encountered ~ 110 m (a), and the temperature differences between surface and bottom waters encountered by macaroni and rockhopper (ROCK) penguins in relation to depth (b) showing the approximate position of the thermocline (grey line)

Inter-annual variation

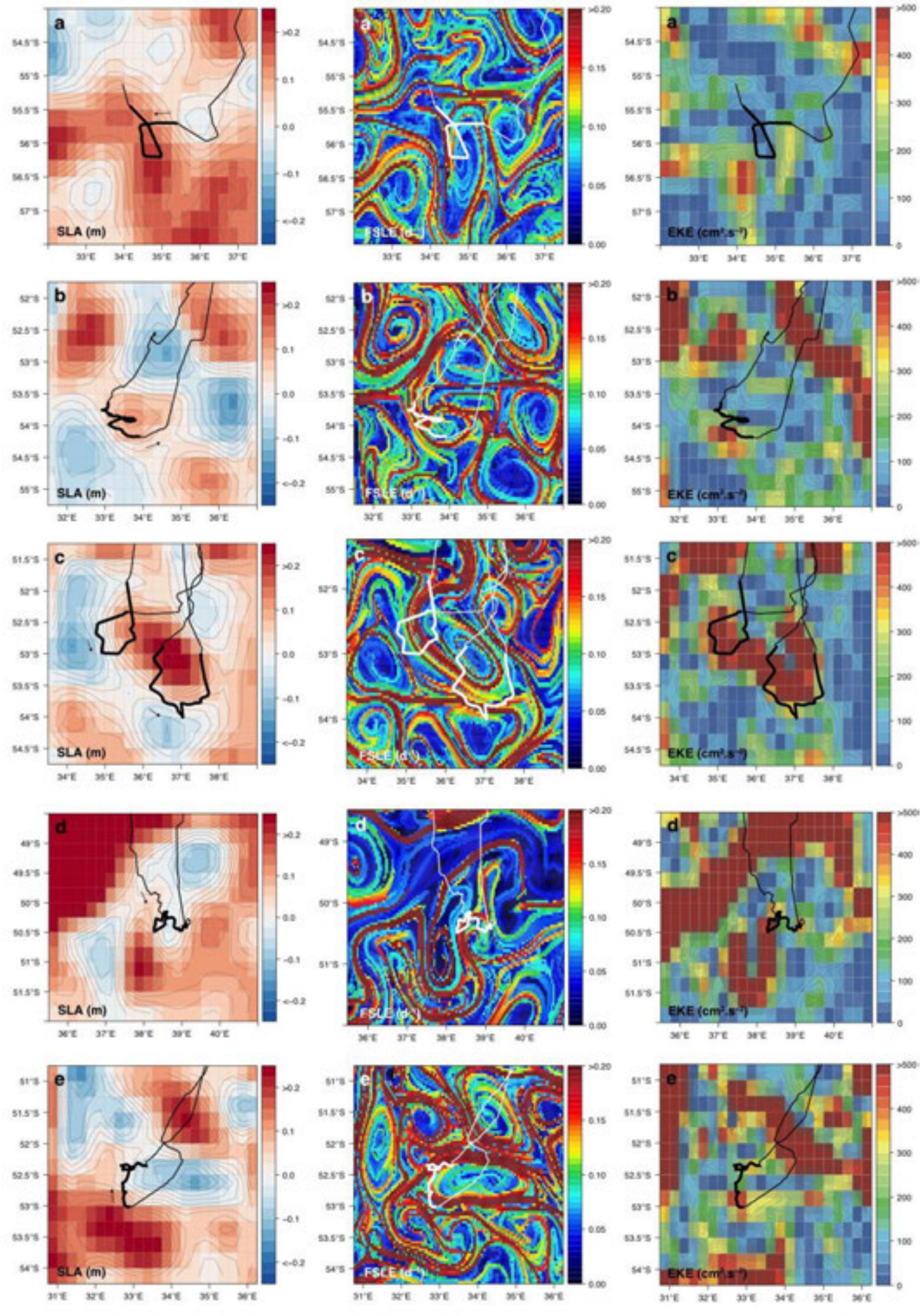
Due to the highly dynamic and complex nature of Southern Ocean ecosystems, the limited period during which this study was undertaken, and rather small sample sizes, it was difficult to identify specific environmental drivers of inter-annual variation in foraging trip characteristics. Positions of the APF and SACCF, and cooler isotherms (2-4 °C) south of the islands varied marginally between years (Fig. 4.1; see also Fig. S6), with the core AAZ and 3.5 °C isotherm located slightly nearer (~ 80 km) to the islands in 2013. This difference appears insufficient to account for the inter-annual variation in maximum foraging ranges, suggesting the influence of other factors. Perhaps the most distinct difference between years was the early disintegration of the summer bloom in 2014; resulting in decreased surface chlorophyll-a concentrations both within core foraging areas and upstream at the SWIR. This may explain why both species spent significantly more time at sea in 2014 compared to 2013, but does not account for the longer trips performed by macaroni penguins in 2012. Reduced primary productivity is likely to reduce prey availability, forcing penguins to spend more time searching for and/or pursuing prey. Reasons for the decreased productivity are unclear, but as mesoscale processes are key drivers of primary productivity (Kahru et al. 2007; Frenger 2013), such conditions may be linked to the structure of the mesoscale environment. Mesoscale activity in this region is largely determined by the interaction of the ACC with the SWIR (Durgadoo et al. 2011) and thus fluctuations in the positions of major frontal boundaries associated with the ACC may indirectly influence primary productivity. The mesoscale environment was most distinctly different in 2013 due to a corridor of extreme eddies upstream of the Prince Edward Islands (Fig. S8, S10) which might have resulted from the close proximity of the APF and SACCF over the SWIR (Ansorge et al. 2009). Continued monitoring is required in order to better understand how environmental conditions drive inter-annual variation in pre-moult foraging trip characteristics.

Diving behaviour

Both species dived actively throughout trips, but exhibited diving behaviour more typical of intensive foraging in cooler waters (< 4.5 °C; i.e. more dives > 10 m, increased VTD, deeper dives, and steeper descent and ascent rates; Table 4.4), supporting the importance of these waters as core foraging areas. As macaroni and rockhopper penguins are visual predators that forage predominantly during the day (Tremblay and Cherel 2003; Green et al. 2005), the more frequent night dives in warmer waters were likely associated with travelling. In cooler waters, diving activity of both species was concentrated in the mornings and evenings (Fig. 4.7). Euphausiids and fish are well known to exhibit diel vertical migration patterns and are probably more accessible to penguins during these periods (Hulley 1990). To my knowledge, this chapter provides the first evidence of the utilisation of thermoclines by crested penguins (Fig. 4.8), but such features were not important for rockhopper penguins due to their low encounter rate (0.6 % of dives > 10 m) as a consequence of a reduced ability to dive to such depths (Fig. 4.5). Thermoclines are important features for penguins as they structure the vertical habitat of prey (Charrassin and Bost 2001; Ropert-Coudert et al. 2009; van Eeden et al. 2016).

Macaroni penguins in this study exhibited similar diving behaviour to chick-rearing penguins at Marion Island (Pichegru et al. 2011), as also observed for macaroni penguins at South Georgia (Green et al. 2005). However, dive depths and durations of macaroni penguins in this study were greater than those during breeding and pre-moult at South Georgia and more akin to those during the over-wintering period at South Georgia (Green et al. 2005) and incubation period at Kerguelen (Sato et al. 2004). This study is the first to reveal insights into the diving behaviour of rockhopper penguins during the pre-moult period. Dive depths and durations were similar to those during the breeding season at Marion (Chapter 3) and Crozet Islands (Tremblay and Cherel 2003), but were deeper and longer than those during the breeding season at Macquarie Island (Hull 2000). In comparison to southern rockhopper penguins in the south-west Atlantic Ocean, dive depths and durations were greater at Marion Island, perhaps owing to differences in prey distribution and availability (Schiavini and Raya Rey 2004; Putz et al. 2006; Raya Rey et al. 2009; Ludynia et al. 2013). Interestingly, a male rockhopper penguin in this study performed the deepest dive recorded for this species (122.3 m).

Figure 4.9 (next page). Movements of macaroni (a, b) and rockhopper penguins (c, d, e) in relation to maps of sea level anomaly (SLA), finite-size Lyapunov exponent (FSLE) and eddy kinetic energy (EKE). Thicker line represents 3 days prior to and after the date of mapped environmental variables; 17 March 2012 (a), 4 March 2013 (b), 22 March 2013 (c), 17 March 2013 (d) and 17 March 2014 (e). Arrows indicate direction of movement


a
b
c
d
e
SLA (m)
FSLE (d⁻¹)
EKE (cm².s⁻²)
>0.2
0.1
0.0
−0.1
<−0.2
>0.20
0.15
0.10
0.05
0.00
>500
400
300
200
100
0
54.5°S
55°S
55.5°S
56°S
56.5°S
57°S
33°E
34°E
35°E
36°E
37°E
52°S
52.5°S
53°S
53.5°S
54°S
54.5°S
55°S
32°E
51.5°S
38°E
49°S
49.5°S
50°S
50.5°S
51°S
39°E
40°E
31°E

Comparison between species

Macaroni and rockhopper penguins exhibited similar habitat preferences and at-sea distributions during the pre-moult foraging trip (Fig. 4.3), but spatiotemporal overlap is considerably reduced by the two to three-week difference in departure dates (Table 4.1; Fig. 4.4), linked to differences in the onset of breeding (Brown 1987). This phenological difference may have evolved to reduce interspecific competition during the breeding season when foraging pressure near the islands is high, but it also appears to reduce potential interspecific competition during the pre-moult foraging period, and possibly during the initial and final weeks of the winter trip (Thiebot et al. 2012). Royal and rockhopper penguins, and Adélie and chinstrap penguins also exhibit allochrony throughout their annual cycle (Trivelpiece et al. 1987; Hull 2000). This time shift appears to be a vital aspect of segregation during the pre-moult period as it allows rockhopper penguins to exploit similar habitats to macaroni penguins whilst minimising potential competition. Contrastingly, these two species exhibit markedly different habitat preferences during the winter period (Thiebot et al. 2013). Comparisons of diving behaviour revealed a large overlap in their use of the water column (Fig. 4.5), however, macaroni penguins dived more frequently to depths > 80 m (Table 4.4) and thus encountered thermoclines more often. This suggests that the size or type of prey taken during the pre-moult period might differ slightly between species, and prompts further investigations into potential dietary differences; however, isotopic studies at other localities suggest that macaroni and rockhopper penguins forage at a similar trophic level during the pre-moult period (Cherel et al. 2007; Thiebot et al. 2014). If the same prey are targeted, it is important to consider that intense foraging by macaroni penguins at core foraging areas during the two weeks leading up to the period when rockhopper penguins are at sea may reduce prey availability unless new prey are advected into the region. Additionally, the greater abundance of macaroni penguins and their increased ability to dive deeper and for longer than rockhopper penguins, as expected from their larger body size and oxygen storage capacity, suggests that if foraging areas overlapped and resources were limited, they would likely outcompete rockhopper penguins. Thus, in less productive years when both species spend more time concurrently at sea, such as 2014, the potentially larger spatiotemporal overlap may negatively affect the foraging efficiency of rockhopper penguins. However, inspection of SSTs exploited in 2014 revealed that macaroni penguins foraged in marginally cooler or warmer waters than rockhopper penguins whilst both species were concurrently at sea (Fig. 4.4). Further studies with larger sample sizes are, however, needed to determine whether such fine-scale segregation occurs.

Table 4.5. Characteristics of the pre-moult foraging trip of macaroni penguins from different breeding localities (*March 1st). GPS = global positioning system; GLS = geolocation; BGL = behavioural geolocation; PTT = platform terminal transmitter; [a]data only available for one individual

Locality	Year	N	Technique	Departure date	Duration (days)	Maximum range (km)	Direction	Distance to 3.5 °C isotherm (km)*	Distance to core AAZ (km)*	Reference
Marion (47°S)	1985	2	speed meter	-	-	945 ± 332	-	738	-	Brown (1987)
	2012	5	GPS	19-Feb ± 1	35 ± 7	1018 ± 166	S	657	724	This study
	2013	6	GPS	16-Feb ± 2	29 ± 3	780 ± 60	S	606	677	
	2014	9	GPS	18-Feb ± 1	38 ± 7	873 ± 104	S	681	734	
Crozet (47°S)	2009	9	GLS	14-Feb ± 4	50 ± 7	824 ± 343	S, SE	796	810	Thiebot et al. (2014)
Kerguelen (49°S)	2011	13	GLS	17-Feb ± 1	42 ± 4	941 ± 271	SE	667	813	Thiebot et al. (2014)
South Georgia (54°S)	1976	29	-	-	13 ± 1	-	-	-	-	Williams and Croxall (1991)
	2002	17	BGL	20-Feb ± 4	21 ± 1	634 ± 115	N, NW, W	142	378	Green et al. (2009b)
	2003	15	BGL	21-Feb ± 4	18 ± 1	697 ± 88	N, NW	175	384	
	2004	4	PTT	19-Feb	18 ± 7	489 ± 80	N, NW, W	175	435	Waluda et al. (2010)
	2012	4	GPS	24-Feb ± 1	17 ± 1	357 ± 40	NW	154	374	Horswill (2015)
Bouvetøya (54°S)	2008	3	PTT	1-Mar ± 0	20[a]	444 ± 111	N, NW	437	411	Lowther et al. (2014)

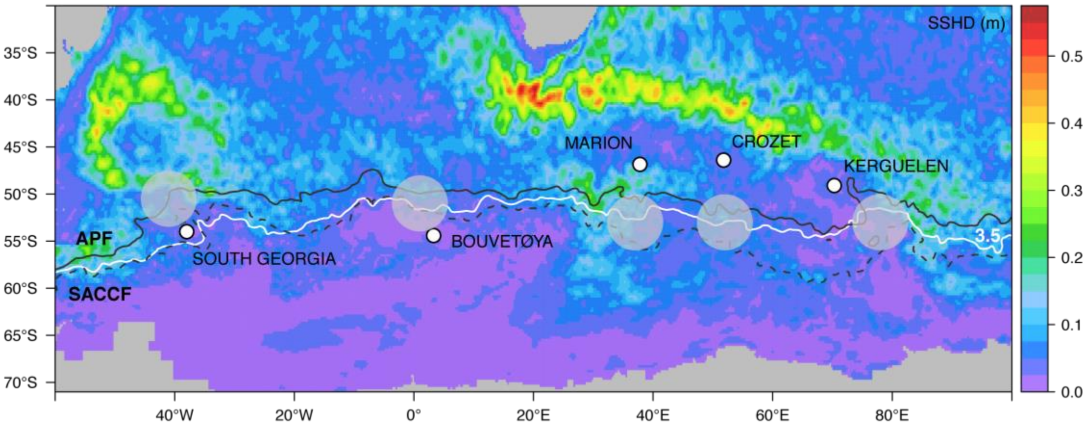


Figure 4.10. Macaroni penguin breeding localities (white circles) and approximate foraging areas (grey circles, see Table 4.5) during the pre-moult foraging trip. Colour represents sea surface height variability (SSHD; $m^2.s^{-2}$) across the Atlantic and Indian Ocean sectors of the Southern Ocean at the end of February during 2002 – 2014 (data source: Aviso). Mean positions of the 3.5 °C isotherm, Antarctic Polar Front (APF) and Southern Antarctic Circumpolar Current Front (SACCF) are shown

Pre-moult habitat and trip characteristics in a circumpolar context

Throughout the range of macaroni penguins, the duration of pre-moult foraging trips varies considerably (Table 4.5). For instance, macaroni penguins at South Georgia conduct relatively short trips (13 to 21 d; Williams and Croxall 1991; Green et al. 2009b) compared to birds at Crozet and Kerguelen (50 d and 42 d, respectively; Thiebot et al. 2014). SST preferences of penguins in this study were remarkably similar to macaroni penguins at Crozet and Kerguelen that reached waters ~ 3.5 °C (Thiebot et al. 2014). Thiebot et al. (2014) suggested that the duration of trips was related to the distance from the colony to the 3.5 °C isotherm (~ 796 km from Crozet and 667 km from Kerguelen). The proximity of the 3.5 °C isotherm to Marion Island (~ 635–681 km) is similar to Kerguelen and closer than Crozet, and penguin trip durations are appreciably shorter (~ 33 d). At South Georgia, the 3.5 °C isotherm is generally located to the south of the island during the pre-moult period yet macaroni penguins travel > 350 km northwest of the island to slightly warmer waters (~ 5 °C; Waluda et al. 2010; Horswill 2015). The inter-island differences in preferred SST at foraging areas suggests that while SST may play an important role as an environmental cue to local populations, other processes ultimately determine favourable foraging areas. At a broad scale, macaroni penguins forage predominantly in AAZ waters between the APF and the SACCF (Fig. 4.10), although behavioural geolocation of penguins from South Georgia suggests they also forage north of the APF in the PFZ (Green et al. 2009b). Both the APF and SACCF are associated with high mesoscale activity and productivity (Strass et al. 2002; Kahru et al. 2007; Frenger 2013) and the shedding of eddies into AAZ waters may provide penguins with a rich mesoscale environment in which to forage. The strong relationships between the distance of the colony to the core AAZ and the duration and maximum range of the pre-moult foraging trip (Fig. 4.11) further emphasises the global importance of this region for macaroni penguins.

To my knowledge there are no previous records of foraging ranges or habitats of rockhopper penguins during the pre-moult period, however, trip durations of 9 and 13 days have been reported for rockhopper penguins at Macquarie Island (Hull et al. 2004; 1995 and 1996, respectively; core AAZ ~ 189 and 277 km S, respectively), and 20 to 25 days for southern rockhopper penguins at the Falklands (Strange 1982; core AAZ ~ 580 km S). Future studies at other localities are required to validate the importance of the core AAZ to both macaroni and rockhopper penguins during the pre-moult period, and to determine whether penguins at these localities associate with eddies and/or sub-mesoscale filaments.

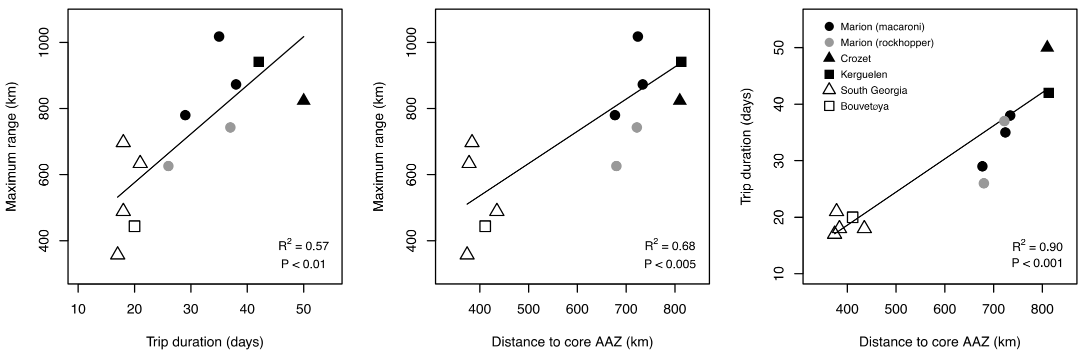


Figure 4.11. Linear regressions of pre-moult foraging trip characteristics of macaroni penguins at various breeding localities in relation to their distance to the core AAZ (midpoint of the APF and SACCF). Rockhopper penguins also included for comparison. Note that multiple years are shown

Conclusions

At a broad scale, the consistent movement of both macaroni and rockhopper penguins from Marion Island to cooler waters (~ 3.5 °C) south of the APF in the lee of the SWIR documents for the first time the importance of this region as a predictable foraging area for these penguins after the breeding season. The association of penguins with mesoscale eddies (and sub-mesoscale filaments) further supports the value of such features in sustaining top predator populations at the Prince Edward Islands (Nel et al. 2001; Massie et al. 2015). Both macaroni and eastern (subspecies of southern) rockhopper penguins are listed as Vulnerable (BirdLife International 2015) due to recent population declines (30 % and 70 % since 1994/95, respectively, at the Prince Edward Islands; Crawford et al. 2009). Changes in the prey environment at pre-moult foraging areas may have implications for adult survival during and after the moult, and may thus be an important driver of population dynamics. Given the recent changes documented in the Southern Ocean, such as increasing SST (Gille 2002;

Melice et al. 2003) and the southward shift in major frontal boundaries (Hunt et al. 2001), continued monitoring is necessary in order to determine how penguins might adapt to associated changes in this dynamic region of the Southern Ocean (Péron et al. 2012).

Supplementary material

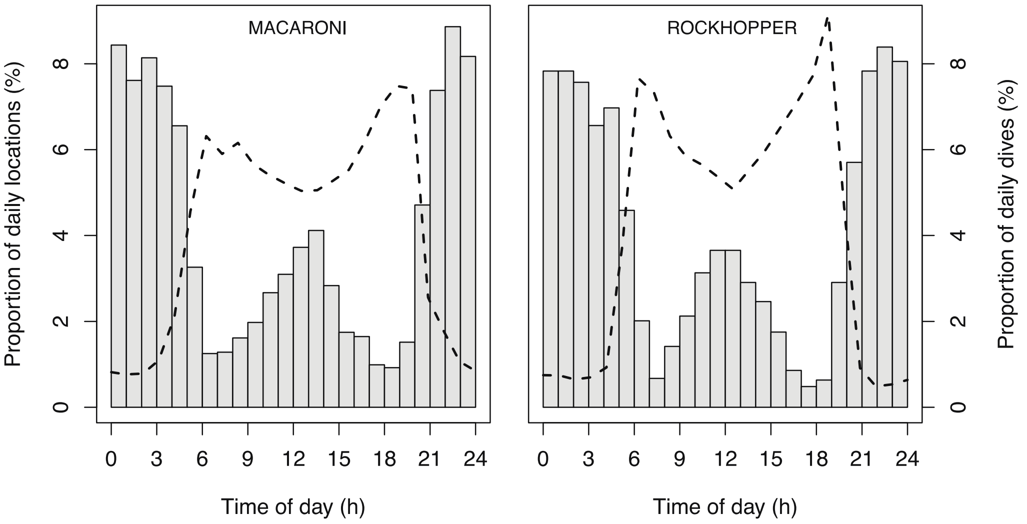


Figure S4.1. Proportion of raw GPS locations acquired (grey bars; 2013 and 2014) and proportion of total dives (dotted line; 2014) of macaroni and rockhopper penguins during pre-moult foraging trips relative to time of day

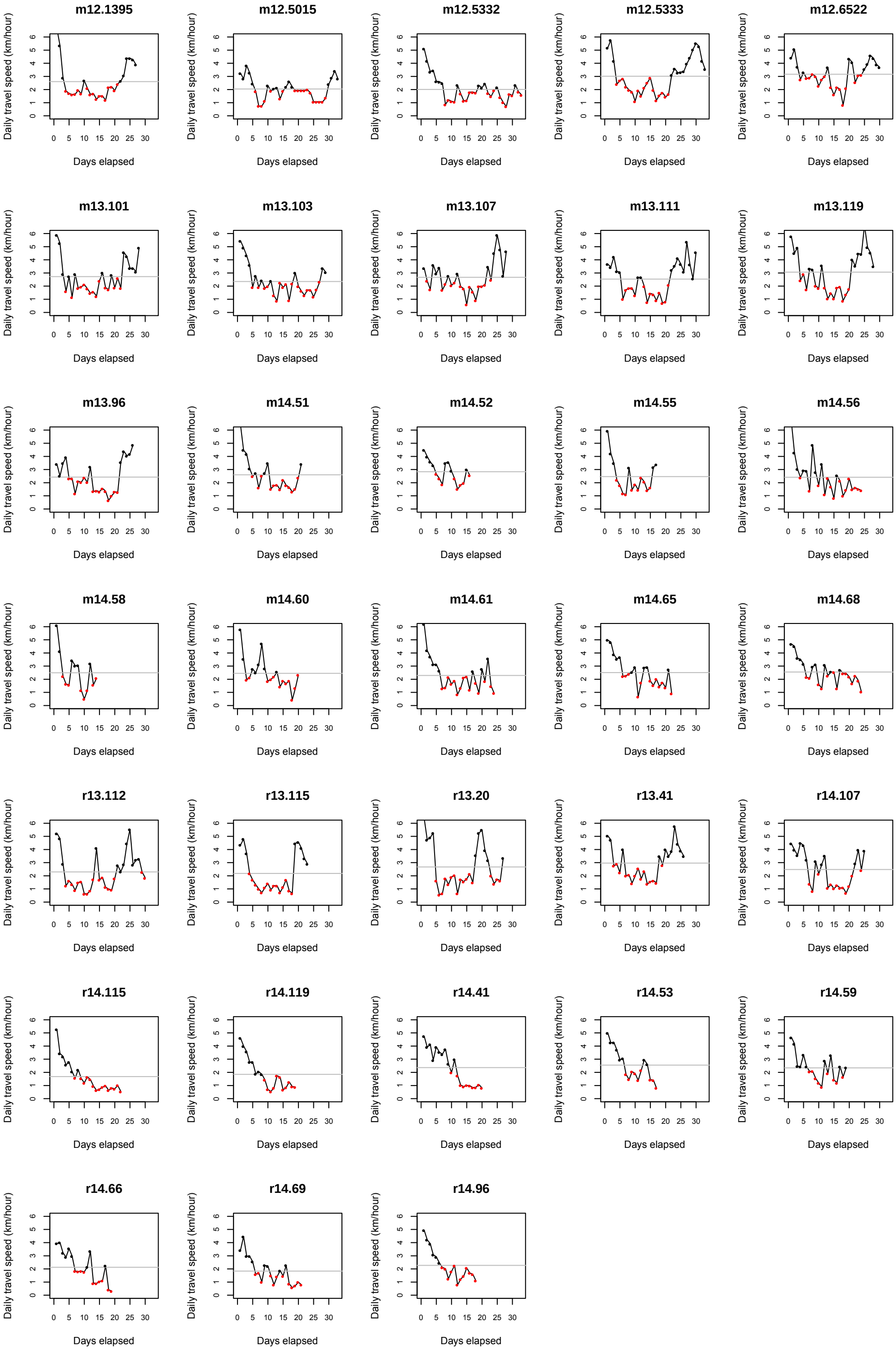


Figure S4.2. Daily travel speeds of individual macaroni and rockhopper penguins in relation to the number of days elapsed during the pre-moult foraging trip. Grey lines indicate the individual's mean travel speed and red dots represent days considered as core foraging phases

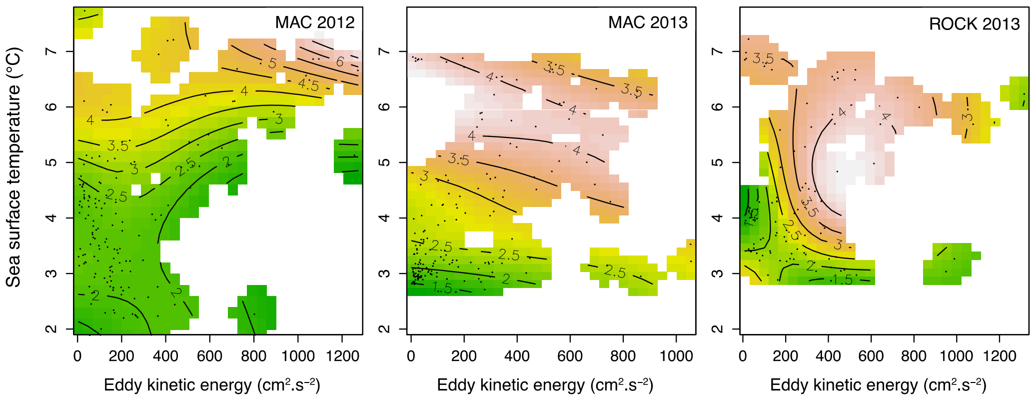


Figure S4.3. Generalised additive model outputs of daily travel speeds of macaroni (MAC) and rockhopper (ROCK) penguins in relation to the interaction between sea surface temperature and eddy kinetic energy in 2012 and 2013. Interaction in 2014 was not significant. Contours and colours depict predicted daily travel speeds, with light pink to green indicating fast to slow. Black dots represent daily locations

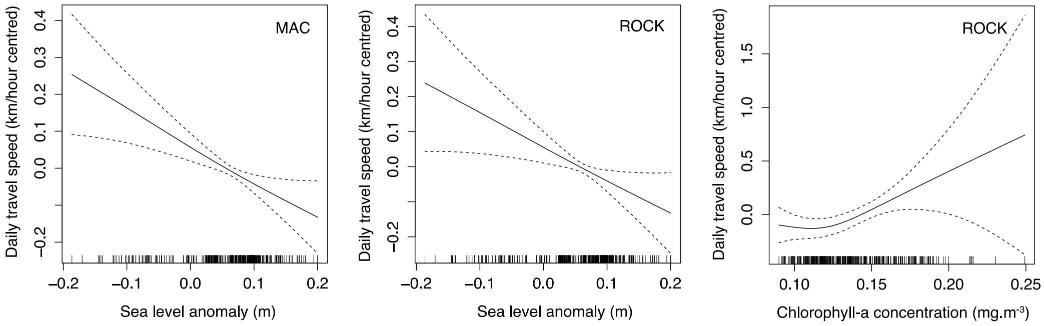


Figure S4.4. Generalised additive model (GAM) outputs of daily travel speeds of macaroni (MAC) and rockhopper (ROCK) penguins in relation to sea level anomaly (left and centre panels) and chlorophyll-a concentrations (right panel) in 2014

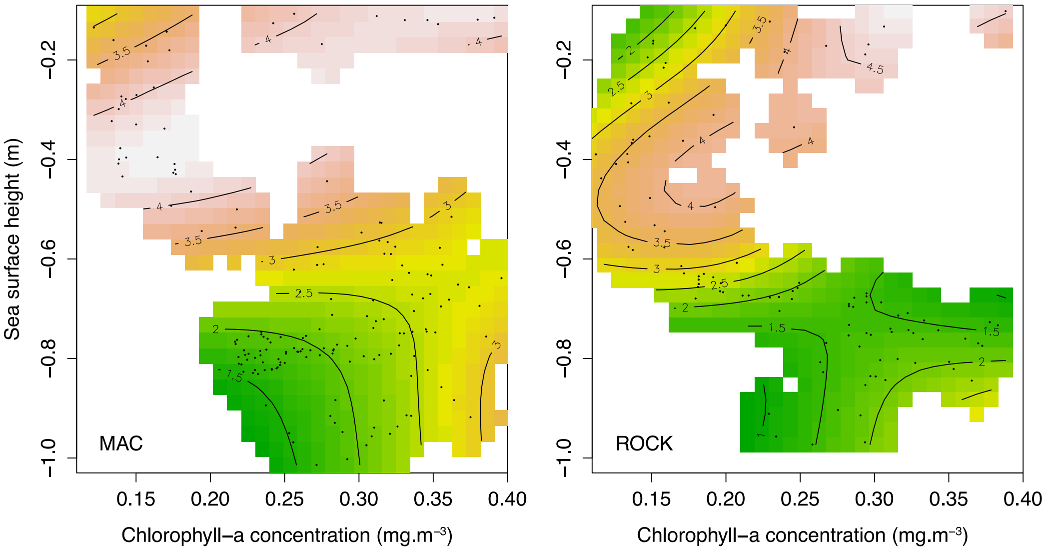


Figure S4.5. Generalised additive model outputs of daily travel speeds of macaroni (MAC) and rockhopper (ROCK) penguins in relation to the interaction between sea surface height and chlorophyll-a concentrations in 2013. Interactions in 2012 and 2014 were not significant. Contours and colours depict predicted daily travel speeds, with light pink to green indicating fast to slow. Black dots represent daily locations

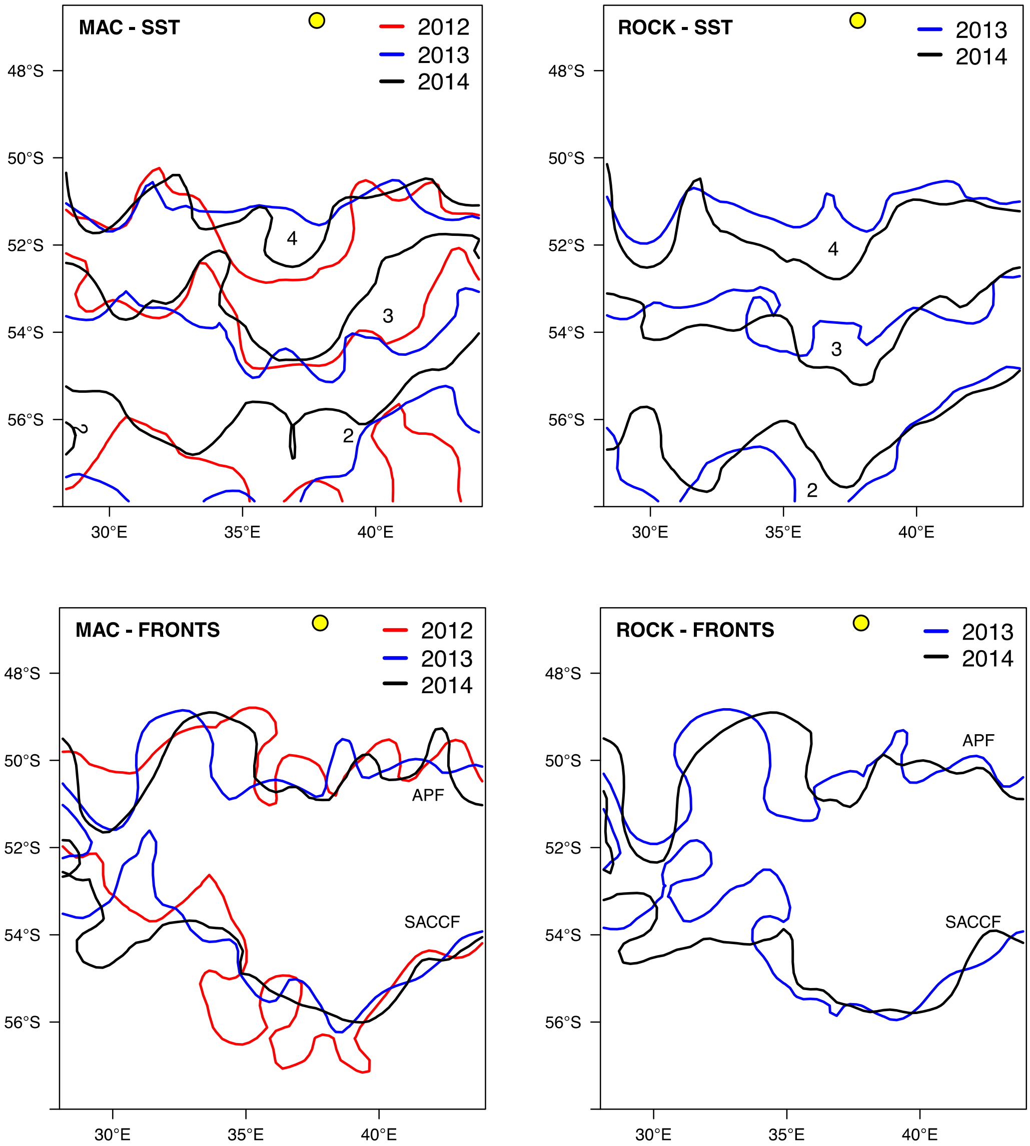


Figure S4.6. Positions of cooler sea surface temperature isotherms (2–4 °C; top row) and major frontal boundaries (bottom row) during the pre-moult foraging trip of macaroni (MAC) and rockhopper (ROCK) penguins. APF = Antarctic Polar Front, SACCF = Southern Antarctic Circumpolar Front

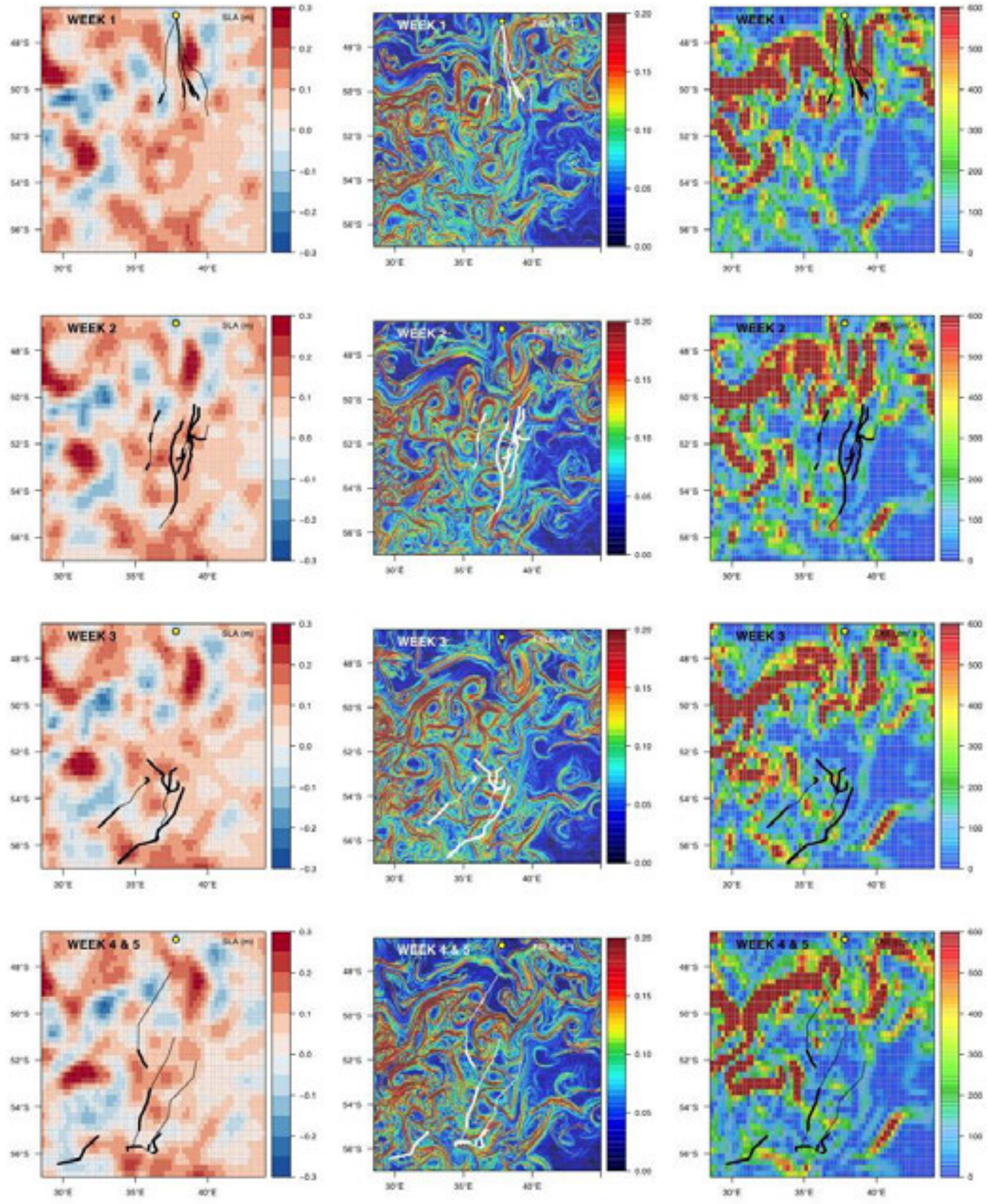


Figure S4.7. Weekly maps of sea level anomaly (SLA; m), finite-size Lyapunov exponent (FSLE; FLSE.d^{-1}) and eddy kinetic energy (EKE; cm^2.s^{-2}) showing tracks of macaroni penguins during the 2012 pre-moult foraging trip. Black dots represent phases where daily travel speeds were less than the individual's mean

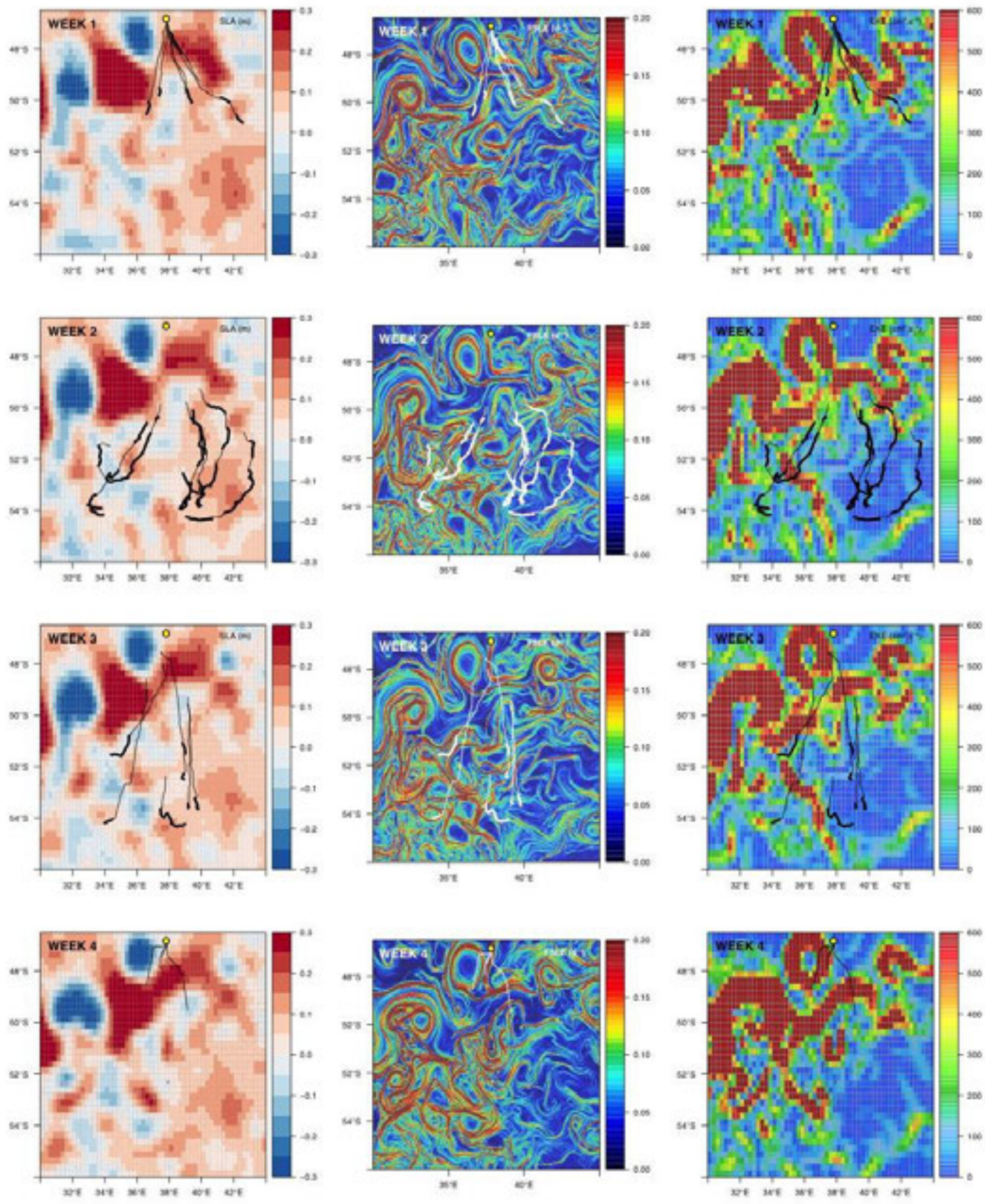


Figure S4.8. Weekly maps of sea level anomaly (SLA; m), finite-size Lyapunov exponent (FSLE; FLSE.d^{-1}) and eddy kinetic energy (EKE; cm^2.s^{-2}) showing tracks of macaroni penguins during the 2013 pre-moult foraging trip. Black dots represent phases where daily travel speeds were less than the individual's mean

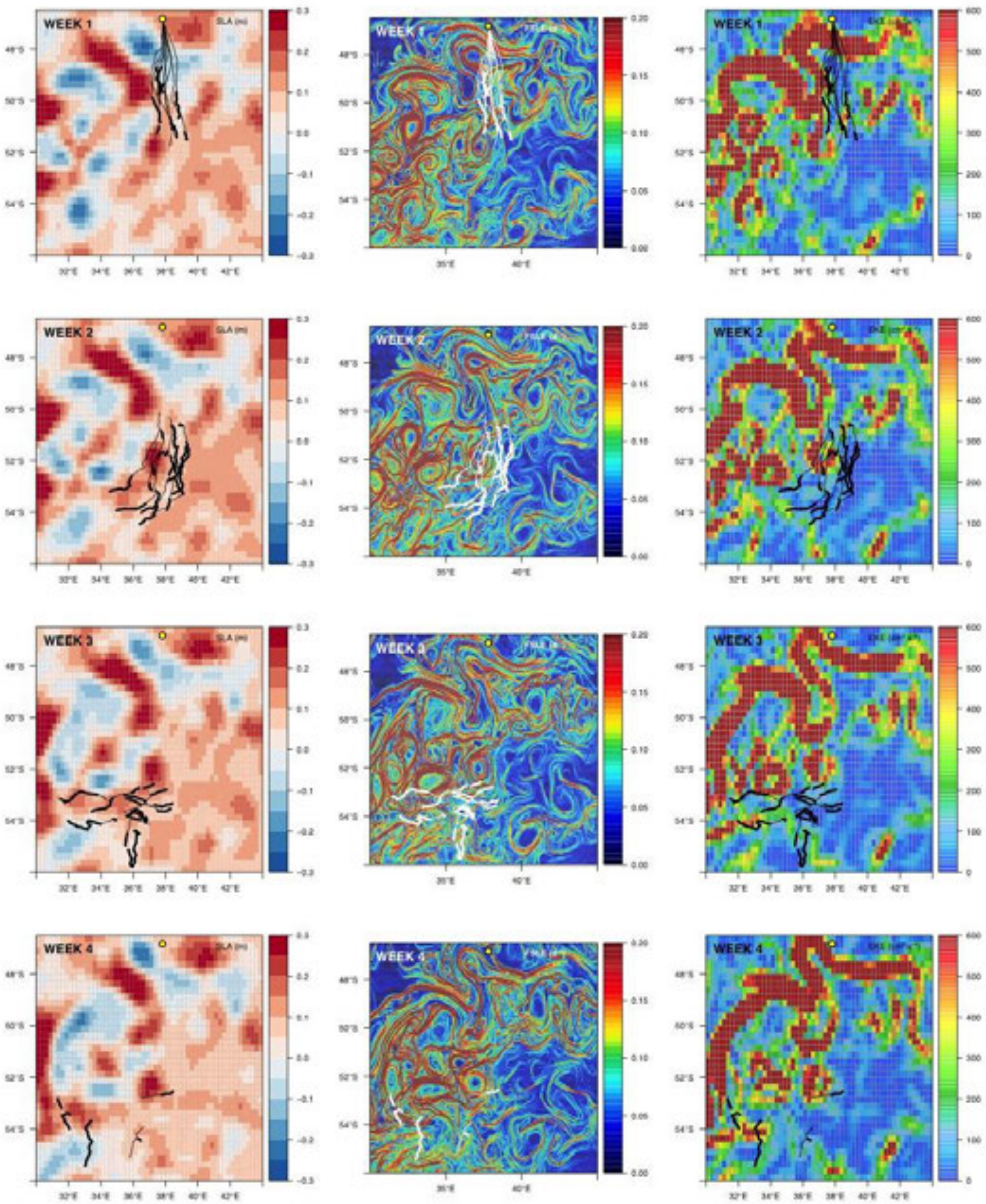


Figure S4.9. Weekly maps of sea level anomaly (SLA; m), finite-size Lyapunov exponent (FSLE; FLSE.d^{-1}) and eddy kinetic energy (EKE; cm^2.s^{-2}) showing tracks of macaroni penguins during the 2014 pre-moult foraging trip. Black dots represent phases where daily travel speeds were less than the individual's mean

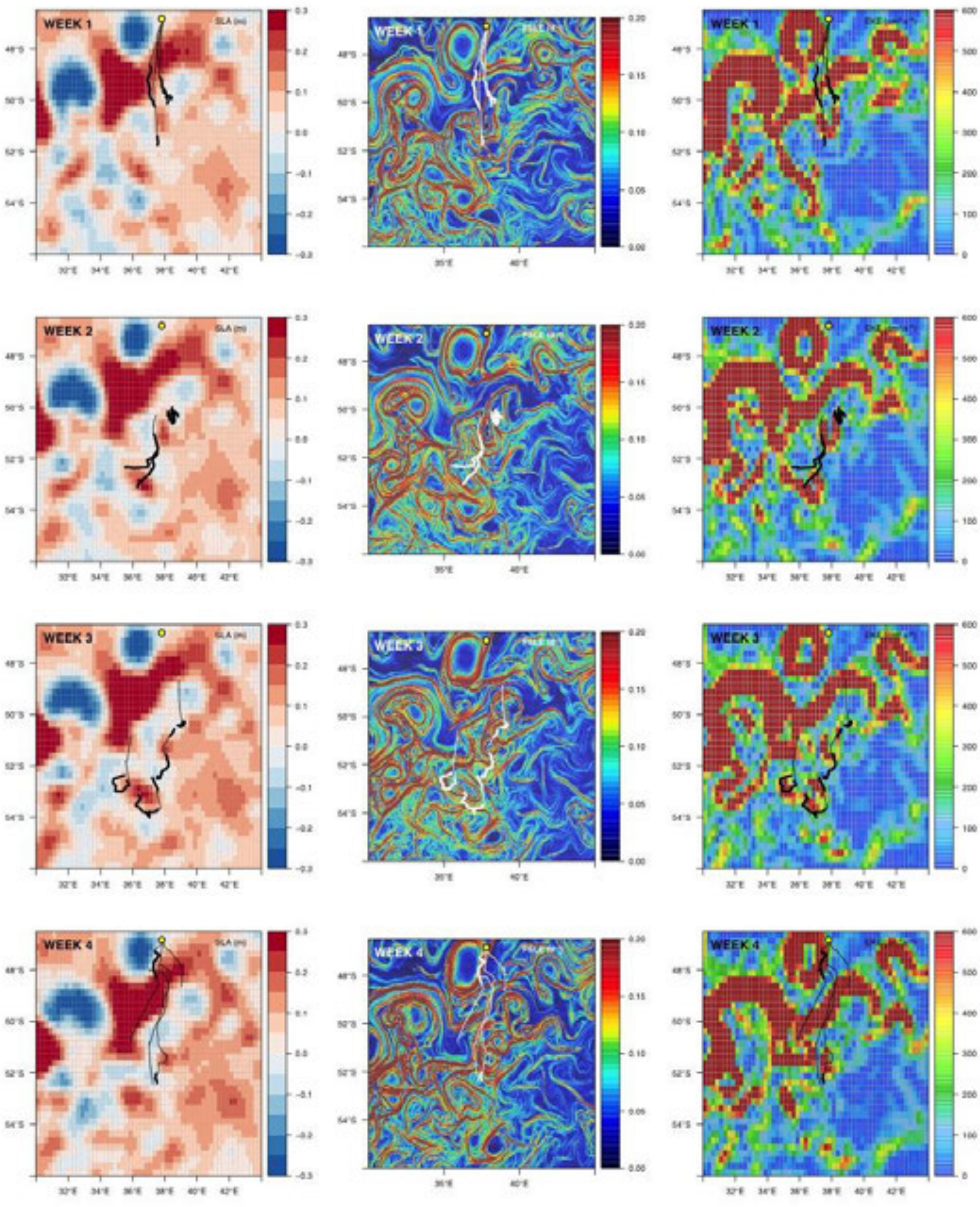


Figure S4.10. Weekly maps of sea level anomaly (SLA; m), finite-size Lyapunov exponent (FSLE; FLSE.d^{-1}) and eddy kinetic energy (EKE; cm^2.s^{-2}) showing tracks of rockhopper penguins during the 2013 pre-moult foraging trip. Black dots represent phases where daily travel speeds were less than the individual's mean

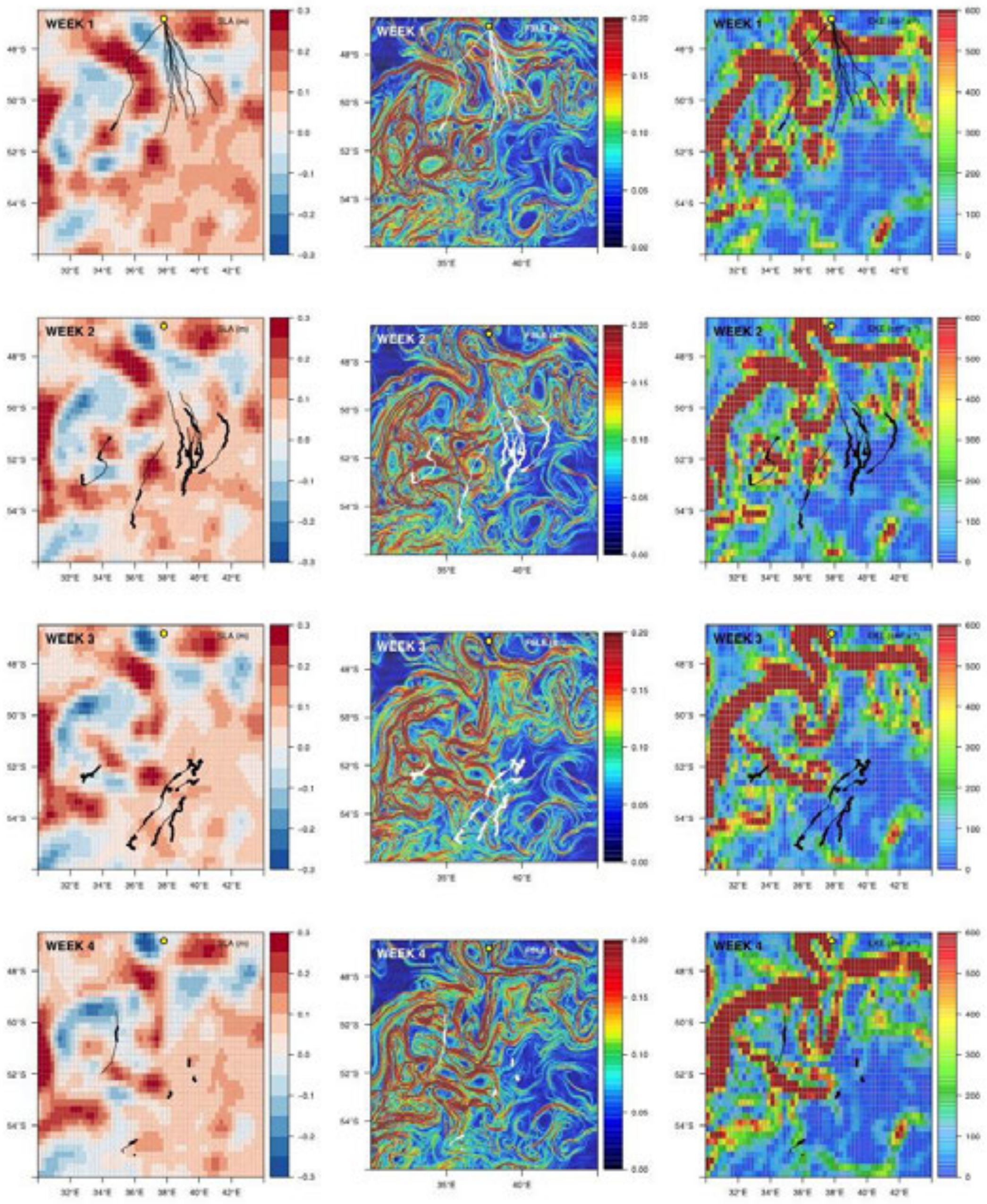


Figure S4.11. Weekly maps of sea level anomaly (SLA; m), finite-size Lyapunov exponent (FSLE; FLSE.d^{-1}) and eddy kinetic energy (EKE; cm^2.s^{-2}) showing tracks of rockhopper penguins during the 2014 pre-moult foraging trip. Black dots represent phases where daily travel speeds were less than the individual's mean

Table S4.1. Summary of tracking and diving data from GPS and time-depth recorders deployed on macaroni and rockhopper penguins from Marion Island during their pre-moult foraging trip

		GPS			TDR	
Species	Year	Number of tracks (male-female)	Complete tracks	Sampling interval	Number of datasets (male-female)	Sampling interval
Macaroni penguin	2012	5 (2-3)	3 (2-1)	12 h	3 (1-2)	3 s
	2013	6 (3-3)	4 (3-1)	90 min	*	*
	2014	9 (5-4)	0 (0-0)	60 min	4 (3-1)	5 s
	ALL	20 (10-10)	7 (5-2)		7 (4-3)	
Rockhopper penguin	2013	4 (4-0)	3 (3-0)	90 min	*	*
	2014	9 (5-4)	0 (0-0)	60 min	7 (4-3)	5 s
	ALL	13 (9-4)	3 (3-0)		7 (4-3)	

GPS – global positioning system; TDR – time-depth recorders; *no TDRs deployed

Table S4.2. Dates of deployment, departure, arrival, retrieval, duration and maximum range for macaroni and rockhopper penguins for the pre-moult foraging trip in 2012, 2013 and 2014

Species	Year	Penguin ID	Sex	Date deployed	Date departed	Date arrived	Date retrieved	% complete	Duration (days)	Max range (km)
Macaroni	2012	m12.1395	M	18-Feb	20-Feb	18-Mar	23-Mar	100	27	747
		m12.5015	F	17-Feb	18-Feb	01-Apr[a]	13-Apr	74	43	1181
		m12.5332	F	17-Feb	18-Feb	01-Apr[a]	13-Apr	74	43	1045
		m12.5333	F	18-Feb	19-Feb	23-Mar	23-Mar	100	33	999
		m12.6522	M	18-Feb	19-Feb	20-Mar	23-Mar	100	30	1116
	2013	m13.101	M	14-Feb	17-Feb	16-Mar	03-Apr	100	27	697
		m13.103	F	14-Feb	14-Feb	21-Mar[a]	03-Apr	83	35	843
		m13.107	M	14-Feb	16-Feb	15-Mar	03-Apr	100	27	728
		m13.111	F	14-Feb	17-Feb	18-Mar	03-Apr	100	29	784
		m13.119	M	14-Feb	17-Feb	17-Mar	03-Apr	100	28	844
		m13.96	F	14-Feb	16-Feb	16-Mar[a]	03-Apr	93	28	781
	2014	m14.51	F	17-Feb	18-Feb	-	23-Mar	-	-	991
		m14.52	F	17-Feb	18-Feb	03-Apr[b]	15-Apr	34	44	905[c]
		m14.55	M	17-Feb	18-Feb	-	30-Mar	-	-	770[c]
		m14.56	F	17-Feb	17-Feb	21-Mar[a]	23-Mar	75	32	884
		m14.58	F	17-Feb	18-Feb	-	27-Mar	-	-	657[c]
		m14.60	M	17-Feb	19-Feb	20-Mar[a]	21-Mar	69	29	813
		m14.61	M	17-Feb	17-Feb	21-Mar[b]	21-Mar	72	32	726
		m14.65	M	17-Feb	18-Feb	22-Mar[b]	23-Mar	66	32	838
		m14.68	M	17-Feb	19-Feb	03-Apr[b]	05-Apr	53	43	988
Rockhopper	2013	r13.112	M	07-Mar	08-Mar	07-Apr	15-Apr	100	30	618
		r13.115	M	07-Mar	07-Mar	29-Mar	15-Apr	100	22	401
		r13.20	M	06-Mar	08-Mar	03-Apr	15-Apr	100	26	697
		r13.41	M	06-Mar	08-Mar	02-Apr[a]	15-Apr	96	25	788
	2014	r14.107	F	02-Mar	02-Mar	30-Mar[b]	30-Mar	83	28	749
		r14.115	F	02-Mar	03-Mar	13-Apr[b]	15-Apr	51	41	614
		r14.119	F	02-Mar	06-Mar	08-Apr[b]	22-Apr	55	33	611
		r14.41	M	02-Mar	03-Mar	10-Apr[b]	15-Apr	53	38	929
		r14.53	M	02-Mar	05-Mar	-	15-Apr	-	-	906[c]
		r14.59	F	02-Mar	06-Mar	-	22-Apr	-	-	916[c]
		r14.66	M	02-Mar	03-Mar	15-Apr[b]	22-Apr	40	43	667[c]
		r14.69	M	02-Mar	04-Mar	15-Apr[b]	15-Apr	50	42	670
		r14.96	M	02-Mar	04-Mar	09-Apr[b]	15-Apr	50	36	882

[a]GPS incomplete, estimated using mean travel speed (see below); [b]GPS incomplete, determined from temperature data; [c]not used in analyses

Table S4.3. Environmental variables and sources

Variable	**Abbreviation**	**Spatial resolution**	**Temporal resolution**	**Source**
Chlorophyll-a concentration (mg.m^{-3})	-	0.04° x 0.04°	8 days	Aqua MODIS, NPP, L3SMI[a]
Eddy kinetic energy	EKE	0.33° x 0.33°	daily	Aviso[b,c]
Finite Size Lyapunov Exponent (d^{-1})	FSLE	0.04° x 0.04°	4 days	Aviso[b]; LOcean[d]; CTOH[e]
Sea level anomaly (m)	SLA	0.33° x 0.33°	daily	Aviso[b]
Sea surface height (m)	SSH	0.33° x 0.33°	daily	Aviso[b]
Sea surface temperature (°C)	SST	0.25° x 0.25°	daily	GHRSST Level 4 AVHRR_OI Global Blended Sea Surface Temperature Analysis[f]

[a] NASA Goddard Space Flight Center OceanColor Group (http://oceancolor.gsfc.nasa.gov/); data were downscaled to 0.25° x 0.25° and a monthly composite generated for the period two weeks prior to two weeks after departure (macaroni = 01/02 – 01/03, rockhopper = 14/02 – 17/03)

[b] Produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (www.aviso.altimetry.fr/duacs/)

[c] Downloaded as geostrophic velocities (U and V components) and computed as EKE = 0.5 x ($U^2 + V^2$)

[d] Laboratory of Oceanography and Climate: Experiments and Digital Approaches (www.locean-ipsl.upmc.fr)

[e] Center for Topographic studies of the Ocean and Hydrosphere (http://ctoh.legos.obs-mip.fr/)

[f] NASA Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center (http://podaac.jpl.nasa.gov/)

Table S4.4 (next page). Ranking of generalised additive models explaining variance in daily travel speed of macaroni and rockhopper penguins in relation to environmental covariates according to Akaike's information criterion (AIC). SSH and SST were not included in the same model as they were highly correlated ($r_s = 0.94 – 0.96$). The most parsimonious best fitting models ($\Delta AIC < 2$) are indicated for SSH and SST each year. NULL model includes individual identity as a random effect

	2012			**2013**			**2014**		
MODELS + ID	**AIC**	**ΔAIC**	**Dev. (%)**	**AIC**	**ΔAIC**	**Dev. (%)**	**AIC**	**ΔAIC**	**Dev. (%)**
SSH + SLA + CHLA + EKE	30.4	14.68	0.55	170.28	28.56	0.47	48.42	18.62	0.62
SSH + SLA + CHLA	**30.4**	**14.68**	**0.55**	179.6	37.88	0.43	47.8	18.00	0.62
SSH + SLA + EKE	35.28	19.56	0.51	175.8	34.08	0.44	48.43	18.63	0.62
SSH + SLA	35.28	19.56	0.51	179.58	37.86	0.43	43.13	13.33	0.62
SSH + CHLA + EKE	29.18	13.46	0.55	176.19	34.47	0.45	58.69	28.89	0.61
SSH + CHLA	29.18	13.46	0.55	188.1	46.38	0.42	54.53	24.73	0.6
SSH + EKE	36.36	20.64	0.5	186.02	44.30	0.41	57.68	27.88	0.61
SSH*SLA + CHLA + EKE	29.75	14.03	0.55	172.29	30.57	0.48	48.7	18.90	0.63
SSH*SLA + CHLA	29.83	14.11	0.55	183.27	41.55	0.46	44.9	15.10	0.63
SSH*SLA + EKE	37.63	21.91	0.51	172.29	30.57	0.48	45.75	15.95	0.63
SSH*SLA	37.63	21.91	0.51	183.26	41.54	0.46	42.13	12.33	0.62
SSH*CHLA + SLA + EKE	36.4	20.68	0.55	**158.26**	**16.54**	**0.51**	47.06	17.26	0.63
SSH*CHLA + SLA	36.4	20.68	0.55	167.26	25.54	0.49	44.64	14.84	0.62
SSH*CHLA + EKE	38.06	22.34	0.54	165.56	23.84	0.49	60.76	30.96	0.61
SSH*CHLA	38.06	22.34	0.54	173.62	31.90	0.47	60.24	30.44	0.61
SSH*EKE + CHLA + SLA	31.82	16.10	0.54	176.48	34.76	0.47	**35.82**	**6.02**	**0.63**
SSH*EKE + SLA	31.82	16.10	0.54	176.47	34.75	0.47	40.58	10.78	0.63
SSH*EKE + CHLA	35.4	19.68	0.52	180.75	39.03	0.45	53.29	23.49	0.62
SSH*EKE	35.09	19.37	0.55	181.49	39.77	0.44	53.72	23.92	0.62
SST + SLA + CHLA + EKE	27.63	11.91	0.56	178.64	36.92	0.42	30.96	1.16	0.63
SST + SLA + CHLA	27.63	11.91	0.56	197.15	55.43	0.39	30.96	1.16	0.63
SST + SLA + EKE	29.56	13.84	0.53	178.64	36.92	0.42	30.96	1.16	0.63
SST + SLA	29.56	13.84	0.53	196.89	55.17	0.39	30.96	1.16	0.63
SST + CHLA + EKE	27.63	11.91	0.56	178.64	36.92	0.42	29.81	0.01	0.63
SST + CHLA	27.63	11.91	0.56	197	55.28	0.38	29.81	0.01	0.63
SST + EKE	29.56	13.84	0.53	178.64	36.92	0.42	29.81	0.01	0.63
SST*SLA + CHLA + EKE	33.82	18.10	0.54	183.53	41.81	0.45	38.61	8.81	0.63
SST*SLA + CHLA	33.82	18.10	0.54	200.78	59.06	0.41	37.61	7.81	0.63
SST*SLA + EKE	37.9	22.18	0.52	183.53	41.81	0.45	38.61	8.81	0.63
SST*SLA	37.9	22.18	0.52	202.64	60.92	0.41	37.61	7.81	0.63
SST*CHLA + SLA + EKE	30.87	15.15	0.56	171.56	29.84	0.47	32.09	2.29	0.63
SST*CHLA + SLA	30.87	15.15	0.56	184.95	43.23	0.44	32.14	2.34	0.63
SST*CHLA + EKE	30.87	15.15	0.56	171.56	29.84	0.47	31.46	1.66	0.63
SST*CHLA	30.87	15.15	0.56	184.95	43.23	0.44	31.23	1.43	0.63
SST*EKE + CHLA + SLA	15.72	0.00	0.61	141.72	0.00	0.54	32.05	2.25	0.63
SST*EKE + SLA	15.72	0.00	0.61	**141.72**	**0.00**	**0.54**	32.05	2.25	0.63
SST*EKE + CHLA	15.72	0.00	0.61	148.22	6.50	0.52	32.59	2.79	0.63
SST*EKE	**15.72**	**0.00**	**0.61**	173.62	31.90	0.47	60.24	30.44	0.61
CHLA	102.76	87.04	0.24	262.45	120.73	0.2	290.48	260.68	0.2
EKE	88.89	73.17	0.29	258.91	117.19	0.18	280.09	250.29	0.22
SLA	100.29	84.57	0.23	291.47	149.75	0.05	314.76	284.96	0.14
SSH	36.36	20.64	0.5	191.08	49.36	0.4	53.08	23.28	0.6
SST	29.56	13.84	0.53	196.39	54.67	0.37	**29.8**	**0.00**	**0.63**
NULL	107.52	91.80	0.17	302.75	161.03	0.01	348.1	318.30	0.03

CHAPTER 5

Trophic ecology of sympatric crested penguins during the pre-moult period

Abstract

Niche partitioning plays an important role in minimising interspecific competition for resources. Using carbon and nitrogen stable isotopic analysis of feathers, trophic niche partitioning between macaroni penguins and eastern rockhopper penguins breeding at the Prince Edward Islands was investigated during the critical pre-moult period over five consecutive years (2011 to 2015). Both species consistently foraged immediately south of the Antarctic Polar Front, with macaroni penguins foraging farther south in years of reduced primary productivity, minimising spatiotemporal overlap between species. Macaroni penguins consistently foraged at a higher trophic level than rockhopper penguins, indicating trophic niche differentiation. Male rockhopper penguins fed at a higher trophic level than females, but macaroni penguins showed no differences between sexes. The observed dietary differences, partial allochrony and species-specific spatial responses to reduced primary productivity (i.e. prey availability) indicate that macaroni and rockhopper penguins exhibit contrasting foraging strategies that limit interspecific competition during the pre-moult period.

Introduction

The ecological niche is defined as the role or position of a species in its environment, particularly with respect to the utilisation of resources needed to survive and reproduce. In cases where sympatric species compete for a limited resource, ecological theory predicts that each species should evolve to exploit different parts of the resource (Hardin 1960). Niche partitioning may occur along several ecological axes (Hutchinson 1957), including spatial (e.g. horizontal or vertical segregation), temporal (e.g. asynchrony in peak resource use) and/or trophic (e.g. dietary differences) (Trivelpiece et al. 1987; Field et al. 2005; Nakano et al. 1999).

Penguins (Spheniscidae) are one of the most numerous mesopelagic predators in the Southern Ocean, consuming more than 23 million tonnes of marine resources every year (Brooke 2004). The most diverse and abundant group is the crested penguins (genus Eudyptes), ranging from temperate to Antarctic climates (Williams 1995). Eudyptids breed sympatrically at many localities, usually involving the smaller rockhopper and the larger royal, erect-crested or macaroni penguins (Warham 1975). Most eudyptids occupy broadly similar ecological niches, feeding primarily on swarming crustaceans and myctophid fish in offshore waters (Cooper et al. 1990). Owing to the high potential for interspecific competition for resources, sympatric eudyptids provide a good model by which to explore niche partitioning.

Approximately 302 000 and 80 000 pairs of macaroni and eastern rockhopper penguins, respectively, breed at the Prince Edward Islands in the Indian Ocean sector of the Southern Ocean (Crawford et al. 2009). During the breeding season, diet and foraging areas overlap considerably (Brown 1987; Brown and Klages 1987; Adams and Brown 1989), with the only major difference being that macaroni penguins commence breeding two to three weeks earlier (Brown 1987). This difference extends into the pre-moult period, when penguins must head to sea to replenish body condition and fatten up for their annual moult ashore. As penguins lose 40 to 50 % of their body mass during the moult (Brown 1986), finding sufficient resources during the pre-moult foraging trip is critical, as failure to do so may impact survival. In such circumstances it is expected that each species should maximise foraging gain by adopting strategies that minimise energetic costs, such as avoiding interspecific competition for resources. Although macaroni and rockhopper penguins exhibit similar habitat preferences during their month-long foraging trip to waters 400 to 1000 km south of the islands, temporal segregation exists for the initial two to three weeks (Chapter 4). However, potential interspecific competition may still occur while both species are concurrently at sea, particularly in years when reduced productivity prolongs temporal overlap (Chapter 4). It is possible that trophic niche differentiation may further reduce interspecific competition for resources; however, few studies have focused on dietary comparisons during this period (Jaeger and Cherel 2011).

In this chapter, I used stable isotope ratios in the feathers of macaroni and rockhopper penguins at the Prince Edward Islands to investigate niche partitioning during the pre-moult period over five consecutive years (2011 to 2015). As knowledge of how penguins respond to fluctuations in the marine environment is vital to better understand their susceptibility to ecosystem changes, I also investigated inter-annual variation of stable isotopic ratios and niche overlap in relation to at-sea conditions. I predicted that in years of reduced prey availability, penguins would adopt strategies that minimise competition for resources.

Methods

Data collection

Marion Island, the larger of the two Prince Edward Islands, supports 96 and 53% of the population of macaroni and rockhopper penguins breeding at the islands, respectively (Crawford et al. 2009). Penguins depart for the pre-moult foraging trip in mid-February and early March, respectively, returning in late March or April (Chapter 4). Feathers were collected in April from moulting penguins at two colonies, Funk Bay and Ship's Cove, in April 2012, 2013 and 2015. As melanin is known to influence the isotopic values of feathers (Michalik et al. 2010), only white feathers were used in this study. Old and new feathers were plucked from the breast of each individual and stored in sealed bags at room temperature until laboratory analysis. As feathers remain chemically inert after synthesis, old and new feathers represent the previous and current year's pre-moult foraging trip, respectively (Jaeger and Cherel 2011). Thus, I could investigate the diet of the eudyptids in 2011, 2012, 2013, 2014 and 2015. Each bird was sexed based on bill morphometrics (Williams and Croxall 1991; Poisbleau et al. 2010), except in 2013, when the sex of macaroni penguins was not recorded. See Chapter 2 for details on sample preparation and stable isotope analyses. Replicate measurements of internal laboratory standards indicated minimal standard deviations (Merck gel: $\delta^{13}C = 0.2‰$, $\delta^{15}N < 0.1‰$; valine: $\delta^{13}C = 0.1‰$, $\delta^{15}N = 0.1‰$; seal bone: $\delta^{13}C = 0.2‰$, $\delta^{15}N < 0.1‰$).

Environmental data

Surface chlorophyll-a concentrations (chl a; $mg.m^{-3}$) and SSTA (°C) were used as monthly composites. As conditions leading up to the pre-moult period may influence prey availability, mean chl a concentrations (proxy for primary productivity) and mean SSTA within a region corresponding to the core pre-moult foraging area of penguins (49 to 54° S, 33 to 40° E; Chapter 4) were calculated for January, February and March each year. Means were calculated using the 'calc' function in the R package 'raster'. The southern extent of the APF was characterised using the -0.63 m SSH contour (Swart et al. 2010).

Statistical analysis

Data were analysed using R (version 3.1.0; R Development Core Team 2016). To validate the assumption that old and new feathers represented the previous and current pre-moult periods, respectively, linear models (LMs) were used to test for the influence of feather age on $\delta^{13}C$ and $\delta^{15}N$ in feathers representative of the 2012 pre-moult foraging trip. Differences in $\delta^{13}C$ and $\delta^{15}N$ between species and sexes were determined using linear mixed-effects models (LMEs) (R package 'nlme'; Pinheiro et al. 2013). To account for repeated observations from the same individual (old and new feathers) and the potential influence of sampling year, individual identity nested within year was included as a random effect. Within-year comparisons of $\delta^{13}C$ and $\delta^{15}N$ between species and sexes were made using LMs. All model residuals were checked to ensure normality. Bivariate ellipses were used to plot the isotopic niche of each species using the 'Stable Isotopes Bayesian ellipses in R' (SIBER) package

(Jackson et al. 2011). The total and core niche space and overlap between species were calculated within each year and overall, with a correction for small sample sizes. To investigate potential drivers of inter-annual variation, mean annual $\delta^{13}C$ and $\delta^{15}N$ of each species were modeled in relation to mean primary productivity and SST anomalies during January, February and March using LMs. Models were weighted by the standard deviation of $\delta^{13}C$ and $\delta^{15}N$ each year to account for differences in variation between years. Model selection was performed according to Akaike's information criterion (AIC), with the most parsimonious of the top models ($\Delta AIC < 4$) selected. To reconstruct the diet of penguins during the pre-moult foraging trip, a two-source isotopic mixing model was used (Phillips 2001, Forero et al. 2002). This simplistic approach uses a single isotopic axis to estimate the relative contribution of two sources to consumer diet. This method was preferred over the two-axis approach ($\delta^{13}C$ and $\delta^{15}N$) as the $\delta^{13}C$ values of available isotopic data of potential prey species were unlikely to be representative of prey at known foraging areas south of the APF (Chapter 4). Mean $\delta^{15}N$ values of the two dominant prey groups, crustaceans and fish (Adams and Brown 1989), were calculated based on available isotopic data (Table S5.1). Owing to the potential variation of isotopic signatures within prey groups (i.e. according to species, life history stage, year, locality), $\delta^{15}N$ values used are not definite but approximate. The following equation was used to estimate relative contribution of fish in the diet from isotopic data:

$$P_A\,(\%) = 100 \times (D_T - D_B)/(D_A - D_B)$$

where P_A is the proportion of source A in consumer diet, D_T is the isotopic value of consumer tissue, D_A and D_B are the isotopic values of sources A and B (fish and crustaceans), respectively, after the addition of discrimination factors. I used the mean of known discrimination factors for feathers derived from captive penguin studies: $\Delta\delta^{15}N_{\text{diet feathers}} = 4.1 \pm 0.7$ ‰ (Table S5.2; Connan et al. 2016).

Results

Feathers were collected from 28 macaroni and 40 rockhopper penguins, representing 53[*] and 80 pre-moult foraging trips, respectively. Feather age (old and new) had no influence on isotopic signatures of macaroni ($\delta^{13}C$: $t = -2.0$, $p = 0.07$; $\delta^{15}N$: $t = 1.1$, $p = 0.29$) and rockhopper penguins ($\delta^{13}C$: $t = 1.4$, $p = 0.19$; $\delta^{15}N$: $t = 0.2$, $p = 0.86$). No correlations between $\delta^{13}C$ and $\delta^{15}N$ were present in macaroni ($t = -0.3$, $p = 0.75$) or rockhopper penguins ($t = 0.01$, $p = 0.99$).

Interspecific differences

Overall, the core isotopic niche space of both species was 0.39 ‰^{2} with an overlap of 0.01 ‰^{2} (Fig. 5.1). Within-year comparisons also revealed minimal overlap (Fig. 5.1; Table S5.3). Feathers of rockhopper penguins were $\delta^{13}C$ enriched by 0.2 ± 0.0 ‰ (mean ± SD) compared to those of macaroni penguins ($t = 6.2$, $p < 0.001$; Table 5.1). This difference varied between years, being similar in 2012, 2013 and 2015, but significantly higher in rockhopper penguins

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[*] both old and new feathers (representing previous and current year's pre-moult foraging trips) could not be sampled from all penguins

in 2011 and 2014 (Fig. 5.1). Overall, feathers of macaroni penguins were $\delta^{15}N$ enriched by 0.8 ± 0.1 ‰ compared to rockhopper penguins ($t = 9.7$, $p < 0.001$; Table 5.1). This difference varied between years, being similar in 2011 and 2013, but significantly higher in macaroni penguins in 2012, 2014 and 2015 (Fig. 5.1). $\delta^{15}N$ of both macaroni and rockhopper penguins reflected a mixed diet of crustaceans and myctophid fish, with macaroni penguins consuming ~ 40 % more fish (Table 5.1).

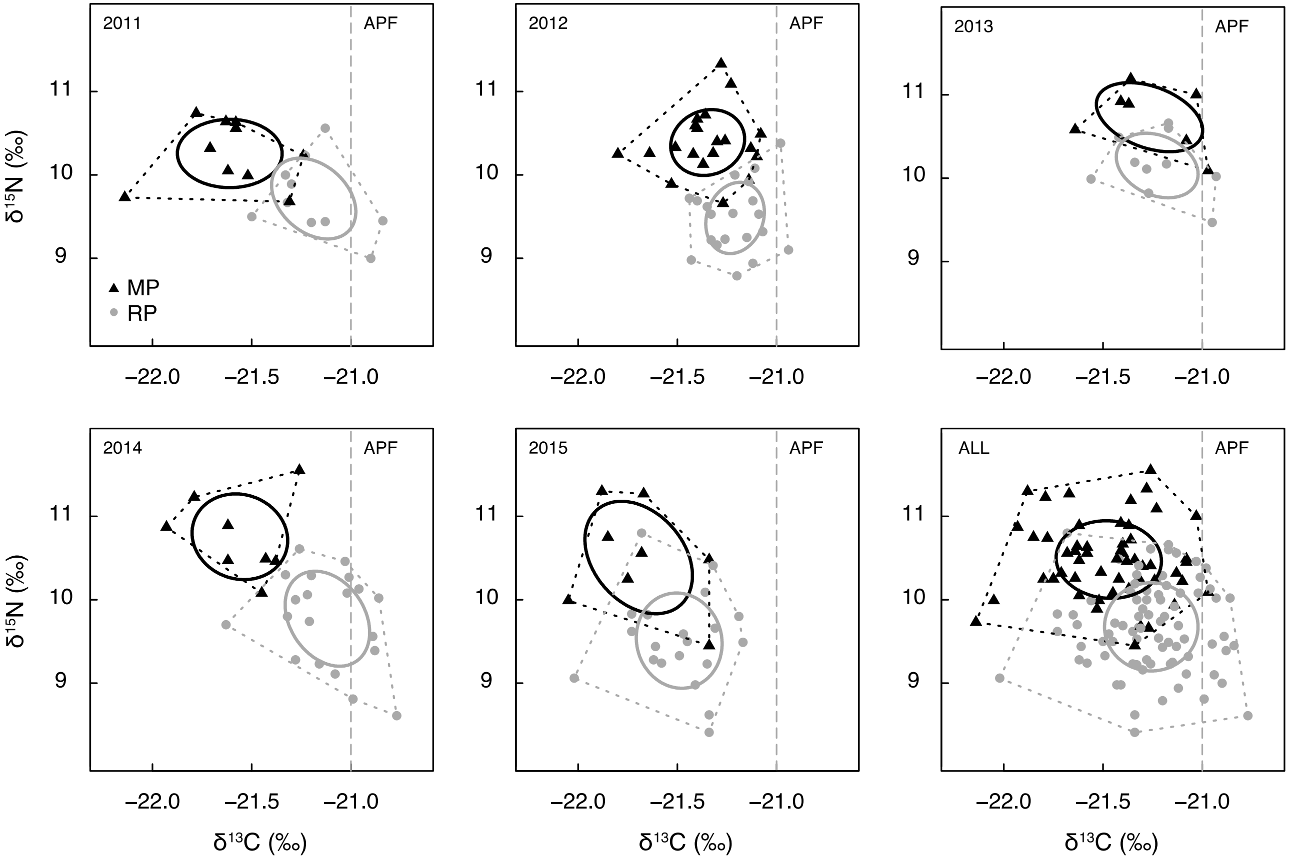


Fig. 5.1. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios in feathers of macaroni (MP; black triangle) and eastern rockhopper (RP; grey circle) penguins. Total isotopic niche space (dotted convex hulls), core isotopic niche space corrected for small samples size (solid ellipses) and the estimated position of the APF (dashed vertical grey line) are shown

Table 5.1. Summary of carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios in feathers of macaroni and eastern rockhopper penguins in 2011 to 2015 and the estimated percentage of fish in the diet (mean ± SD (range)) (see Methods)

Species	Sex	N individuals (n feathers)	δ^{13}C (‰)	δ^{15}N (‰)	C:N ratio	Percentage of fish in diet	
Macaroni penguin	Male	10 (20)	-21.5 ± 0.2	10.5 ± 0.5	3.12 ± 0.03	51 ± 11	(30–77)
	Female	8 (16)	-21.5 ± 0.3	10.3 ± 0.5	3.12 ± 0.03	46 ± 12	(25–70)
	Both	28 (53)	-21.5 ± 0.3	10.5 ± 0.5	3.12 ± 0.03	50 ± 11	(25–77)
Eastern rockhopper penguin	Male	21 (42)	-21.3 ± 0.2	9.9 ± 0.4	3.11 ± 0.02	37 ± 11	(19–58)
	Female	19 (38)	-21.2 ± 0.2	9.4 ± 0.5	3.11 ± 0.02	23 ± 11	(0–43)
	Both	40 (80)	-21.3 ± 0.2	9.7 ± 0.5	3.11 ± 0.02	30 ± 13	(0–58)

Sexual differences

Macaroni penguins exhibited no sexual differences in δ^{13}C ($t = 0.8$, $p = 0.45$) or δ^{15}N ($t = 0.5$, $p = 0.65$) overall, or in any within-year comparison when data were available (Fig. 5.2; Table S5.4). Rockhopper penguins also lacked sexual differences in δ^{13}C overall ($t = 0.5$, $p = 0.62$) and in each year (Fig. 5.2; Table S5.4), but δ^{15}N of male rockhopper penguins was 0.6 ± 0.1‰ higher than females ($t = 5.8$, $p < 0.001$). This was consistent for all within-year comparisons except in 2011, when both sexes had similar δ^{15}N values (Table S5.4).

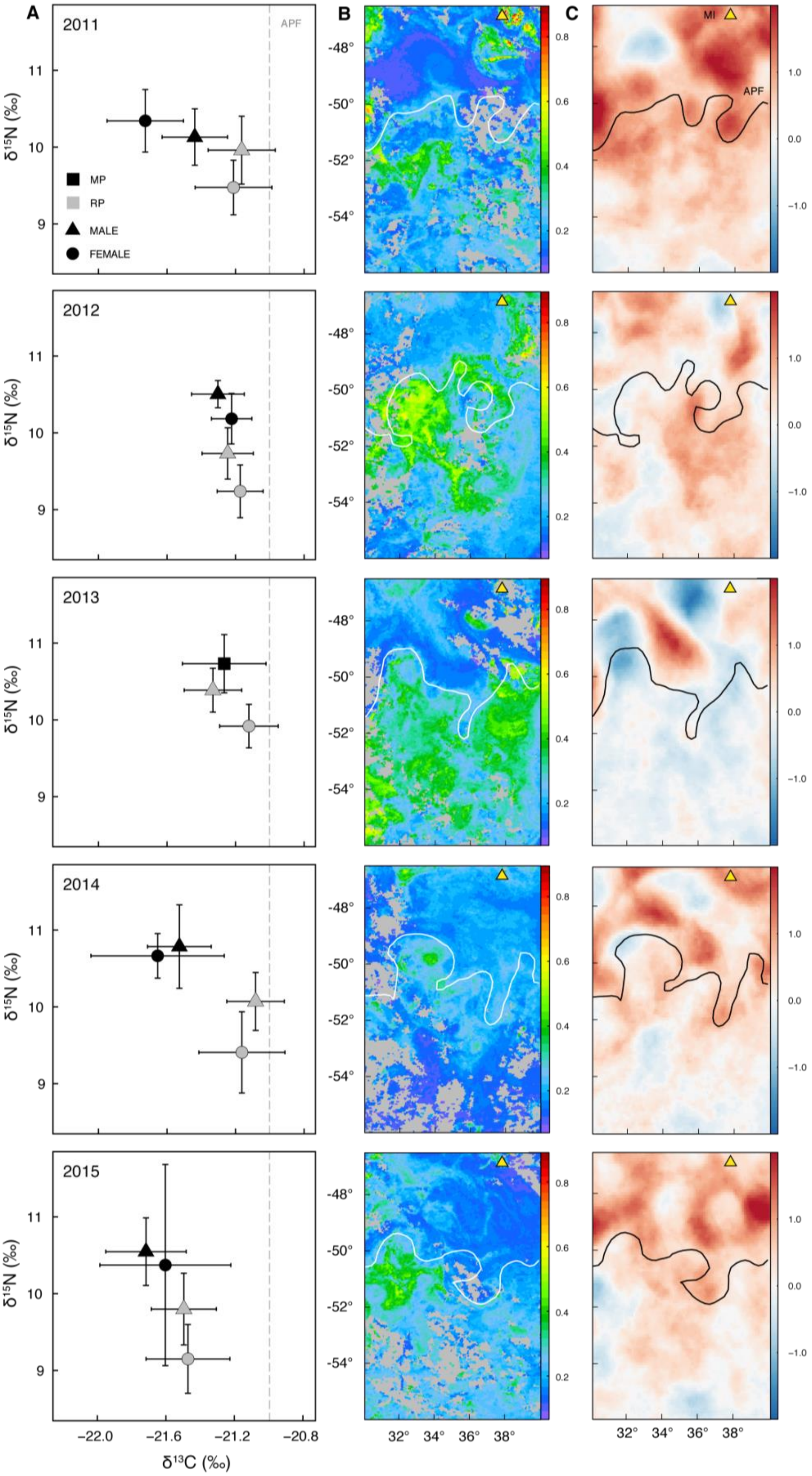
Inter-annual variation

Primary productivity was higher in 2012 and 2013 compared to other years (Fig. 5.2). Mean annual $\delta^{13}C$ of macaroni penguins was significantly related to primary productivity in January and February (Table S5.5), with February explaining the most variation. When years were categorised into high and low productivity in February (> 0.30 mg.m^{-3} versus <0.22 mg m^{-3}), feathers of macaroni penguins were $\delta^{13}C$ enriched by 0.3 ± 0.1‰ in more productive years ($t = 5.2$, $p < 0.05$). There were no significant trends in $\delta^{15}N$ of macaroni penguins or $\delta^{13}C$ and $\delta^{15}N$ of rockhopper penguins in relation to primary productivity (Table S5.5). Similarly, there were no trends in mean annual $\delta^{13}C$ or $\delta^{15}N$ in relation to SST anomalies (Table S5.5). When years were categorised into cooler (< 0 °C) and warmer (>0.4°C) SST anomalies in February, feathers of rockhopper penguins were $\delta^{15}N$ enriched by 0.5 ± 0.2 ‰ in cooler years, i.e. 2013 ($t = 3.2$, $p < 0.05$). $\delta^{13}C$ of macaroni penguins was significantly higher in 2012 and 2013 than 2011 and 2015, with 2014 intermediate between these two sets of years (Table 5.2). There were no inter-annual differences in $\delta^{15}N$ of macaroni penguins (Table 5.2). $\delta^{13}C$ of rockhopper penguins was significantly lower in 2015 than other years, and $\delta^{15}N$ was significantly higher in 2013 compared to 2012 and 2015, but similar for other comparisons (Table 5.2).

Table 5.2. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios in feathers of macaroni and eastern rockhopper penguins (mean ± SD). ^{a,b}Different letters indicate significant within-species inter-annual differences ($p < 0.05$)

Species	Year	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ratio
Macaroni penguin	2011	10	-21.6 ± 0.3^{a}	10.3 ± 0.4	3.12 ± 0.02
	2012	20	-21.4 ± 0.2^{b}	10.4 ± 0.4	3.12 ± 0.03
	2013	7	-21.3 ± 0.2^{b}	10.7 ± 0.4	3.10 ± 0.01
	2014	8	-21.6 ± 0.2^{ab}	10.8 ± 0.5	3.15 ± 0.03
	2015	8	-21.7 ± 0.3^{a}	10.5 ± 0.6	3.13 ± 0.03
Eastern rockhopper penguin	2011	10	-21.2 ± 0.2^{b}	9.7 ± 0.5^{ab}	3.10 ± 0.01
	2012	20	-21.2 ± 0.1^{b}	9.5 ± 0.4^{a}	3.12 ± 0.02
	2013	10	-21.2 ± 0.2^{b}	10.2 ± 0.4^{b}	3.12 ± 0.03
	2014	20	-21.1 ± 0.2^{b}	9.8 ± 0.6^{ab}	3.11 ± 0.02
	2015	20	-21.5 ± 0.2^{a}	9.5 ± 0.6^{a}	3.13 ± 0.02

Fig. 5.2 (next page). (a) Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes in feathers of male (triangle) and female (circle) macaroni (MP; black) and eastern rockhopper (RP; grey) penguins representative of diet during the pre-moult foraging trip across 5 consecutive years. Mean (b) chl a concentrations (mg.m^{-3}) and (c) SST anomalies (°C) during February each year, showing positions of the APF and Marion Island (MI; yellow triangle)


A
B
C
2011
2012
2013
2014
2015
APF
MI
δ15N (‰)
δ13C (‰)
MP
RP
MALE
FEMALE
11
10
9
−22.0
−21.6
−21.2
−20.8
-48°
-50°
-52°
-54°
32°
34°
36°
38°
0.8
0.6
0.4
0.2
1.0
0.0
−1.0

Discussion

This study provides evidence for trophic niche differentiation between macaroni and rockhopper penguins during the pre-moult period. By monitoring resource use over 5 successive years, it was possible to compare trophic niches across a range of environmental conditions, revealing species-specific responses to changes in primary productivity. However, niche overlap was very limited, irrespective of inter-annual variation in productivity in their preferred foraging areas. This is also the first time consistent sexual differences in the diet of rockhopper penguins have been observed during the pre-moult foraging trip, which contrasts with the lack of sexual differences among macaroni penguins. Potential reasons for these inter- and intraspecific niche differences are discussed below.

Trophic differences

The consistently higher trophic level at which macaroni penguins foraged during this study is indicative of a greater proportion of myctophid fish in the diet and/or potentially larger prey, as larger individuals of some fish and crustaceans may be δ^{15}N enriched (Pakhomov et al. 1994; Schmidt et al. 2003). This concurs with dietary comparisons during the breeding season at Marion Island and at other localities, where macaroni penguins may consume nearly twice as much fish as rockhopper penguins (Cooper et al. 1990). The size class of myctophids consumed may also differ; for example, at the Crozet Islands, macaroni penguins feed mainly on adult myctophids whereas rockhopper penguins mainly target post-larval myctophids (Cherel et al. 2010). Dietary differences may be linked to vertical distribution of prey, as macaroni penguins spend more time foraging at >80 m (22%) than rockhopper penguins (4%) during the pre-moult foraging trip (Chapter 4). Diving deeper may increase encounters with myctophid fish, as macaroni penguins at Heard Island consumed more fish when performing deeper dives (Deagle et al. 2008), and specialist myctophid-feeding king penguins dive to considerably deeper depths (Adams and Brown 1989; 100 to 200 m, Scheffer et al. 2012). Bill size might also influence prey selection; macaroni penguins have larger bills (Agnew and Kerry 1995) that may better equip them to handle larger prey. Ultimately, dietary differences between macaroni and rockhopper penguins appear to be a function of body size, as larger-bodied animals are able to load greater O_2 stores and have lower mass-specific metabolic rates (Schreer and Kovacs 1997), presumably resulting in species-specific optimal foraging depths, such as with pygoscelids (Wilson 2010). Being larger, macaroni penguins also have higher energetic requirements (Brown 1989) and thus it may be more energy-efficient to feed on energy-dense, lipid-rich myctophids (Cherel and Ridoux 1992; Meynier et al. 2008) to acquire sufficient energy stores for their upcoming moult ashore. Compared to sympatric macaroni and rockhopper penguins at the Crozet Islands, conspecifics in this study fed at a higher trophic level (Fig. 5.3), which either indicates a greater availability of higher trophic level prey or a higher baseline $\delta^{15}N$ in waters south of the Prince Edward Islands. Macaroni penguins at South Georgia fed at a similar trophic level to macaroni penguins from Marion Island. The higher $\delta^{15}N$ of southern rockhopper penguins *E. c. chrysosome* at the Falklands is likely due to differences in stable isotopic values at the base of the food web influenced by productivity over the Patagonian Shelf (Dehnhard et al. 2011).

Spatial differences

Previous studies estimate the isotopic position of the APF as -21.2‰ $\delta^{13}C$ based on data from king penguins (Cherel and Hobson 2007) and wandering albatrosses *Diomedea exulans* (Jaeger et al. 2010). Given that macaroni and rockhopper penguins forage almost exclusively in Antarctic zone waters south of the APF during the pre-moult trip (Chapter 4), and that most $\delta^{13}C$ values are -21.8 to -21.0‰ $\delta^{13}C$ (Fig. 5.1), these values are likely representative of Antarctic zone waters. Conspecifics at Crozet and South Georgia also feed in Antarctic waters (see Chapter 4) and feather $\delta^{13}C$ has a similar range to those in the present study (Fig. 5.3). It is possible that species-specific tissue characteristics (e.g. metabolic routing, turn-over rates and discrimination factors) may result in different estimates of $\delta^{13}C$ at the APF, and thus I redefined the isotopic position of the APF for macaroni and rockhopper penguins for this study as -21‰ $\delta^{13}C$. This indicates that rockhopper penguins consistently foraged in Antarctic zone waters south of the APF (with the exception of 2015), whereas macaroni penguins foraged in similar areas in productive years but farther south in less productive years (Fig. 5.2). Therefore, although spatial overlap between species was high in productive years, the shorter foraging trips associated with such conditions (Chapter 4) means that spatiotemporal overlap was negligible. Similarly, in years of reduced productivity when both species spend more time concurrently at sea (Chapter 4), spatial overlap would have been reduced because macaroni penguins forage farther south. It is important to note that although variation in $\delta^{13}C$ may be attributed to phytoplankton-driven shifts in baseline $\delta^{13}C$ of the food web (Jaeger and Cherel 2011), the contrasting variation of $\delta^{13}C$ in macaroni and rockhopper penguin feathers (Fig. 5.2) indicates that fluctuations in $\delta^{13}C$ are primarily driven by species-specific behavioral responses to productivity rather than productivity itself. These contrasting responses may be related to species-specific energetic requirements and dietary preferences that force the larger macaroni penguins to travel farther south in search of more energy-rich myctophids.

Sexual differences

Although macaroni penguins did not exhibit sex-specific feeding differences, male rockhopper penguins fed at a higher trophic level compared to females, indicating a larger contribution of fish and/or larger-sized prey in the diet. As both macaroni and rockhopper penguins exhibit similar degrees of sexual dimorphism (Agnew and Kerry 1995), it is surprising that sex has a contrasting influence on diet. Macaroni penguins at other localities also lack sexual differences in diet during the pre-moult period (Thiebot et al. 2014; Horswill et al. 2016), as well as during the breeding period (Bearhop et al. 2006; Horswill et al. 2016). Although male southern rockhopper penguins in the southwest Atlantic Ocean forage at a higher trophic level than females during the late winter and incubation periods (Dehnhard et al. 2011; Ludynia et al. 2013), no sexual differences in diet were recorded during the pre-moult period (Dehnhard et al. 2011). Sexual differences in diet exist in Adélie, gentoo and Magellanic penguins *Spheniscus magellanicus* (Ainley and Emison 1972; Volkman et al. 1980, Forero et al. 2002), as well as other sexually dimorphic seabirds (Kato et al. 1996; Forero et al. 2005; Quillfeldt et al. 2011), with larger males generally feeding on larger and/or higher trophic level prey.

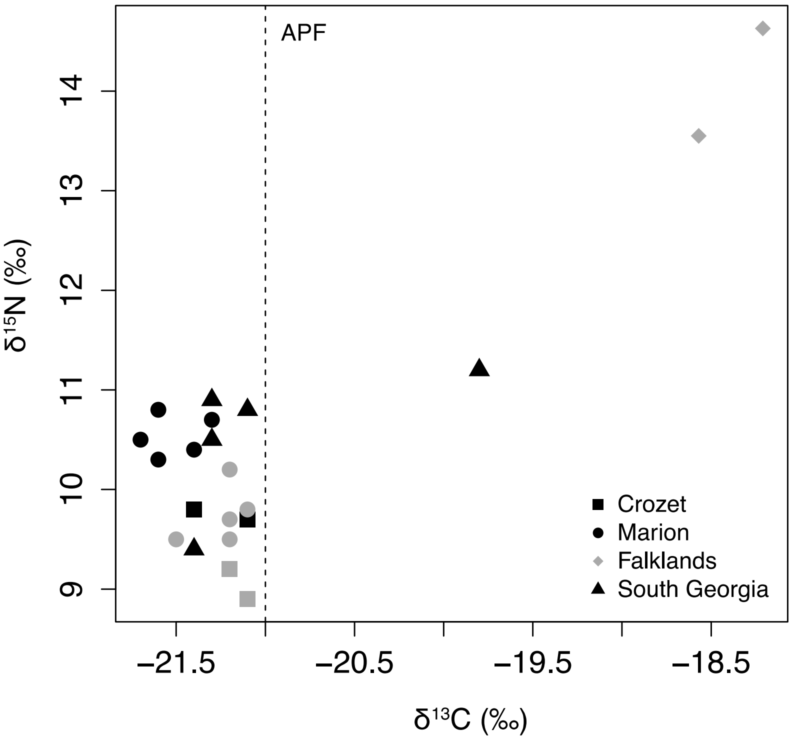


Fig. 5.3. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes in feathers of macaroni (black) and eastern/southern rockhopper penguins (grey) at Marion Island, Crozet (Jaeger and Cherel 2011), Falklands (Dehnhard et al. 2011) and South Georgia (Horswill et al. 2016)

Environmental drivers

The fact that macaroni penguins foraged farther south during years of reduced primary productivity suggests that such conditions are likely associated with reduced availability of myctophid fish immediately south of the APF. With the exception of 2012, poor productivity coincided with strong positive SST anomalies near the APF (Fig. 5.2). Warmer surface waters may force ectothermic myctophids to migrate farther south or deeper in the water column, making them less accessible to penguins (Péron et al. 2012). Conversely, when cooler waters were present in 2013, rockhopper penguins foraged at a higher trophic level (Fig. 5.2), possibly due to increased accessibility to fish. Warmer SSTs have been linked to a global shift of rockhopper penguins to a lower trophic level diet over the last century (Hilton et al. 2006), which is suggested to have caused the decline of rockhopper penguin populations in the sub-Antarctic (Cunningham and Moors 1994). However, extremely cool SST anomalies are also known to negatively affect the survival of rockhopper penguins at the Falklands (Dehnhard et al. 2013), and local warming has been shown to have a positive effect on the survival of adult macaroni penguins at South Georgia (Horswill et al. 2014), suggesting that the effects of SST on the distribution and abundance of preferred prey may be regional. It is also important to consider that the foraging strategies that penguins have evolved to buffer the consequences of environmental variability may be regional. For instance, macaroni penguins at South Georgia exhibited high intrapopulation variation and low sensitivity to fluctuations in krill density (Horswill et al. 2016), which contrasts with the low intrapopulation variation and high sensitivity to primary productivity (i.e. prey availability) observed in this study.

Conclusions

The trophic niche differentiation observed between macaroni and rockhopper penguins during the relatively unconstrained pre-moult period indicates that subtle, but inherently different dietary preferences exist between the 2 species. The combination of such differences with partial allochrony and species-specific spatial responses to reduced primary productivity/prey availability provides a better perspective of the overall niche differentiation in space, time and diet, limiting interspecific competition during the pre-moult period. As it is vital that penguins accumulate enough resources in order to endure the moult ashore and retain sufficient energy stores for their return to winter foraging areas, any changes in the availability of preferred prey during the pre-moult period may have severe consequences for adult survival. With the predicted southward shift of major fronts and increasing SST in the Southern Ocean (Hunt et al. 2001; Mélice et al. 2003), it is possible that penguins may have to travel farther and/or dive deeper to find sufficient energy-rich myctophids (Péron et al. 2012), exacerbating energetic constraints during the most critical stage of their annual cycle. Continued monitoring of penguin foraging behaviour during the pre-moult period coupled with annual survival estimates is needed to determine whether changes in at-sea conditions during the pre-moult period are key drivers of population dynamics in macaroni and rockhopper penguins at the Prince Edward Islands.

Supplementary material

Table S5.1. Carbon and nitrogen stable isotope ratios of potential prey species of macaroni and eastern rockhopper penguins (APF: Antarctic Polar Front; PEI: Prince Edward Islands)

Prey	**$\delta^{13}C$**	**$\delta^{15}N$**	**Location**	**Reference**
Crustaceans				
Euphausia vallentini	-20.0	5.2	Kerguelen	Cherel et al. (2008)
Euphausia vallentini	-20.9	2.95	PEI (downstream)	Kaehler et al. (2000)
Euphausia vallentini	-23.7	3.95	PEI (upstream)	Kaehler et al. (2000)
Euphausia frigida	-24.2	4.2	APF	Schmidt et al (2003)
Themisto gaudichaudii	-22.8	5.0	Kerguelen	Cherel et al. (2008)
Thysanoessa spp.	-22.2	4.8	APF	Schmidt et al (2003)
Average	**-22.3 ± 1.6**	**4.4 ± 0.8**		
Fish				
Krefftichthys anderssoni	-22.3	7.6	Kerguelen	Cherel et al. (2008)
Protomyctophum tenisoni	-22.1	8.1	Kerguelen	Cherel et al. (2010)
Electrona carlsbergi	-21.6	9.5	Kerguelen	Cherel et al. (2008)
Average	**-22.0 ± 0.4**	**8.4 ± 1.0**		

Table S5.2. Species-specific discrimination factors between penguin feathers and food taken from captivity studies (adapted from Connan et al. 2016)

Species	$\delta^{13}C$	$\delta^{15}N$	Reference
Gentoo penguin *Pygoscelis papua*	1.3 ± 0.5	3.5 ± 0.4	Polito et al. (2011)
Humboldt penguin *Spheniscus humboldti*	-	4.8	Mizutani et al. (1992)
King penguin *Aptenodytes patagonicus*	0.1	3.5	Cherel et al. (2005)
Rockhopper penguin *Eudyptes chrysocome*	0.1	4.4	Cherel et al. (2005)
Average	**0.5 ± 0.7**	**4.1 ± 0.7**	

Table S5.3. Core niche widths (‰^{2}) of macaroni and rockhopper penguins and overlap between species (following Jackson et al. 2011)

Year	Macaroni	Eastern rockhopper	Overlap (‰^{2})
2011	0.34	0.30	< 0.001
2012	0.23	0.19	< 0.001
2013	0.32	0.24	0.04
2014	0.39	0.36	< 0.001
2015	0.54	0.39	0.03
Overall	**0.39**	**0.39**	**0.01**

Table S5.4. Carbon and nitrogen stable isotope ratios in feathers of male and female macaroni and rockhopper penguins. Significance of within-year sex comparisons are shown; not significant (ns), $P < 0.05$ (*) and $P < 0.01$ (**). Sex of macaroni penguins in 2013 was unknown.

Species	Year	Sex	N	δ^{13}C (‰)		δ^{15}N (‰)		C:N
Macaroni penguin	2011	Male	4	-21.4 ± 0.2	ns	10.1 ± 0.4	ns	3.11 ± 0.01
		Female	6	-21.7 ± 0.2		10.3 ± 0.4		3.12 ± 0.01
	2012	Male	4	-21.3 ± 0.2	ns	10.5 ± 0.2	ns	3.10 ± 0.02
		Female	6	-21.2 ± 0.1		10.2 ± 0.3		3.10 ± 0.01
	2013	Both	7	-21.3 ± 0.2	-	10.7 ± 0.4	-	3.10 ± 0.01
	2014	Male	6	-21.5 ± 0.2	ns	10.8 ± 0.5	ns	3.14 ± 0.03
		Female	2	-21.7 ± 0.4		10.7 ± 0.3		3.17 ± 0.04
	2015	Male	6	-21.7 ± 0.2	ns	10.6 ± 0.4	ns	3.13 ± 0.03
		Female	2	-21.6 ± 0.4		10.4 ± 1.3		3.13 ± 0.03
Eastern rockhopper penguin	2011	Male	5	-21.2 ± 0.2	ns	10.0 ± 0.4	ns	3.10 ± 0.02
		Female	5	-21.2 ± 0.2		9.5 ± 0.4		3.09 ± 0.01
	2012	Male	10	-21.3 ± 0.1	ns	9.7 ± 0.3	**	3.12 ± 0.02
		Female	10	-21.2 ± 0.2		9.2 ± 0.3		3.12 ± 0.02
	2013	Male	5	-21.3 ± 0.2	ns	10.4 ± 0.3	*	3.13 ± 0.03
		Female	5	-21.1 ± 0.2		9.9 ± 0.3		3.11 ± 0.03
	2014	Male	11	-21.1 ± 0.2	ns	10.1 ± 0.4	**	3.10 ± 0.02
		Female	9	-21.2 ± 0.3		9.4 ± 0.5		3.11 ± 0.02
	2015	Male	11	-21.5 ± 0.2	ns	9.8 ± 0.5	**	3.11 ± 0.01
		Female	9	-21.5 ± 0.2		9.2 ± 0.4		3.12 ± 0.02

Table S5.5. Summary of best explanatory variables of carbon and nitrogen stable isotopes of macaroni and rockhopper penguins

Species		Chlorophyll-a concentration			Sea surface temperature anomalies			*P*-value	F-statistic	R^2
		JAN	FEB	MAR	JAN	FEB	MAR			
Macaroni	$\delta^{13}C$	+	+					0.005	203.2	0.99
	$\delta^{15}N$						+	0.06	8.9	0.66
Rockhopper	$\delta^{13}C$				+	+		0.15	5.9	0.71
	$\delta^{15}N$	+	+				+	0.25	8.5	0.85

CHAPTER 6

Where do crested penguins go in winter? Insights from tracking and stable isotopes

'Among the real mysteries that remain is the off-season life of the crested penguins. They all go to sea from between four to six months after they are finished with breeding and molting. What they do there, how they groom themselves, what social groupings they have, their feeding behaviour during that time – all these questions are open.'

James Gorman, The Complete Penguin, 1990

Abstract

During the austral winter, crested penguins spend 4 – 6 months entirely at sea. Knowledge of their foraging ecology during winter is fundamental to understanding potential drivers of population dynamics and how they might respond to climate-driven changes in the Southern Ocean. The lack of provisioning constraints during this period allows greater flexibility in terms of habitat selection, and provides an opportunity to compare habitat preferences of sympatric species and identify mechanisms that reduce potential intra- and interspecific competition. This chapter investigates the winter habitat use and trophic ecology of sympatric macaroni and eastern rockhopper penguins from the Prince Edward Islands. Movement data were collected using satellite transmitters and geolocation loggers and related to environmental covariates. Habitat selection models indicated that both species preferred waters with high eddy kinetic energy, weak sea level anomalies and the presence of submesoscale filaments, revealing the importance of the mesoscale environment in structuring prey availability. During the core winter months (June to August), macaroni penguins targeted areas characterised by cooler waters (~ 3 °C) near the Southern Antarctic Circumpolar Current Front, while rockhopper penguins foraged in slightly warmer waters of the Polar Frontal Zone (5-6 °C), resulting in spatial segregation. During late winter (September/October), carbon and nitrogen stable isotopes revealed that both species foraged in the Polar Frontal Zone, and typically at a lower trophic level than in summer; except female rockhopper penguins that foraged at a higher trophic level. Although isotopic niche overlap was high during late winter, the wider spatial niche of female rockhopper penguins reduced potential intraspecific competition. Foraging areas and trophic level of macaroni

penguins, as inferred from stable isotopes, did not influence mass on arrival, but both geolocation and stable isotope data revealed that rockhopper penguins that fed in cooler waters, farther south, returned to the colony in better condition (greater body mass).

Introduction

Penguins represent more than 90 % of seabird biomass in the Southern Ocean, consuming more than 23 million tons of marine resources every year (Brooke 2004). Crested penguins (*Eudyptes*) are the most abundant and diverse group of penguins, ranging from temperate to Antarctic waters (Williams 1995). During the breeding season, eudyptids are constrained to forage close to land by the need to relieve incubating partners and provision offspring, and must come ashore for several weeks during the annual moult. However, these constraints are absent over winter, between their moult and the following breeding season, when they spend 4-6 months at sea (Thiebot et al. 2013; Ratcliffe et al. 2014). For a mesopelagic predator, finding adequate resources during winter in the Southern Ocean is challenging, as deeper mixed layers, due to more frequent storms, and reduced primary productivity result in low prey densities in surface waters (Venables and Moore 2010; Béhagle et al. 2016). Indeed, eudyptids may travel thousands of kilometres to find adequate foraging areas (Thiebot et al. 2013) and macaroni penguins dive deeper during winter than during other seasons (Green et al. 2005). Environmental conditions that exacerbate a penguin's ability to find sufficient resources may thus have implications for survival and influence population dynamics (Crawford et al. 2006, 2008).

At Marion Island, the proportion of macaroni and eastern rockhopper penguins that initiate breeding each year is related to their mass on arrival after the winter period (a proxy for winter foraging success; Crawford et al. 2006). Additionally, heavier on-arrival rockhopper penguins fledge heavier chicks, suggesting that environmental conditions during winter have carry-over effects that may influence post-fledging survival (Crawford et al. 2008). Given the recent population declines of macaroni and rockhopper penguins at Marion Island (30 % and 70 % since 1994/95, respectively; Crawford et al. 2009) and the apparent influence of winter conditions on population dynamics, it is important to better understand their foraging ecology during this period.

The primary objectives of this chapter were to 1) determine broad- and fine-scale winter habitat preferences of macaroni and rockhopper penguins at Marion Island using geolocation and satellite tracking techniques, respectively, and 2) compare winter and summer trophic ecology, within and between the two species, using carbon and nitrogen stable isotopes. Additionally, as eudyptids are sexually dimorphic and sexes may differ in their energetic constraints (Agnew and Kerry 1995), sex-specific foraging strategies were investigated as a potential mechanism to reduce intraspecific competition.

Methods

See Chapter 2 for description of study site and species.

Geolocation

Macaroni and rockhopper penguins were caught at their nests at the end of the moulting period (early and late April, respectively) at Funk Bay (2013) and Ship's Cove (2013 and 2014), respectively. A GLS logger was leg-mounted to each penguin (see Chapter 2) and retrieved the following summer. Light and temperature data were extracted using BAStrack software. To estimate the most probable foraging path from light data, R packages 'SGAT' and 'BAStag' (Wotherspoon and Sumner 2015) were used, which incorporates land and sea surface temperature (SST) masks (Reynold's weekly). Movement parameters were constrained by a mean travelling speed of 3.0 ± 1.8 km.h^{-1} following Thiebot et al. (2012). The following parameters were calculated for each trip; 1) trip duration (time elapsed between first and last ambient sea temperature records), 2) total distance travelled (sum of distances between successive locations), and 3) maximum range (distance between the colony and the furthest point of the trip).

Satellite tracking

Macaroni and rockhopper penguins were caught and fitted with PTTs in April/May 2007, 2008 and 2012 by Bruce Dyer and field assistants working for Oceans and Coasts at the Department of Environmental Affairs. Unreliable locations from PTT data were removed using the R package 'argosfilter' and a maximum travel speed of 7.6 km.h^{-1} (Chapter 4). Data were linearly interpolated at an interval of 12 hours using the R package 'trip' (Sumner 2016). To avoid using tracks where penguins may have not even reached preferred foraging areas, data were only used when penguins were tracked for at least 1 month. For broader interpretation of foraging areas, analyses were restricted to April to August when data were available for at least three individuals of each species. See Chapter 2 for more details on the deployment of PTTs.

Environmental data

SST and SSH were used to characterise the broad-scale marine environment used by penguins (see Table S6.1 for data sources and resolutions). To investigate the distribution based on relatively fine-scale PTT data, EKE and SLA were used to characterise the mesoscale environment. FSLE was used to identify submesoscale filaments (defined as > 0.1 FSLE.day^{-1} following d'Ovidio et al. 2004) and the proximity of each location to a filament calculated, with locations delineated as < or > 10 km.

Habitat selection

All data were analysed in R 3.2.0 (R Development Core Team 2015). Habitat selection models were constructed for each species by comparing utilised habitat to available habitat using a logistic regression-based approach (Aarts et al. 2008). To represent available habitat, five pseudo-absences were generated – using a uniform spatial Poisson process – for every observed location and these were assigned the same date (Cleasby et al. 2015). In order to provide realistic pseudo-absence data, distribution was constrained to within 100 km of the distance of the observed location from the colony and within a bounding box defined by the latitudinal and longitudinal extent of penguin locations (7° to 55° E, -42° to -62° S). Due to the non-linearity between response variables and environmental covariates that commonly occur in species-habitat studies (Cotté et al. 2015), generalized additive models (GAMs) were used for their ability to detect relationship shapes through flexible smoothers. Models were fit with a binomial error distribution using the R package 'mgcv' and a separate model constructed for each species. Smoothers were applied to each environmental covariate and fitted using cubic regression splines with extra shrinkage, which avoids over-parameterisation by allowing variables to be penalised out of the model during fitting (Wood 2006). To account for repeated observations for each individual and potential variation between years, individual identity and year were included as random effects. Prior to modelling, environmental covariates were log(x+1)-transformed if data were heavily skewed, and all covariates scaled to 0 ± 1 (mean ± SD). As SST and SSH were highly correlated with latitude (r_s = 0.89), these variables were not included in the same models. To check for spatial autocorrelation, variograms were constructed using the R package 'gstat'. If spatial autocorrelation was present, models were ranked by means of K-folds cross-validation (K = 5) using the function 'CVgam' in the R package 'gamclass' (Cleasby et al. 2015), as this allows for the fact that the assumption of independence between data points is not met. The overlap between each species' distribution (based on PTT data) was computed using the function 'kerneloverlapHR' and the 'Bhattacharyya's affinity' (BA) method (Fieberg and Kochanny 2005).

GLS-based at-sea distribution of rockhopper penguins (no data retrieved from loggers deployed on macaroni penguins; see ‘Results’) was broadly characterised by computing 50 % and 95 % utilization distributions (UDs) using kernel analysis in the R package ‘adehabitatHR’. A smoothing parameter of 1° was used following Thiebot et al. (2014). The overlap of penguin distributions in 2013 and 2014 was computed using the function ‘kerneloverlapHR’ and the BA method (Fieberg and Kochanny 2005). To test for inter-annual differences in GLS-derived sea temperatures experienced by rockhopper penguins, a linear-mixed effect model (LME) was used with individual identity included as a random effect. To compare satellite-derived SST between species, an LME was used with month included as a fixed effect and individual identity nested within year as a random effect. For each species, monthly variations in SST were investigated using LMEs, with individual identity nested within year as a random effect. The function ‘glht’ in the R package ‘multcomp’ was used for post-hoc comparisons.

To determine whether winter foraging areas influenced the condition of penguins arriving to breed, mass on arrival of individuals was modeled in relation to sea temperature they experienced in each month (May to October), with year and sex included as fixed effects (only possible for rockhopper penguins). A global model was constructed and the function ‘dredge’ in the R package ‘MuMIn’ (Barton 2016) was used to rank models according to AIC. The most parsimonious of the top models (ΔAIC < 2) was selected.

Stable isotope analysis

See Chapter 2 for details on the application of stable isotopes to studying the trophic ecology of marine predators. To investigate the penguins' winter trophic ecology, 25 macaroni (12 males, 13 females) and 25 rockhopper penguins (12 males, 13 females) were caught on arrival at Funk Bay in October and November 2011, respectively, and blood was collected via venipuncture in the medial metatarsal vein using a sterile slightly heparinized syringe with a 25G needle. These samples represent a 2-month period leading up to the arrival of penguins at the island (Cherel et al. 1994). To provide a baseline from which to interpret winter trophic ecology, summer trophic ecology (Chapter 3) was included in analyses as penguins forage near the island in summer (Chapter 3). Replicate measurements of internal laboratory standards indicated minimal standard deviations of $\delta^{13}C$ and $\delta^{15}N$ (Merck gel: $\delta^{13}C = 0.2$ ‰, $\delta^{15}N < 0.1$ ‰; valine: $\delta^{13}C = 0.1$ ‰, $\delta^{15}N < 0.1$ ‰; seal bone: $\delta^{13}C = 0.2$ ‰, $\delta^{15}N < 0.1$ ‰).

Bivariate ellipses were used to plot the isotopic niche of each sex for each species and for each stage (winter/summer) using the Stable Isotopes Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011). Total (TA) and core niche (SEA_c) space and overlap of each TA ellipse were calculated. Linear models were used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ between sex and species within each season. When variances were unequal, linear models were fit using generalized least squares (GLS). To determine differences in trophic ecology between winter and summer within each species, $\delta^{13}C$ and $\delta^{15}N$ were modeled in relation to stage with sex included as a fixed effect. Models were ranked according to AIC and the most parsimonious (ΔAIC < 2) were selected. To determine how mass on arrival was influenced by $\delta^{13}C$ and $\delta^{15}N$, a global model was constructed with sex included as a fixed effect. The function 'dredge' was used to rank models according to AIC and the most parsimonious (ΔAIC < 2) was selected.

Results

GLS logger retrieval rates were high, with 19/20 (95%) and 16/18 (89%) recovered from rockhopper penguins in 2013 and 2014, respectively, and 17/18 (94%) recovered from macaroni penguins in 2014. Unfortunately, due to technical problems with loggers, particularly in 2014, data were restricted to 16 rockhopper penguins in 2013 and 9 in 2014 (Table 6.1); no data were obtained from macaroni penguins, precluding interspecific comparisons using GLS data. The distribution of rockhopper penguins in 2013 and 2014 was similar (BA = 0.94) and therefore data were pooled. PTTs attached to 12 macaroni and eight rockhopper penguins transmitted for > 1 month (Table 6.2), with mean transmission periods of 105 ± 62 days and 93 ± 30 days, respectively.

Table 6.1. Trip characteristics (mean ± SD (range)) of rockhopper penguins tracked during the winter period using GLS

Year	Sex	N	Departure date	Return date	Trip duration (days)	Maximum range (km)	Minimum total distance travelled (km)	Mass (kg)	Mass gain (%)[*]
2013	Male	8	28-Apr ± 1 (26-Apr – 30-Apr)	4-Nov ± 4 (30-Oct – 11-Nov)	191 ± 5 (183 – 199)	820 ± 262 (477 – 1386)	8406 ± 892 (7052 – 9395)	3.2 ± 0.2 (2.8 – 3.4)	39 ± 15 (21 – 72)
	Female	8	27-Apr ± 1 (26-Apr – 30-Apr)	09-Nov ± 4 (4-Nov – 16-Nov)	197 ± 3 (192 – 203)	1191 ± 412 (781 – 1998)	9206 ± 1291 (7639 – 11641)	3.3 ± 0.1 (3.2 – 3.6)	51 ± 10 (38 – 65)
	All	16	27-Apr ± 1 (26-Apr – 30-Apr)	06-Nov ± 5 (30-Oct – 16-Nov)	194 ± 5 (183 – 203)	1005 ± 385 (477 – 1998)	8806 ± 1149 (7052 – 11641)	3.2 ± 0.2 (2.8 – 3.6)	45 ± 14 (21 – 72)
2014	Male	4	1-May ± 2 (28-Apr – 3-May)	3-Nov ± 0 (29-Oct – 3-Nov)	183 ± 5 (179 – 189)	960 ± 377 (683 – 1483)	7348 ± 778 (6634 – 8215)	3.5 ± 0.3 (3.1 – 3.8)	39 ± 9 (32 – 52)
	Female	5	3-May ± 1 (3-May – 4-May)	3-Nov ± 1 (3-Nov – 4-Nov)	184 ± 1 (183 – 185)	841 ± 218 (689 ± 1212)	7584 ± 1295 (6261 – 9212)	3.5 ± 0.3 (3.1 – 3.8)	42 ± 5 (37 – 49)
	All	9	2-May ± 2 (28-Apr – 4-May)	3-Nov ± 0 (3-Nov – 4-Nov)	184 ± 4 (179 – 189)	894 ± 285 (683 – 1483)	7479 ± 1040 (6261 – 9212)	3.5 ± 0.3 (3.1 – 3.8)	41 ± 7 (32 – 52)

[*] as a proportion of initial body mass

Table 6.2. Summary of PTT data from macaroni and rockhopper penguins during the over-wintering period

Species	Year	PTT	Sex	Depart	Termination	Transmission period (days)	Max range (km)	Min total distance travelled (km)	Average speed (km.h^{-1})
Macaroni	2007	57336	F	14-Apr	05-Jun	52	652	1417	1.1
	2007	57340	-	14-Apr	17-Jun	65	2012	2809	1.8
	2007	57342	M	13-Apr	26-May	43	1204	1649	1.6
	2008	80735	M	03-Apr	17-Sep	168	1338	5616	1.4
	2008	80740	F	03-Apr	19-Nov	230	1481	7694	1.5
	2008	80742	F	12-Apr	08-Aug	118	2249	4579	1.6
	2008	80745	M	09-Apr	30-Sep	175	1777	6569	1.6
	2008	80752	M	03-Apr	19-Jun	77	1107	2905	1.6
	2008	80753	F	03-Apr	31-Aug	150	1294	5070	1.4
	2012	98027	M	24-Apr	11-Jul	78	1366	3355	1.8
	2012	98028	F	25-Apr	07-Jun	44	1419	1841	1.7
	2012	98029	M	24-Apr	17-Jun	54	1169	1887	1.4
Rockhopper	2008	80736	-	19-Apr	22-Jun	64	554	1592	1.0
	2008	80743	-	23-Apr	14-Aug	114	1594	4731	1.7
	2008	80746	-	19-Apr	19-Jul	91	600	3104	1.4
	2008	80749	-	25-Apr	07-Aug	105	977	3905	1.5
	2008	80750	-	26-Apr	03-Jul	69	784	2356	1.4
	2008	80751	-	25-Apr	21-Aug	119	1000	4509	1.6
	2012	52913	F	06-May	16-Sep	133	1273	3592	1.1
	2012	52931	M	11-May	29-Jun	49	852	2002	1.7

Habitat preferences

Mean SSTs derived from positions of satellite-tracked macaroni and rockhopper penguins were 3.0 ± 0.5 °C (n = 12; April to August) and 5.3 ± 1.1 °C (n = 8; April to August), respectively, with monthly SSTs of rockhopper penguins being 2.1 ± 0.3 °C warmer (LME, t_{18} = 6.1, $P < 0.001$). *In situ* water temperatures logged by GLSs fitted to rockhopper penguins were similar in 2013 (5.4 ± 0.7 °C) and 2014 (5.6 ± 0.5 °C; LME, t_{22} = 0.6, $P = 0.54$) and there were no differences between sexes (LME, t_{22} = 0.6, $P = 0.53$). The use of major water masses from April to August differed between species, with macaroni penguins spending 89 % of the time in the AAZ and SZ, whereas rockhopper penguins spent > 90 % of the time in the AAZ and PFZ (Table 6.3). Interspecific overlap of utilization distributions was moderate (BA = 0.49) during this period and occurred mostly in the AAZ. From September to November, rockhopper penguins foraged almost exclusively (88 %) in the PFZ (Table 6.3). Although the investigation of monthly movements of macaroni penguins was limited to the period between April and August, they generally remained in the vicinity of the SACCF (Fig. 6.1) where SSTs were 2-3 °C (Fig. 6.2). Rockhopper penguins foraged near the APF during April and May, and thereafter moved north into the PFZ for the remainder of winter (Fig. 6.1). Both species preferred waters with elevated EKE (Tables S6.2, S6.3, S6.4; Fig. 6.4a), with rockhopper penguins exhibiting a preference for weak positive SLA and macaroni penguins for negative SLA (Tables S6.2, S6.3, S6.4; Fig. 6.4b). Both species foraged in waters close to submesoscale filaments (Tables S6.2, S6.3, S6.4; Figs. 6.4c, d; Fig. 6.6).

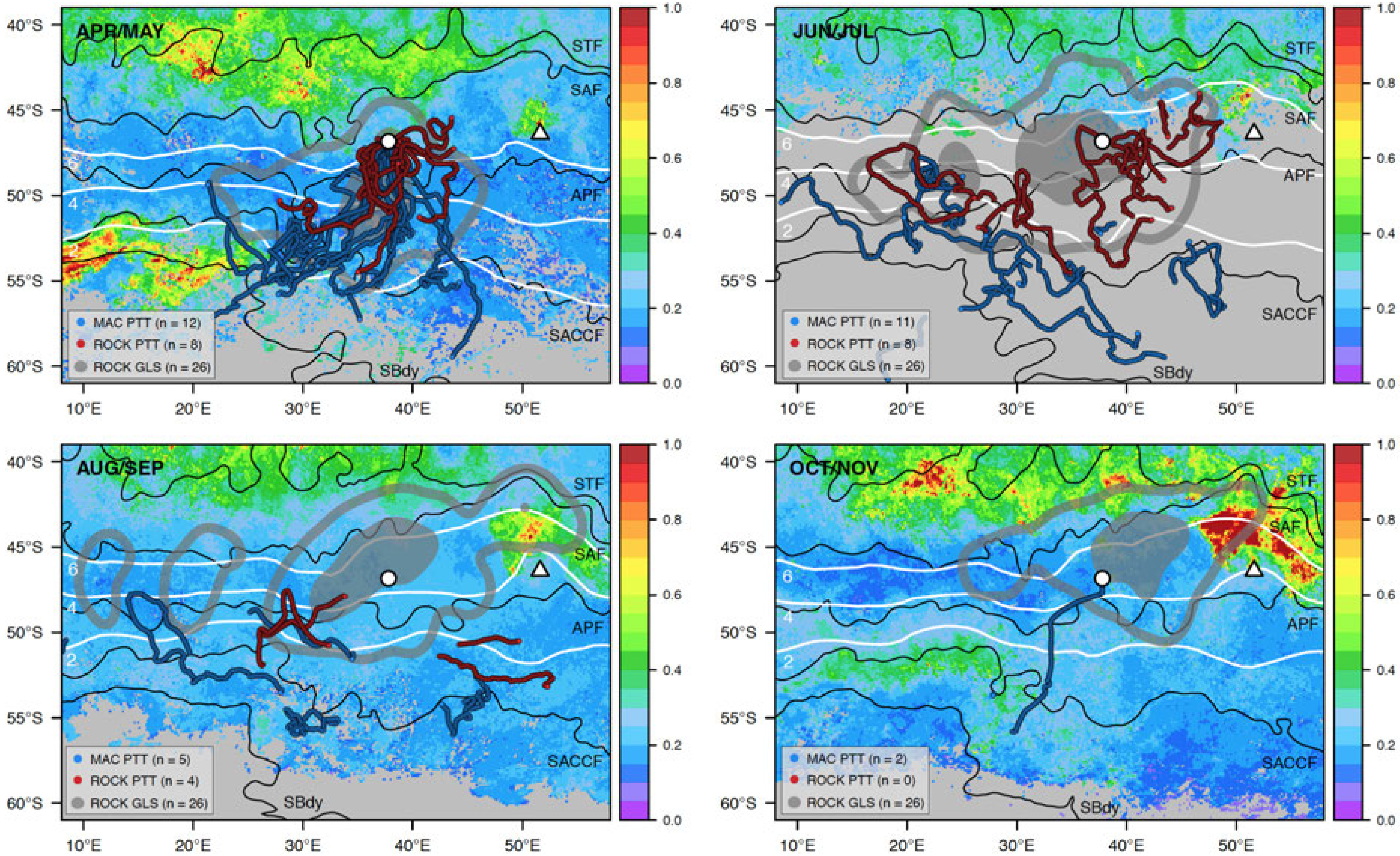

APR/MAY
JUN/JUL
AUG/SEP
OCT/NOV
STF
SAF
APF
SACCF
SBdy
6
4
2
MAC PTT (n = 12)
ROCK PTT (n = 8)
ROCK GLS (n = 26)
MAC PTT (n = 11)
ROCK PTT (n = 8)
ROCK GLS (n = 26)
MAC PTT (n = 5)
ROCK PTT (n = 4)
ROCK GLS (n = 26)
MAC PTT (n = 2)
ROCK PTT (n = 0)
ROCK GLS (n = 26)
40°S
45°S
50°S
55°S
60°S
10°E
20°E
30°E
40°E
50°E
0.0
0.2
0.4
0.6
0.8
1.0

Figure 6.1. (previous page). Satellite tracks of macaroni (blue) and rockhopper penguins (red) from Marion Island (white circle). Kernel density polygons (50 % and 95 %) represent GLS locations of rockhopper penguins. Map represents mean surface chl-a concentrations (mg.m^{-3}) in 2013 and 2014 during GLS deployments (light grey = missing data due to cloud cover). Crozet Islands (white triangle), mean positions of the Sub-Tropical Front (STF), sub-Antarctic Front (SAF), Antarctic Polar Front (APF), Southern Antarctic Circumpolar Front (SACCF) and Southern Boundary (SBdy), and 2 °C, 4 °C and 6 °C isotherms are shown

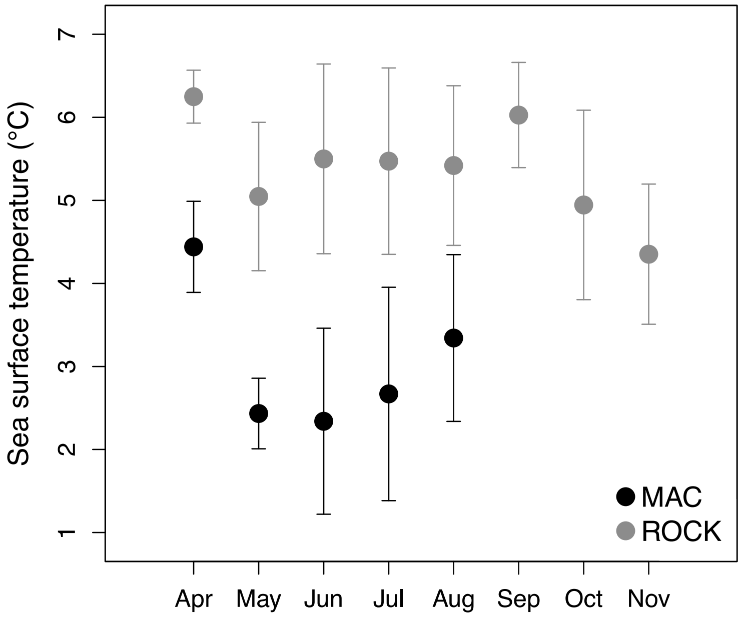


Figure 6.2. Mean ± SD sea surface temperatures experienced by macaroni (MAC) and rockhopper (ROCK) penguins during winter (based on PTT locations for macaroni penguins, and PTT and GLS data for rockhopper penguins). Only months with data available for at least 4 individuals were included

Table 6.3. Percentage of time spent by macaroni (MAC) and rockhopper (ROCK) penguins from Marion Island in major water masses during winter

Water mass	Apr - Aug		Sep - Nov
	MAC	ROCK	ROCK
Sub-Antarctic Zone	0	2	10
Polar Frontal Zone	11	57	88
Antarctic Zone	46	39	2
Southern Boundary Zone	43	2	0

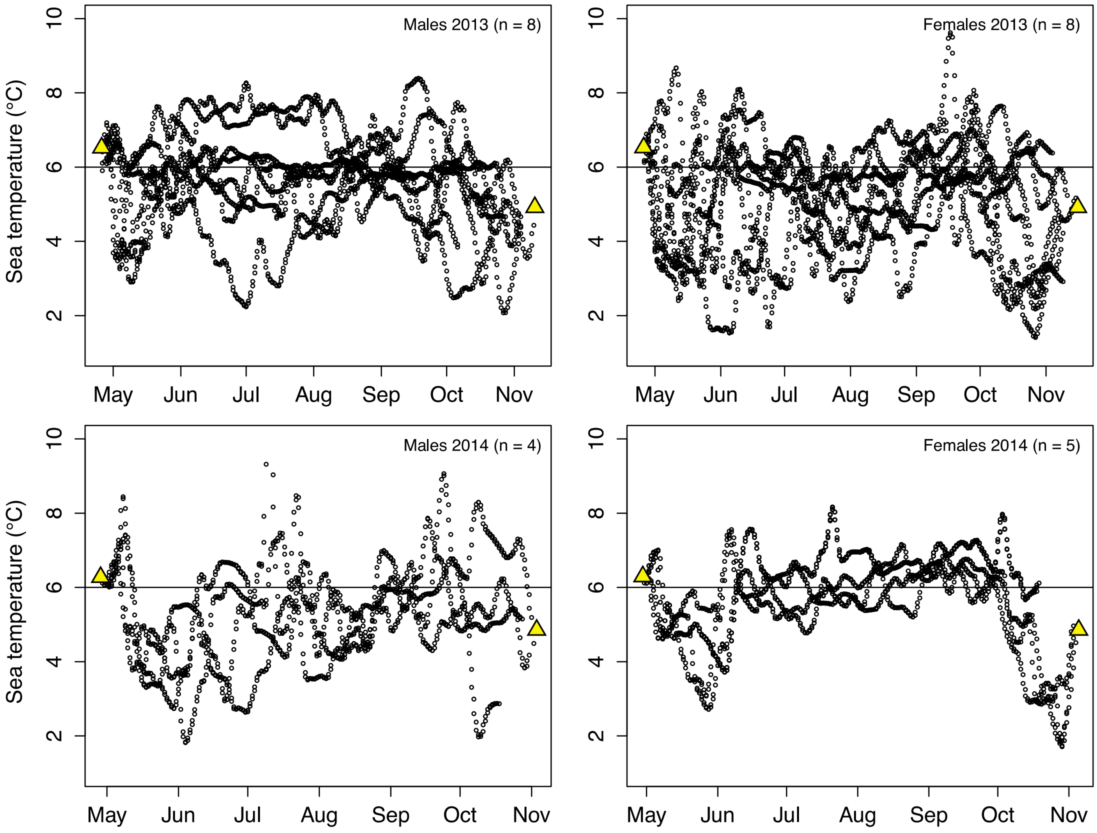


Figure 6.3. *In situ* sea temperatures logged by GLS loggers attached to rockhopper penguins. Yellow triangle represents approximate sea temperatures at Marion Island

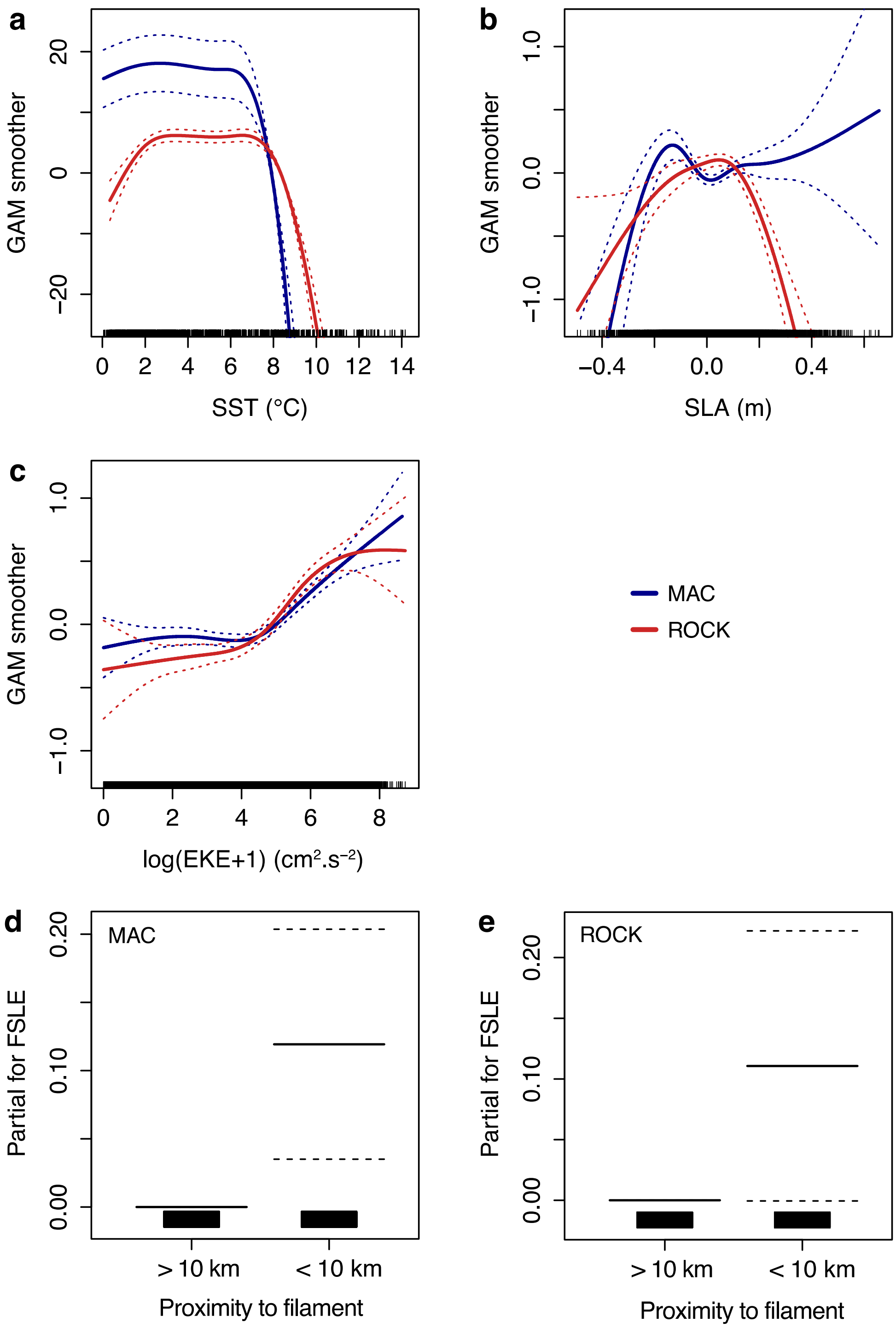


Figure 6.3. Habitat selection functions for (a) sea surface temperature (SLA), (b) sea level anomaly (SLA), (c) eddy kinetic energy (EKE) and (d, e) proximity to submesoscale filaments. Solid lines are predicted curves from generalized additive models (GAM) and dashed lines are 95 % confidence intervals

Stable isotopes

In winter, $\delta^{13}C$ ratios for erythrocytes were 0.2 ± 0.1 ‰ higher in males than females but this was only near significant (GLS, $t_{42} = 2.0$, $P = 0.054$; Table S6.5). Female rockhopper penguins exhibited larger variation than males (Table 6.4; Fig. 6.5). Erythrocyte $\delta^{15}N$ values were not influenced by sex (GLS, $t_{42} = -1.1$, $P = 0.29$) or species (GLS, $t_{42} = 1.0$, $P = 0.31$) alone, but when an interaction term was specified, rockhopper penguins were 0.5 ± 0.2 ‰ higher than macaroni penguins (GLS, $t_{40} = 2.5$, $P < 0.05$) owing to the higher $\delta^{15}N$ of female rockhopper penguins (Table 6.4). Female rockhopper penguins had a larger isotopic niche than male rockhopper penguins, and both sexes of macaroni penguins (Table 6.5). Total niche areas of macaroni and rockhopper penguins were 0.29 and 0.71 ‰^{2}, respectively, with overlaps of 88 and 36 %, respectively. In summer, erythrocyte $\delta^{13}C$ values were similar between species (LM, $t_{44} = -0.9$, $P = 0.4$) and sexes (LM, $t_{44} = -0.9$, $P = 0.35$). Erythrocyte $\delta^{15}N$ values were 0.7 ± 0.2 ‰ higher in macaroni penguins (GLS, $t_{42} = -3.5$, $P < 0.005$), with no influence of sex (GLS, $t_{42} = 0.7$, $P = 0.48$) or interactions (GLS, $t_{42} = 1.9$, $P = 0.06$). Total niche areas of macaroni and rockhopper penguins were 0.20 and 0.35 ‰^{2}, respectively, with overlaps of 53 and 30 %.

For macaroni penguins, $\delta^{13}C$ values were 0.3 ± 0.1 ‰ higher (GLS, $t_{42} = 5.1$, $P < 0.001$; Table S6.6) and $\delta^{15}N$ values were 1.1 ± 0.1 ‰ lower during winter than in summer (GLS, $t_{42} = -8.7$, $P < 0.001$). For rockhopper penguins, $\delta^{13}C$ values were 0.5 ± 0.1 ‰ higher during winter than in summer (GLS, $t_{44} = 5.4$, $P < 0.001$) but $\delta^{15}N$ values were influenced by both stage and sex (GLS, $t_{42} = -3.8$, $P < 0.001$), with $\delta^{15}N$ of males being higher in summer and lower in winter compared to females. The higher $\delta^{13}C$ values of both species during winter compared to summer, when adults are spatially constrained, suggests that they foraged near or north of the Prince Edward Islands during late winter (Fig. 6.5).

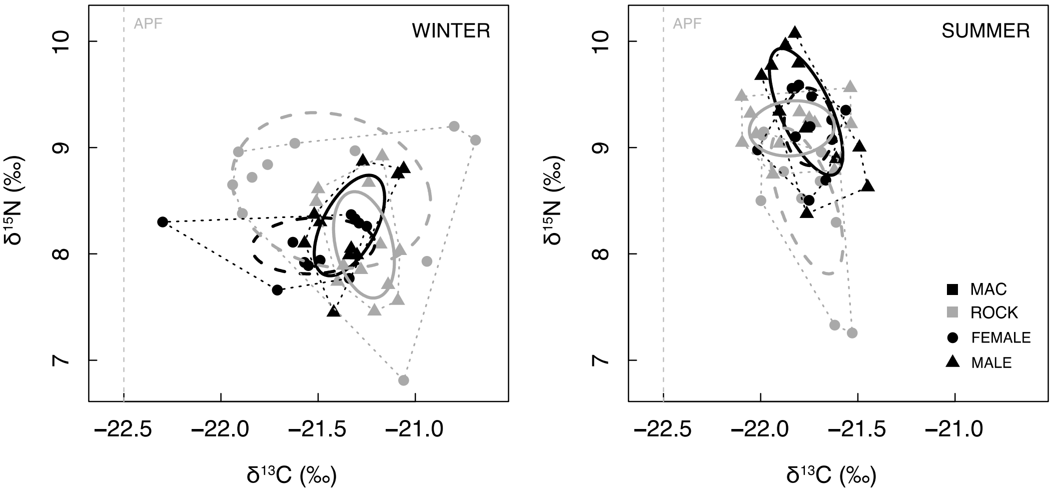


Figure 6.5. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios in erythrocytes of male (triangles) and female (circles) macaroni (black) and rockhopper (grey) penguins representative of trophic ecology during late winter (September – November) and summer (December – February). Total isotopic niche space (dotted convex hulls), core isotopic niche space corrected for small samples size (solid and dashed ellipses for males and females, respectively), and the position of the Antarctic Polar Front south of where penguins were foraging (APF, dashed vertical grey line, estimated for whole blood by Jaeger et al. 2011) are shown

Table 6.4. Summary of stable isotope ratios in erythrocytes of macaroni and rockhopper penguins. Mean ± SD and range are shown.

Species	Sex	N	Winter				Summer		
			$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ratio	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ratio
Macaroni penguin	Male	12	-21.3 ± 0.2 (-21.6 – -21.1)	8.3 ± 0.4 (7.5 – 8.9)	3.3 ± 0.0 (3.3 – 3.3)	12	-21.8 ± 0.2 (-22.0 – -21.5)	9.3 ± 0.6 (8.4 – 10.1)	3.3 ± 0.0 (3.3 – 3.3)
	Female	13	-21.5 ± 0.3 (-22.3 – -21.3)	8.1 ± 0.3 (7.7 – 8.4)	3.3 ± 0.0 (3.3 – 3.4)	11	-21.8 ± 0.1 (-22.0 – -21.6)	9.2 ± 0.3 (8.5 – 9.6)	3.3 ± 0.0 (3.3 – 3.3)
Rockhopper penguin	Male	12	-21.3 ± 0.1 (-21.5 – -21.1)	8.1 ± 0.5 (7.5 – 8.9)	3.2 ± 0.0 (3.2 – 3.3)	11	-21.8 ± 0.2 (-22.1 – -21.5)	9.2 ± 0.2 (8.7 – 9.6)	3.2 ± 0.0 (3.2 – 3.3)
	Female	13	-21.4 ± 0.5 (-21.9 – -20.7)	8.6 ± 0.7 (6.8 – 9.2)	3.3 ± 0.0 (3.2 – 3.3)	12	-21.8 ± 0.2 (-22.0 – -21.5)	8.5 ± 0.6 (7.3 – 9.1)	3.2 ± 0.0 (3.2 – 3.2)

Table 6.5. Total isotopic niche area (TA) and percentage overlap between male and female macaroni and rockhopper penguins during winter and summer

			TA (‰^{2})	Macaroni		Rockhopper	
				Female	Male	Female	Male
Winter	MAC	Female	0.26	-	42	77	27
		Male	0.22	50	-	95	55
	ROCK	Female	1.16	17	18	-	15
		Male	0.23	30	52	74	-
Summer	MAC	Female	0.15	-	87	20	67
		Male	0.26	50	-	8	38
	ROCK	Female	0.32	9	6	-	13
		Male	0.18	56	56	22	-

Drivers of variation in mass

For macaroni penguins equipped with GLS loggers, females were 0.3 ± 0.1 kg heavier than males (5.3 ± 0.2 kg, range: 5.0 – 5.7 kg, and 5.0 ± 0.2 kg, range: 4.7 – 5.3 kg, respectively, LM, $t_{15} = -2.7$, $P < 0.05$). For rockhopper penguins equipped with GLS loggers, there were no differences in mass between sexes (LM, $t_{23} = -0.8$, $P = 0.41$), but males were 0.2 ± 0.1 kg heavier in 2014 than in 2013 (LM, $t_{23} = 2.5$, $P < 0.05$, Table 6.1). Mass on arrival of macaroni and rockhopper penguins from which blood was taken for stable isotope analyses were similar to those equipped with GLS loggers (Table S6.7). The best model explaining variance in mass on arrival of rockhopper penguins equipped with GLS loggers included year and sea temperature encountered during October (Table 6.6). Mass on arrival was inversely related to sea temperature experienced, shortly before returning to breed (LM, $t_{22} = - 3.9$, $P < 0.001$, Fig. 6.7). In 2014, the mass of returning rockhopper penguins was 0.28 ± 0.08 kg heavier than in 2013 (LM, $t_{22} = 3.6$, $P < 0.005$). There were no inter-annual differences in productivity at foraging areas during September and October (0.21 ± 0.10 mg.m^{-3} in 2013 and 0.22 ± 0.12 mg.m^{-3} in 2014). With respect to stable isotopes, masses of macaroni penguins on arrival were not influenced by δ^{13}C (LM, $t_{19} = -0.8$, $P = 0.43$) or δ^{15}N (LM, $t_{19} = -0.6$, $P = 0.58$; Table S6.8). Masses of rockhopper penguins on arrival were inversely related to δ^{13}C (LM, $t_{21} = -2.2$, $P < 0.05$, slope = -0.24 ± 0.11) but not to δ^{15}N (LM, $t_{21} = 0.7$, $P = 0.49$). There was no influence of sex on mass on arrival for either species.

Table 6.6. Top (ΔAIC < 2) and null models explaining variance in mass of rockhopper penguins on arrival from winter in relation to sea surface temperatures experienced during different months

Model	AICc	ΔAIC	weight
OCT + year	-7.1	0	0.21
SEP + OCT + year	-7	0.1	0.2
JUL + SEP + OCT + year	-5.4	1.72	0.09
NULL	6.6	13.73	0

Discussion

This chapter provides new insights into the winter habitat preferences and trophic ecology of macaroni and rockhopper penguins. High retrieval rates of GLS loggers (89 – 95 %) indicate high winter survival and strong nest site philopatry in successive breeding seasons, which were expected given the high adult survival estimates reported at other breeding localities (Dehnhard et al. 2013; Horswill et al. 2014). Masses of penguins on arrival at Marion Island were relatively high compared to previous records (Crawford et al. 2003a; Crawford et al. 2008), indicating that resource availability in 2013 and 2014 was particularly good. The at-sea winter distribution of rockhopper penguins was similar between years, which complements previous studies that have observed high winter site fidelity at the population scale in crested penguins (Thiebot et al. 2011, 2012). PTT and GLS data revealed broad-scale species-specific habitat preferences during the core winter months, with macaroni penguins preferring cooler waters than rockhopper penguins. However, stable isotopes revealed high spatial overlap during late winter. PTT data revealed associations of both species with mesoscale eddies and submesoscale filaments, which has been previously documented during incubation (Bón et al. 2015) and pre-moult foraging trips (Chapter 4; Lowther et al. 2014).

Seasonal movements

Immediately following the moult, both macaroni and rockhopper penguins migrated southwards to forage in cooler AAZ waters downstream from the South-West Indian Ridge (Fig. 6.1). This region is an important foraging area during the pre-moult period (Chapters 4 and 5) and likely offers a predictable source of food during the initial few weeks following the moult when penguins need to rapidly replenish energy stores.

During the core winter months (June to August), macaroni penguins foraged in cool (2-3 °C) waters near the SACCF. This frontal zone is associated with strong mesoscale activity and high productivity (Kahru et al. 2007) and is also an important winter foraging area for macaroni penguins at South Georgia (Ratcliffe et al. 2014). By comparison, conspecifics at

Crozet and Kerguelen Islands mainly foraged in PFZ waters (3-4 °C, Thiebot et al. 2011). Rockhopper penguins generally foraged in PFZ waters of 5-6 °C from May to August, but individuals exhibited large variation in SST preferences (Fig. 6.3). Individual variation was lowest in September (Fig. 6.3), perhaps owing to penguins aggregating to exploit abundant resources associated with the spring phytoplankton bloom near the SAF. The preference of rockhopper penguins for PFZ waters near the SAF supports GLS-derived distributions of rockhopper penguins from Crozet and Kerguelen Islands, as well as at-sea observations by Enticott (1988, p. 131) who noted 'two separate individuals some 300 nautical miles NW of the Crozet Islands in May 1983, and two groups of four and 30 birds some 400 nm WNW of the PEIs in September 1979'. This also highlights the high overlap of conspecifics from Marion and Crozet Island populations (see Thiebot et al. 2013). In October, some rockhopper penguins travelled to cooler waters before returning to Marion Island (Fig. 6.3). This may potentially be due to the release of competition with macaroni penguins that start returning to the island in October (Crawford et al. 2003a), and/or potentially greater resource availability in cooler waters. Unfortunately, insufficient data were available to determine the late winter SST preferences of macaroni penguins, but $\delta^{13}C$ values indicated they foraged in PFZ waters from mid-August onwards, and thus potentially competed with rockhopper penguins (Fig. 6.4). Intraspecific competition within rockhopper penguins may have been reduced due to the wider isotopic niche occupied by females (Fig. 6.4; Table 6.9). This might be driven by competitive avoidance with males, as females have larger energetic requirements owing to their need to accumulate resources for egg production.

Trophic ecology

Carbon and nitrogen stable isotope values of macaroni and rockhopper penguins were similar to conspecifics at the Crozet and Kerguelen Islands (Thiebot et al. 2011, 2012). The lower trophic level diet of macaroni and male rockhopper penguins during winter compared to summer may be attributed to a lower contribution of myctophid fish in their diet. The vertical distribution of myctophids typically deepens during winter (Koslov et al. 1991), when the increased frequency of storms and stronger winds results in deeper mixed layers and thermoclines (Venables and Moore 2010), making fish less accessible to penguins (Scheffer et al. 2012). However, the fact that female rockhopper penguins fed at a higher trophic level during late winter compared to summer is surprising. This may result from a greater need to feed on energy-dense myctophids to accumulate resources for egg production, but does not explain why female macaroni penguins did not forage at a higher trophic level. In contrast, female southern rockhopper penguins at the Falkland Islands foraged at a lower trophic level than males during late winter, and both sexes foraged at a higher trophic level compared to summer (Dehnhard et al. 2011), highlighting region-specific foraging strategies between sexes. Sex-specific foraging strategies were not observed among rockhopper penguins during late winter at the Crozet and Kerguelen islands (Cherel et al. 2007; Thiebot et al. 2011, 2012).

Association with meso- and submesoscale features

Habitat preference models revealed that movements of macaroni and rockhopper penguins were influenced by the mesoscale physical environment (Figs. 6.4, 6.6). Additionally, rapid transitions in SST recorded by GLS loggers (Fig. 6.3) could potentially reflect the movement of penguins between neighboring cold- and warm-core mesoscale eddies. Eddies are key drivers of primary productivity due to their physical and biogeochemical properties (Frenger 2013). They aggregate and sustain elevated concentrations of zooplankton and mesopelagic fish (Ansorge et al. 2009) and thus act as important foraging areas for many marine top predators (Nel et al. 2001; Cotté et al. 2007, 2015). The stirring of eddies and the interactions between them create strong filamentary fields, with filaments sometimes stretching for hundreds of kilometres (Lévy et al. 2012). These filaments are associated with reduced vertical mixing and increased water column stability (Lévy et al. 2012) and may support elevated zooplankton concentrations (Labat et al. 2009; Perruche et al. 2011). During winter, when prey availability in surface waters is reduced by strong vertical mixing and reduced primary production (Venables and Moore 2010), eddies and filaments may aggregate prey at depths accessible to penguins, thus providing a predictable source of food. Filaments may also act as transport fronts that accelerate the movement of penguins, reducing energetic costs associated with travel (Bón et al. 2015; Cotté et al. 2015). Visual inspection of penguin movements in relation to maps of SLA and FSLE suggested that penguins continuously track meso- and sub-mesoscale features throughout the winter (Fig. 6.6); with some individuals foraging at individual eddies for up to 2 months (link to animation). Further research into the physical and biological characteristics of eddies and/or filaments targeted by penguins are needed to elucidate fine-scale links between predator, prey and process.

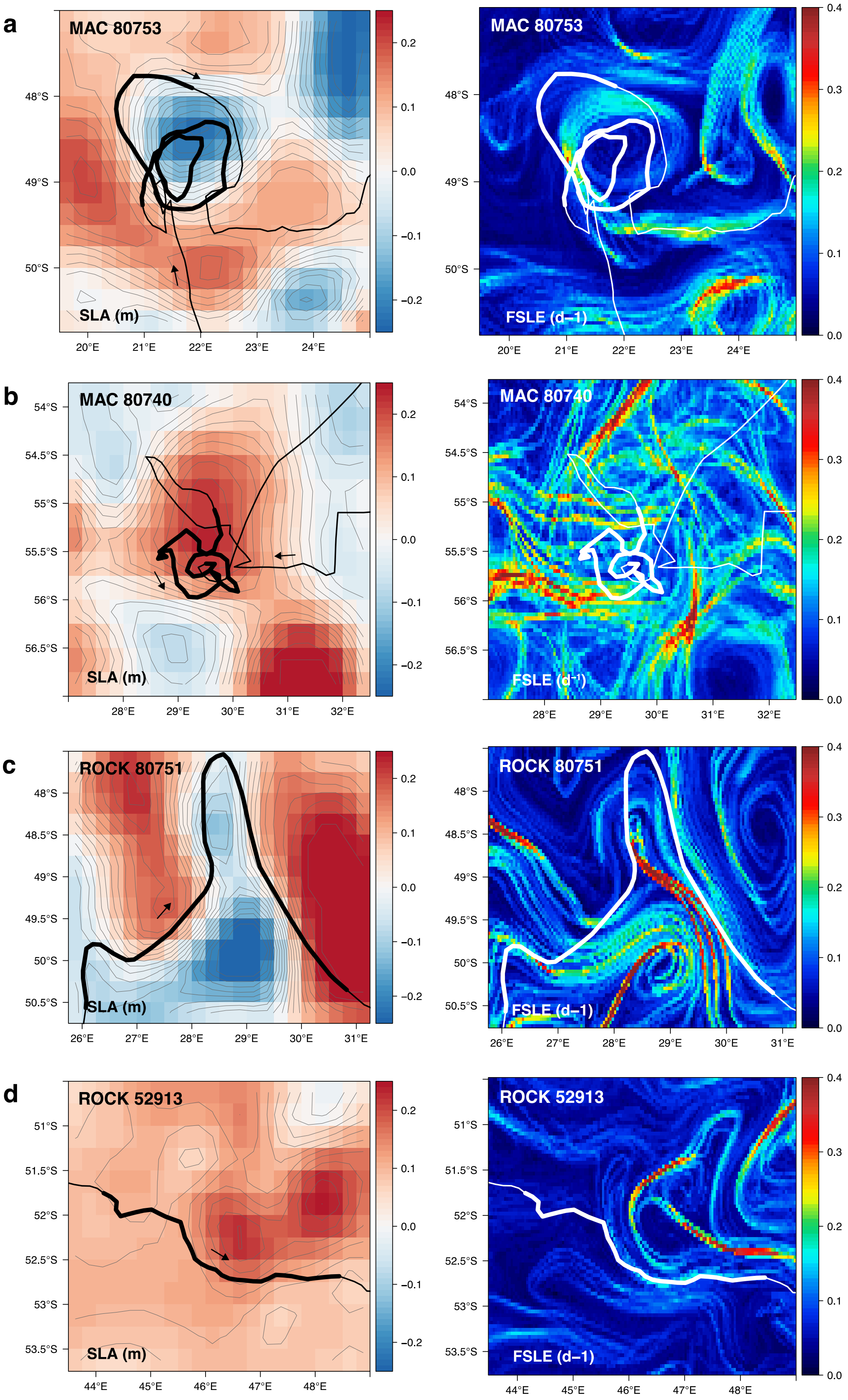

a
MAC 80753
SLA (m)
FSLE (d–1)
48°S
49°S
50°S
20°E
21°E
22°E
23°E
24°E
b
MAC 80740
SLA (m)
FSLE (d⁻¹)
54°S
54.5°S
55°S
55.5°S
56°S
56.5°S
28°E
29°E
30°E
31°E
32°E
c
ROCK 80751
SLA (m)
FSLE (d–1)
48°S
48.5°S
49°S
49.5°S
50°S
50.5°S
26°E
27°E
28°E
29°E
30°E
31°E
d
ROCK 52913
SLA (m)
FSLE (d–1)
51°S
51.5°S
52°S
52.5°S
53°S
53.5°S
44°E
45°E
46°E
47°E
48°E
0.2
0.1
0.0
−0.1
−0.2
0.4
0.3
0.2
0.1
0.0

Figure 6.6 (previous page). Movements of selected satellite-tracked macaroni (MAC) and rockhopper (ROCK) penguins in relation to composite maps of sea level anomaly (SLA) and finite-size Lyapunov exponent (FSLE). Thin line represents entire track and thicker line represents dates of the mapped environmental variables: (a) 11/6 to 11/7/2008, (b) 30/8 to 29/9/2008, (c) 5/8 to 19/8/2008, (d) 8/8 to 22/8/2012. Arrows indicate direction of movement

Interspecific differences

Competition for resources has been shown to result in spatial segregation among closely related penguin species (Kokubun et al. 2010; Wilson 2010). During the core winter months, foraging areas of macaroni and rockhopper penguins partially overlapped in AAZ waters, but contrasting SST preferences indicated broad-scale segregation (Fig. 6.2). SST preferences may be the result of size-related physiological differences in which the larger-bodied macaroni penguins are better equipped to thermoregulate in cooler waters. Alternatively, because mixed layer depths in the AAZ are deeper than in the PFZ during winter (Venables and Moore 2010), the deeper-diving ability of macaroni penguins (Chapters 3 and 4) may allow them access to prey unavailable to rockhopper penguins. In other words, rockhopper penguins may be energetically and physiologically constrained to forage in warmer waters. Habitat segregation of sympatric macaroni and rockhopper penguins during the core winter months has been observed at other South-West Indian Ocean islands – Crozet and Kerguelen Islands (Thiebot et al. 2011, 2012, 2013). However, macaroni penguins from South Georgia and southern rockhopper penguins from a colony in the south of the Falkland Islands overlapped considerably in cooler waters (Ratcliffe et al. 2014). Here it was suggested that the deeper-diving ability of macaroni penguins might result in niche partitioning between the two species (Ratcliffe et al. 2014), such as observed during the pre-moult period at Marion Island (Chapter 5). However, the stable isotope results in this chapter indicate that although spatial overlap was high during late winter, trophic niche differentiation was not evident. This emphasises the importance of the three-week difference in the breeding chronology of crested penguins at Marion Island (Crawford et al. 2003a, b), which means that potential interspecific competition is non-existent during the critical few weeks when rockhopper penguins must undergo hyperphagia to accumulate sufficient energy stores for the upcoming incubation fast ashore. However, it is important to note that intraspecific competition between conspecifics from Marion and Crozet Islands may be high, which contrasts to the clear habitat segregation between Crozet and Kerguelen populations (Thiebot et al. 2013).

Influence of winter foraging on population dynamics

Given that mass on arrival may influence the number of penguins that initiate breeding and/or impact breeding success (Crawford et al. 2008), it was important to identify potential factors that influence mass on arrival. Stable isotopes revealed that rockhopper penguins were heavier on arrival when they fed farther south (Fig. S6.2). Similarly, rockhopper penguins equipped with GLS loggers were heavier when they foraged in cooler waters during October; the month preceding their return to the island. As there were no links between foraging areas and trophic level, the influence of SST on mass on arrival must result from differences in resource quality or availability. This concurs with Dehnhard et al. (2015), who found that female southern rockhopper penguins at the Falklands were in better condition and produced heavier clutches when cooler conditions preceded the incubation period.

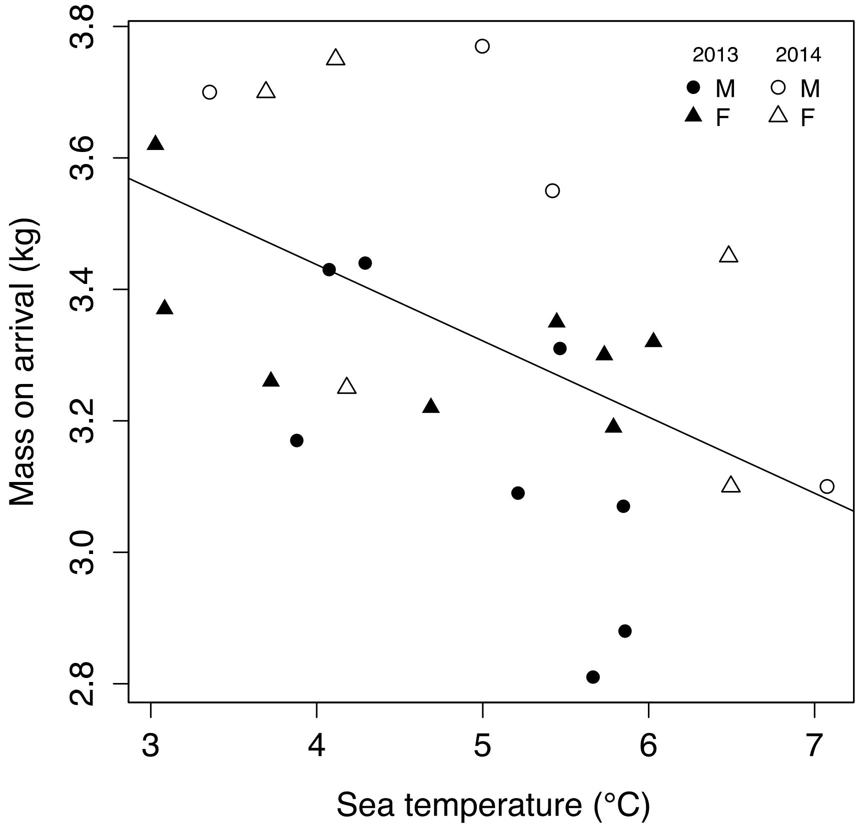


Figure 6.7. Mass on arrival of male (M) and female (F) rockhopper penguins in relation to sea temperatures encountered by penguins in October. Relationship is $y = -0.127x + 0.033$

The limited duration of this study (two years) makes it difficult to ascertain whether high individual variation in SST preferences among rockhopper penguins during late winter is a strategy to reduce intraspecific competition or whether the use of cooler waters by some individuals during this period reflects a recent response to increasingly poor foraging conditions in warmer waters. Further studies linking mass on arrival to conditions at foraging areas during late winter should be conducted over several years to allow for investigations of penguin responses to a wider range of environmental conditions.

Conclusions

During the core winter months, macaroni penguins from Marion Island forage in cooler waters near the SACCF compared to the warmer PFZ waters used by rockhopper penguins. This segregation reduces potential interspecific competition during a period when resources are scarce and potentially limiting to crested penguins. High spatial overlap and lack of niche partitioning during late winter, as inferred from stable isotopes, suggests that potential interspecific competition may occur if resources are limited. This emphasises the importance of the three-week delay in the return of rockhopper penguins to Marion Island, providing them with the opportunity to acquire sufficient resources for the upcoming incubation fast in the absence of potential competition with macaroni penguins. The influence of SST on the mass on arrival of rockhopper penguins suggests that resources in warmer waters are less profitable than in cooler waters, farther south. Given the apparent importance of mesoscale eddies and submesoscale filaments as foraging areas for both macaroni and rockhopper penguins, differences in the biological characteristics of such features in warmer versus cooler waters may explain observed differences in body condition. Further tracking and/or isotopic studies linking mass on arrival to conditions at foraging areas during late winter are needed to better understand if and how penguins might adapt to climate-driven changes in the

Southern Ocean. Future research should identify the fine-scale characteristics of eddies and filaments used by penguins to elucidate potential mechanisms behind such changes.

Supplementary material

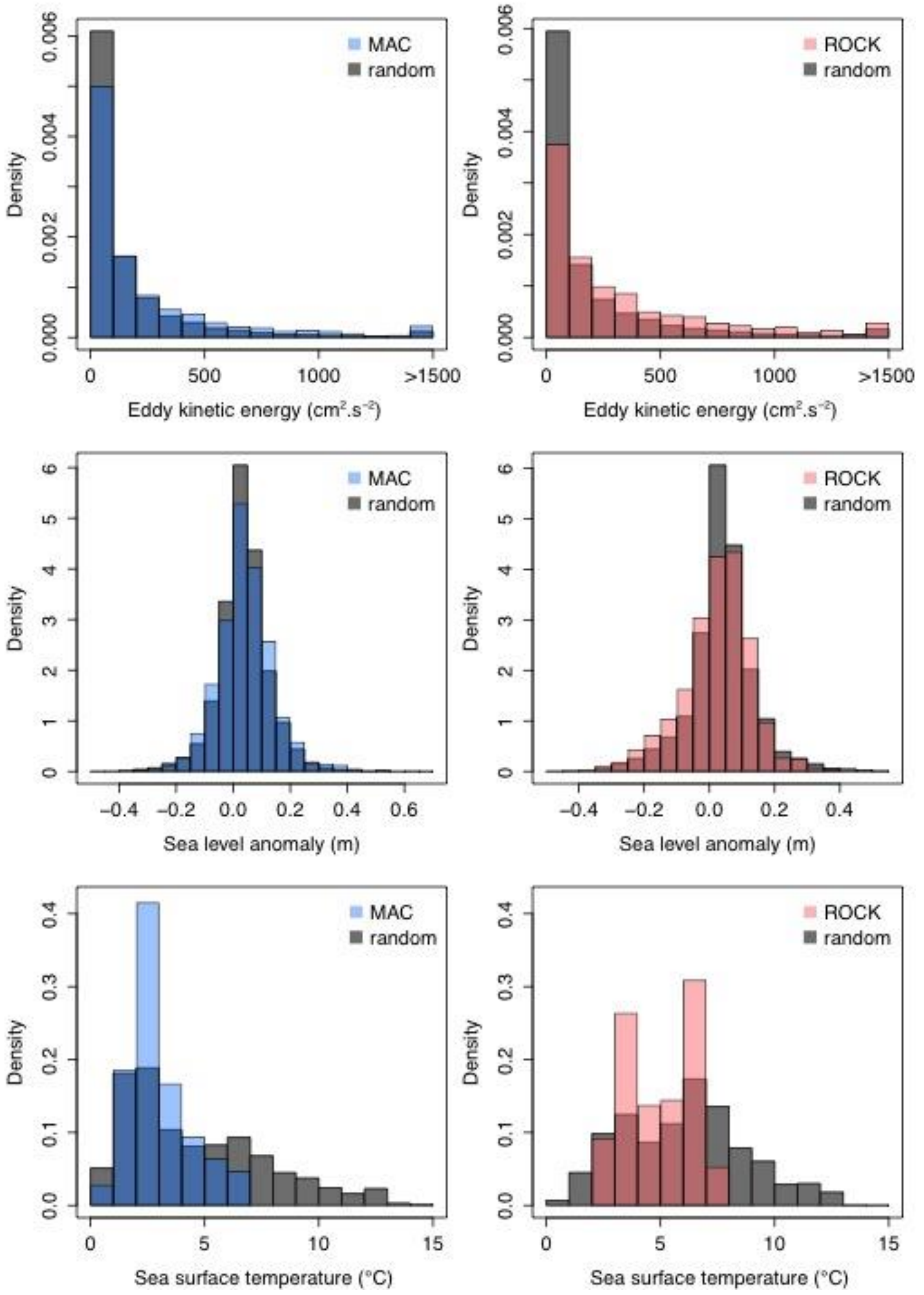


Figure S6.1. Frequency distributions of environmental covariates associated with original and random locations of macaroni (MAC) and rockhopper (ROCK) penguins during the winter period

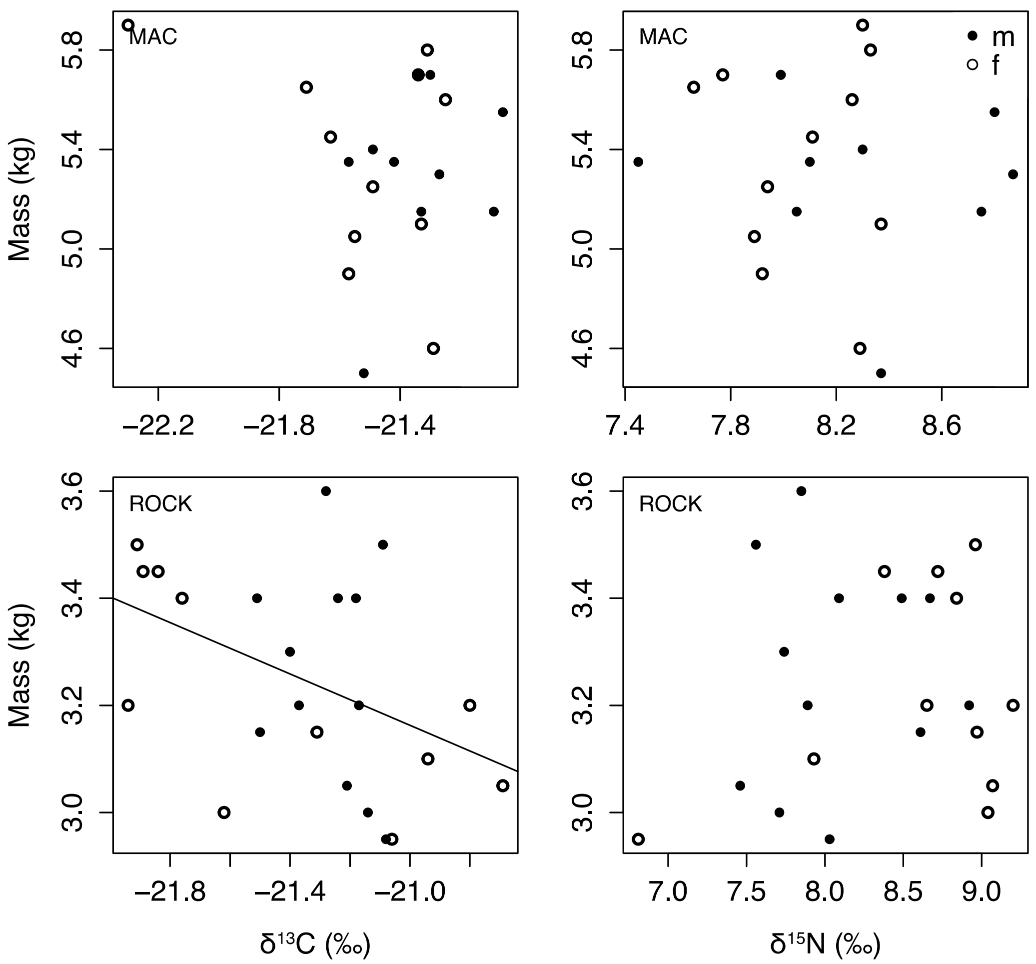


Figure S6.2. Mass of male (closed circles) and female (open circle) macaroni (MAC) and rockhopper (ROCK) penguins on arrival to Marion Island after the winter period in relation to carbon and nitrogen stable isotopes in erythrocytes. The only significant relationship was with $\delta^{13}C$ of rockhopper penguins ($y = -0.24x - 1.9$, $R^2 = 0.15$, $P < 0.05$)

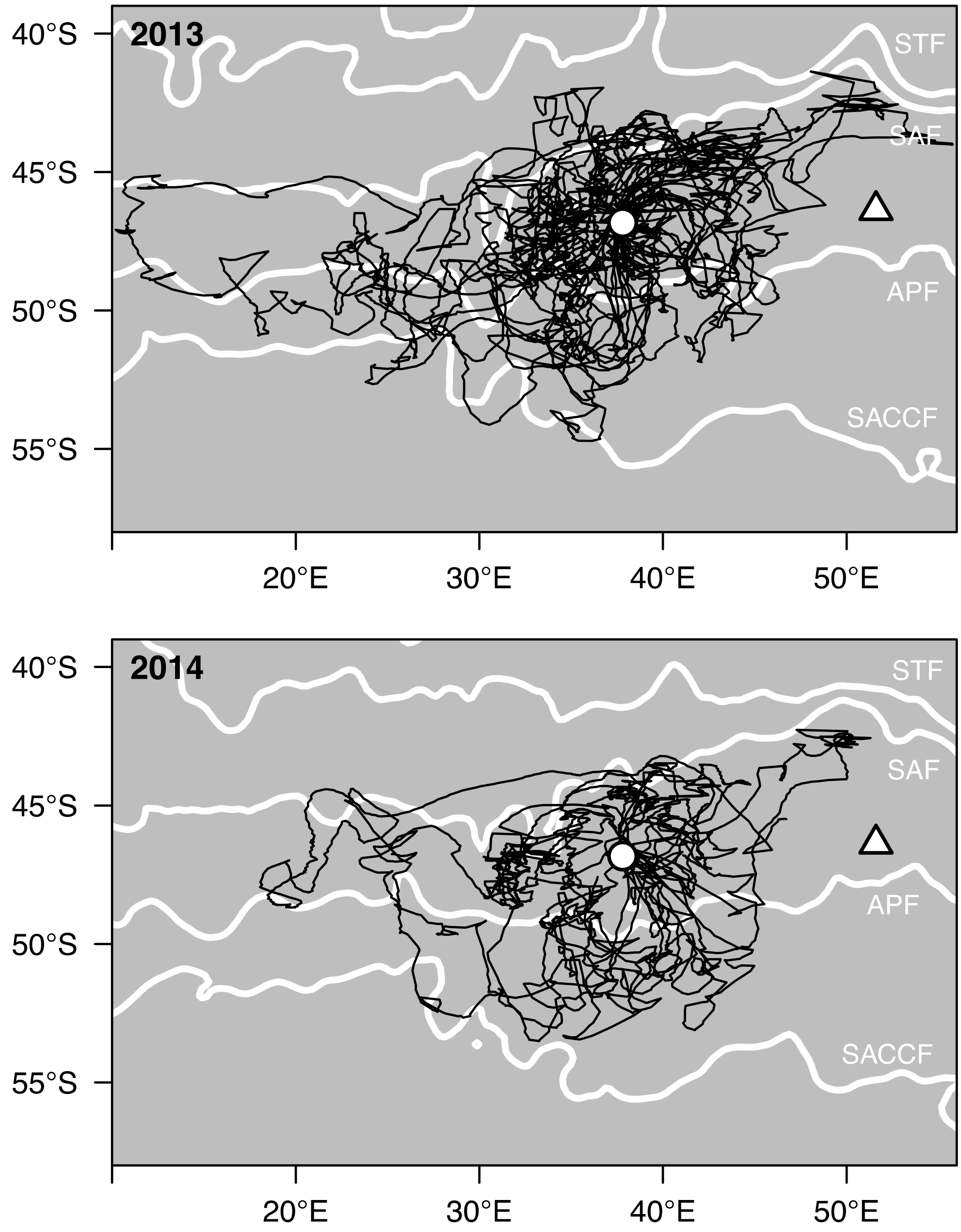


Figure S6.3. Winter movements of rockhopper penguins from Marion Island (white circle) fitted with geolocators. Positions of Crozet Islands (white triangle) and sub-Tropical (STF), sub-Antarctic (SAF), Antarctic Polar (APF) and Southern Antarctic Circumpolar Current Front (SACCF) are shown

Table S6.1. Environmental variables and sources (Abb.: Abbreviations)

Variable	Abb.	Spatial resolution	Temporal resolution	Source
Chlorophyll-a concentration (mg.m^{-3})	-	0.04° x 0.04°	Monthly	Aqua MODIS, NOAA[a]
Eddy Kinetic Energy (cm^{2}.s^{-2})	EKE	0.33° x 0.33°	Daily	Aviso[b]
Finite-size Lyapunov Exponent (d^{-1})	FSLE	0.01° x 0.01°	4-day	Aviso[b]
Sea level anomaly (m)	SLA	0.33° x 0.33°	Daily	Aviso[b]
Sea surface height (m)	SSH	0.33° x 0.33°	Daily	Aviso[b]
Sea surface temperature (°C)	SST	0.1° x 0.1°	Weekly	Reynolds, NASA[c]

[a] NOAA CoastWatch < http://coastwatch.pfel.noaa.gov>

[b] Aviso <http://www.aviso.oceanobs.com/duacs/>

[c] NASA PODAAC< https://podaac.jpl.nasa.gov/>

Table S6.2. Habitat selection models for macaroni and rockhopper penguins from Marion Island in winter

Species	**Model parameters**	**CV-mse**	**ΔCV-mse**
Macaroni penguin	s(SST) + s(SLA) + s(EKE) + filament	0.1267	0.0000
	s(SST) + s(SLA) + s(EKE)	0.1267	0.0000
	s(SST) + s(EKE) + filament	0.1268	0.0001
	s(SST) + s(EKE)	0.1268	0.0002
	s(SST) + s(SLA) + filament	0.1273	0.0007
	s(SST) + s(SLA)	0.1275	0.0008
	s(SST) + filament	0.1276	0.0010
	s(SST)	0.1278	0.0012
	s(SLA) + s(EKE) + filament	0.1366	0.0099
	s(EKE)	0.1372	0.0106
	s(SLA)	0.1384	0.0117
	NULL	0.1389	0.0122
Rockhopper penguin	s(SST) + s(SLA) + s(EKE) + filament	0.1268	0.0000
	s(SST) + s(SLA) + s(EKE)	0.1268	0.0000
	s(SST) + s(EKE) + filament	0.1277	0.0009
	s(SST) + s(EKE)	0.1277	0.0009
	s(SST) + s(SLA) + filament	0.1279	0.0011
	s(SST) + s(SLA)	0.1280	0.0012
	s(SST) + filament	0.1284	0.0016
	s(SST)	0.1285	0.0017
	s(SLA) + s(EKE) + filament	0.1335	0.0067
	s(EKE)	0.1342	0.0074
	s(SLA)	0.1378	0.0110
	NULL	0.1389	0.0121

Table S6.3. Habitat section model output for macaroni penguins during the winter period

Parametric terms	**Estimate**	**SE**	**z-value**	***P***
Intercept	-37.3	5	-7.5	< 0.001
Filament proximity	0.1	0.04	2.6	< 0.01
Smooth terms	**edf**	**Chi.sq**	***P***	
s(SST)	5	609.2	< 0.001	
s(SLA)	4.9	31.3	< 0.001	
s(EKE)	4.2	107.3	< 0.001	
Random effects	**edf**	**Chi.sq**	***P***	
s(ID)	5.9	17.9	< 0.05	
s(YEAR)	1.5	25.4	< 0.05	
Deviance Explained	13.50%			

Table S6.4. Habitat section model output for rockhopper penguins during the winter period

Parametric terms	**Estimate**	**SE**	**z-value**	***P***
Intercept	-13.1	0.9	-14.3	< 0.001
Filament proximity	0.1	0.06	2	< 0.05
Smooth terms	**edf**	**Chi.sq**	***P***	
s(SST)	5	282.5	< 0.001	
s(SLA)	3.9	66.9	< 0.001	
s(EKE)	4.2	124.7	< 0.001	
Random effects	**edf**	**Chi.sq**	***P***	
s(ID)	4	11.3	< 0.01	
s(YEAR)	0	0	0.84	
Deviance Explained	14.80%			

Table S6.5. Ranking of generalized least squares models of stable isotopes for each species in relation to selected variables according to Akaike's Information Criterion (AIC). The selected models are in bold

	Model	$\delta^{13}C$		$\delta^{15}N$	
		AIC	ΔAIC	AIC	ΔAIC
Winter	species	33.7	2.9	**76.7**	**0.1**
	sex	**30.8**	**0.0**	**76.6**	**0.0**
	species + sex	34.9	4.1	79.3	2.7
	species x sex	38.5	7.7	**76.6**	**0.0**
Summer	species	**-27.4**	**0.1**	80.8	4.6
	sex	**-27.5**	**0.0**	81.3	5.1
	species + sex	-26.2	1.3	**77.2**	**1.0**
	species x sex	-24.7	2.8	**76.2**	**0.0**

Table S6.6. Ranking of generalized least squares models of stable isotopes for each season in relation to selected variables according to Akaike's Information Criterion (AIC). The selected models are in bold

	Model	$\delta^{13}C$		$\delta^{15}N$	
		AIC	ΔAIC	AIC	ΔAIC
Macaroni	stage	**-0.4**	**0.0**	**57.6**	**0.0**
	sex	19.1	19.5	100.5	42.9
	stage + sex	3.6	4.0	60.2	2.6
	stage x sex	5.4	5.8	63.1	5.5
Rockhopper	stage	**26.7**	**0.0**	93.7	6.6
	sex	49.2	22.5	101.3	14.2
	stage + sex	31.6	4.9	97.1	10.0
	stage x sex	33.2	6.7	**87.1**	**0.0**

Table S6.7. Mass on arrival of crested penguins at Marion Island

Species	Stage	Sex	N	Mass (kg)	
Macaroni	Winter	Male	10	5.3 ± 0.3	4.5 - 5.7
		Female	11	5.4 ± 0.4	4.6 - 5.9
Rockhopper	Winter	Male	12	3.3 ± 0.2	3.0 - 3.6
		Female	11	3.2 ± 0.2	3.0 - 3.5

Table S6.8. Ranking of linear models of mass on arrival of macaroni and rockhopper penguins at the end of winter in relation to selected variables according to Akaike's Information Criterion (AIC). The selected models with $\delta^{13}C$ and $\delta^{15}N$ are in bold

Model	Macaroni		Rockhopper	
	AIC	ΔAIC	AIC	ΔAIC
sex	23.2	0.6	-4.7	4.6
C	22.6	**0**	-9.3	**0**
sex + C	24.6	2	-8.6	0.7
sex x C	24.6	2	-6.6	2.7
N	23	**0.4**	-5	**4.3**
sex + N	25	2.4	-3.8	5.5
sex x N	27	4.4	-2	7.3
N + C	24.6	2	-7.3	2
sex + N + C	26.5	3.9	-7.2	2.1

CHAPTER 7

Synthesis

Figure 7.1. How do these closely related species co-exist?

Key findings

The primary aim of this thesis is to compare the foraging ecology of macaroni and rockhopper penguins at Marion Island to identify how they partition resources to maintain co-existence, and to assess the conservation implications of this relationship in an era of rapid global change. These questions are particularly relevant given the relatively similar population sizes of the two species at the Prince Edward Islands (Table 7.1). Potential mechanisms of segregation are investigated throughout their annual cycle, including chick-rearing (Chapter 3), pre-moult (Chapters 4 and 5) and winter periods (Chapter 6).

Chapter 3 focuses on foraging strategies during the spatially constrained chick-rearing period. Both species forage in pelagic waters beyond the shelf break, except for rockhopper penguins at Ship's Cove that forage over the inter-island shelf. Most trips last < 3 d and are within 100 km of the island, but penguins occasionally perform long (5 to 14 d) self-provisioning trips up to 500 km south of the island to the APF during crèche. Due to the three-week difference in the onset of breeding, spatiotemporal overlap of foraging areas is minimal until rockhopper penguin chicks hatch. Thereafter, spatiotemporal overlap is high for six weeks until macaroni penguins leave the island for their pre-moult foraging trip. The inter-annual variation in diving behaviour revealed the importance of the Sub-Antarctic Front and local currents in determining local krill availability. Both species dive consistently to 40 – 60 m during years when the SAF is closer to the islands and geostrophic flow is enhanced. However, when the SAF is farther away, geostrophic flow is reduced and dive depths are deeper and more variable. During periods of reduced krill availability, the ability of macaroni penguins to dive deeper, for longer and more efficiently probably allows them access to more myctophid fish than rockhopper penguins, as confirmed by diet samples. This may help macaroni penguins to buffer environmental variability better than rockhopper penguins and potentially explains their lower rate of population decline relative to rockhopper penguins.

Chapter 4 reveals similar habitat preferences of macaroni and rockhopper penguins during the month-long pre-moult foraging trip, when both species forage mainly in Antarctic Zone waters downstream of the South-West Indian Ridge. This makes the three-week temporal segregation integral to reducing spatiotemporal overlap. Both species associate with mesoscale eddies and submesoscale filaments, providing further evidence for the importance of such features for predators in the Southern Ocean. The use of thermoclines by crested penguins is revealed for the first time, although they are more important for macaroni penguins that more often dive deep enough to reach the thermocline. When primary productivity at foraging areas is reduced, both species spend more time at sea before returning to moult.

Chapter 5 uses stable isotopes in feathers to investigate the trophic ecology of crested penguins during the pre-moult period. The consistent use of Antarctic Zone waters over five years supports findings from tracking data in Chapter 4. Species-specific spatial responses to changes in primary productivity are evident, with macaroni penguins travelling farther south in years of reduced productivity. This is likely linked to differences in dietary preferences, as macaroni penguins feed on higher trophic level prey – such as myctophid fish – compared to rockhopper penguins. Overall, crested penguins exhibit subtle but significant niche differentiation during the pre-moult period.

Chapter 6 investigates habitat preferences during winter when both species spend six months at sea. Macaroni penguins forage in cooler waters during the core winter months, minimising spatiotemporal overlap during the period of lowest prey availability. Both species associate with mesoscale eddies and submesoscale filaments, likely due to enhanced prey availability at these features. Stable isotopes reveal that both species spend the late winter months in Polar Frontal Zone waters where they feed at similar trophic levels, suggesting that interspecific competition may be high during late winter. However, the three-week difference in their dates of arrival to Marion Island reduces potential competition during the last few critical weeks when penguins undergo hyperphagia to accumulate sufficient energy stores for the upcoming incubation fast. Mass on arrival of macaroni penguins is not affected by sea surface temperature, but rockhopper penguins that forage in cooler waters farther south prior to arrival are heavier.

Mechanisms of segregation

Segregation may result from a combination of morphological, physiological and/or behavioural differences between species (Hutchinson 1957; Cody 1973). I briefly discuss differences in morphology and physiology before exploring the role of behavioural differences (diet, timing of breeding, diving behaviour and habitat preferences) in minimising interspecific competition and maintaining co-existence.

Morphology and physiology

Macaroni penguins are 70% larger in mass and have larger bills than rockhopper penguins. Larger bills may allow macaroni penguins to handle larger prey. Furthermore, the tip of the upper bill of macaroni penguins has a marginally more pronounced hook compared to rockhopper penguins (Fig. 7.2). The hooks of macaroni and rockhopper penguins are intermediate between Adélie penguins, which are krill-specialists, and *Spheniscus* penguins, which are fish-specialists (Fig. 7.2). The hook is thought to better equip penguins to handle fish. The larger and more hooked bills of macaroni penguins may therefore provide them with a morphological advantage when handling fish. Accurate measurements are required to confirm whether differences are significant, which could be performed using photogrammetry.

Figure 7.2. Bill morphology of Adélie (krill-specialist), Humboldt (fish-specialist), rockhopper and macaroni penguins (mixed-feeders). The edge of the upper bill tip is highlighted (white line). Photo credit: Photovolcanica and Otto Whithead

Animal physiology is closely linked to body size. Larger-bodied animals are able to load greater oxygen stores and have lower mass-specific metabolic rates (Schreer and Kovacs 1997). This accounts for the ability of macaroni penguins to dive for longer than rockhopper penguins and likely results in species-specific optimal foraging depths, such as with pygoscelid penguins (Wilson 2010). Contrasting body sizes may require different thermoregulatory mechanisms but there are no published studies on this topic for macaroni and rockhopper penguins. Little penguins *Eudyptula minor* are adapted to feeding in temperate waters and show signs of stress when subjected to cold water temperatures (Stahel and Nicol 1982). Below 10 °C, little penguins must dramatically increase internal heat production to maintain normal body temperature (~ 39 °C) and they start to lose body temperature in water < 5 °C (Stahel and Nicol 1982). This suggests that size-related thermoregulatory processes limit the southern distribution of little penguins (Stahel and Nicol 1982). Larger body size and increased ability to produce internal heat may therefore account for the ability of macaroni penguins to inhabit more southerly localities than rockhopper penguins, and may even explain cooler SST preferences during the six-month winter sojourn (Chapter 6). On land, however, larger-bodied macaroni penguin adults and chicks may be more susceptible to heat stress during elevated summer temperatures (Frost et al. 1976; Chappell et al. 1990). Penguin species living in warmer climates are either small or utilise shade (tussock/burrows/forest) to avoid hyperthermia. Given that macaroni penguins at Marion Island are at the northern limit of their distribution, continued increases in air temperatures (le Roux and McGeouch 2008) may impact breeding success. Being larger also means that macaroni penguins have higher daily energetic requirements (Brown 1986).

Diet

During the breeding season, macaroni and rockhopper penguins at Marion Island feed primarily on euphausiids *Euphausia vallentini* and *Thysanoessa vicina*, with varying proportions of fish and squid (Brown and Klages 1987; Crawford et al. 2003a, b). The main differences between the diets of the two penguins species are that macaroni penguins tend to feed on more fish and take a wider variety of prey taxa (Brown and Klages 1987; Cooper et al. 1990). However, rockhopper penguins feed on more benthic prey, such as nototheniids, which suggests that they also forage inshore. Previous studies have focused only on the diet of penguins on the east coast of Marion Island (Crawford et al. 2003a, b), but in recent years, samples have also been collected from penguins on the west coast. Preliminary analyses suggest that there are dietary differences between penguins on the east and west coasts (Bruce Dyer, DEA, pers. comm.), likely attributed to differences in prey availability. During the pre-moult period, stable isotope analyses revealed that macaroni penguins consistently fed on larger proportions of higher trophic level prey, such as myctophid fish. However, late winter (pre-breeding) diet was similar between species. Overall, it appears that macaroni penguins at Marion Island pursue a largely krill-based diet, supplemented by deeper-dwelling myctophids, whereas rockhopper penguins also primarily target krill but during the breeding season supplement their diet with neritic prey closer to shore. These subtle differences help to reduce direct competition between the two species. Essentially, if abundant krill stocks are available, both species should be able to co-exist without segregation. However, when krill stocks are limited, alternative foraging strategies should reduce interspecific competition.

Timing of breeding

The three-week difference in the breeding cycles of macaroni and rockhopper penguins at Marion Island is integral to minimising spatiotemporal overlap during late winter (pre-breeding), brood-guard/crèche, pre-moult and immediately following moult. This difference helps stagger peak energy requirements of rockhopper penguins so that they do not overlap with macaroni penguins. Allochrony appears to be consistent throughout the distribution of sympatric eudyptids (Table 7.1) and in other sympatric congeners, such as Adélie and chinstrap penguins (Trivelpiece et al. 1987).

Diving behaviour

Both species primarily forage at 40 to 60 m during chick-rearing and pre-moult periods, which likely reflects the vertical distribution of the main prey species, the euphausiids, during the day. One major difference between species is that macaroni penguins dive to deeper depths more often, which may provide them with access to a wider range of prey, including deeper-dwelling myctophid fish. Rockhopper penguins are likely unable to reach such depths due to size-related limitations in oxygen storage capacity, limiting dive duration (Schreer and Kovacs 1997). Diving behaviour varies between years, with both species diving deeper when krill availability is presumably reduced (Chapter 3). In such circumstances, the ability of macaroni penguins to pursue deeper prey may buffer them from fluctuations in environmental conditions, whereas rockhopper penguin populations may be more susceptible to changes.

Habitat preferences

During the pre-moult period, both species forage in cooler waters (3-4 °C) up to 1000 km south of Marion Island where they associate with mesoscale eddies and submesoscale filaments. Such features are also important during winter but macaroni penguins generally forage in cooler waters (~ 3 °C) near the SACCF compared to rockhopper penguins that forage in warmer PFZ waters (5-6 °C). These contrasting SST preferences may be related to different thermoregulatory processes associated with body size differences. Stable isotope analyses indicate that both species forage in PFZ waters during late winter, perhaps driven by seasonal shifts in prey availability. When provisioning chicks, both species target pelagic waters beyond the shelf break but macaroni penguins forage slightly farther offshore than rockhopper penguins. Rockhopper penguins at Ship's Cove, however, forage over the inter-island shelf in water < 200 m deep. This highlights the ability of rockhopper penguins to forage in a range of marine environments. The shorter trips performed by rockhopper penguins at Ship's Cove indicate better foraging conditions over the inter-island shelf perhaps linked to the availability of different prey and reduced intra- and/or interspecific competition.

There are some lessons to be learnt from the distribution of penguin colonies around their breeding islands. Macaroni penguins generally nest in larger colonies (e.g. Kildalkey and Bullard North which together support > 85 % of the population at Marion Island) with relatively easy beach access, whereas rockhopper penguins nest in smaller colonies scattered along steeper, less accessible stretches of coast. The location of breeding sites may, to some extent, be related to competitive interactions, with the larger macaroni penguins outcompeting rockhopper penguins for preferred nesting sites. However, it more likely reflects at-sea habitat preferences, as penguins should theoretically nest as close as possible to preferred foraging areas to minimise energetic costs associated with travelling. The fact that macaroni penguins are virtually absent from the coasts bordering the inter-island shelf suggests that they much prefer access to deeper waters beyond the island shelf. Rockhopper penguins on the other hand are more flexible. Colony sizes may also reflect carrying capacity of nearby waters (Ballance et al. 2011), with deeper open ocean waters supporting higher prey biomass and renewal rates. Breeding in different areas may reduce spatial overlap between species, but only when foraging ranges are highly restricted, such as with cormorants along the coasts of temperate North America (Cody 1973). The broader context of breeding site preferences and its role in spatial segregation is discussed under *habitat preferences* in the next section.

Co-existence of sympatric eudyptids in a global context

If populations of < 1000 pairs are ignored, there are only eight localities where two species of crested penguins co-exist (Table 7.1); Diego Ramirez and Ildefonso Archipelagos (macaroni and southern rockhopper penguins), Prince Edward Islands, Crozet Archipelago, Kerguelen Archipelago, Heard and McDonald Islands (macaroni and eastern rockhopper penguins), Macquarie Island (royal and eastern rockhopper penguins) and the Antipodes Islands (erect-crested and eastern rockhopper penguins). In all cases sympatry involves a large species and a small species, with the larger species being more numerous at most localities (Table 7.1). This is likely due to the larger species outcompeting the smaller species for preferred nesting sites. For example, rockhopper penguins at Kerguelen, Antipodes and Marion Island often breed at the periphery of colonies of the larger species (Weimerskirch et al. 1988; Sagar et al. 2005; pers. obs.).

Diet

Dietary comparisons of sympatric eudyptids are only available at four localities: Marion, Crozet, Heard and Macquarie Islands (Fig. 7.3). At all localities, the larger macaroni/royal penguins consume a greater diversity of prey taxa – indicating access to a wider range of prey – and a larger proportion of fish (Cooper et al. 1990). The larger macaroni and royal penguins also feed on larger sizes of myctophid fish and consume species that rockhopper penguins did not (Cooper et al. 1990). For instance, at Heard Island, the large icefish *Champsocephalus gunnari* was regularly consumed by macaroni penguins but was absent from the diet of rockhopper penguins (Klages et al. 1989). Although differences in the proportions, types and/or sizes of fish consumed by sympatric eudyptids suggest that dietary segregation exists, the large majority of the diet consists of euphausiids of similar sizes and species (Cooper et al. 1990). This has led previous studies to conclude that dietary segregation of sympatric eudyptids is incomplete, and that either resources are not limited or other factors must contribute towards reducing interspecific competition and maintaining co-existence (Brown and Klages 1987; Cooper et al. 1990).

Table 7.1. Populations of sympatric eudyptids at localities where numbers of both species > 1000 pairs. Data presented is for brood-guard only. Mean dive depth is for dives > 10 m, unless otherwise stated ([a] for dives > 5 m, [b] for dives > 6 m)

Locality	Species	Population (pairs)	Hatching date	Trip duration (d)	Range (km)	Mean dive depth (m)	References
Ildefonso	Macaroni	5,660	-	-	-	-	Kirkwood et al. (2007)
	Southern rockhopper	86,400	-	-	-	-	
Diego Ramirez	Macaroni	15,600	-	-	-	-	Kirkwood et al. (2007)
	Southern rockhopper	132,721	-	-	-	-	
Prince Edward Islands	Macaroni	302,000	10-Dec	1.2 ± 0.7	47 ± 7	55 ± 12	Crawford et al. (2009); Present study
	Eastern rockhopper	80,000	30-Dec	0.8 ± 0.6	35 ± 15	48 ± 10	
Crozet Islands	Macaroni	2,200,000	18-Dec	1.2 ± 0.8	32 ± 18	54 ± 19	Jouventin et al. (1984); Tremblay and Cherel (2003); Bon (2016)
	Eastern rockhopper	152,800	8-Jan	0.5 ± 0.2	-	40 ± 18[a]	
Kerguelen Islands	Macaroni	1,812,000	7-Jan	2.0 ± 0.9	82 ± 41	51 ± 21	Weimerskirch et al. (1988); Tremblay and Cherel (2003); Bon (2016)
	Eastern rockhopper	85,000	21-Jan	0.5 ± 0.1	-	29 ± 14[a]	
Heard and McDonald Islands	Macaroni	1,000,000	20-Dec	1.0 ± 0.7	47 ± 40	36 ± 13	Deagle et al. (2008); BirdLife International (2017a, b)
	Eastern rockhopper	10,000	-	-	-	-	
Macquarie Island	Royal	850,000	1-Dec	4.5 ± 1.1	-	33 ± 26[b]	Copson and Rounsevell (1987); Hull (1997, 2000, 2004); BirdLife International (2017b)
	Eastern rockhopper	37,500	20-Dec	6.4 ± 4.5	-	27 ± 20[b]	
Antipodes Island	Erect-crested	34,226	-	-	-	-	Sagar et al. (2005); Hiscock and Chilvers (2014)
	Eastern rockhopper	2,475	10-Dec	1.4 ± 0.4	36 ± 10	-	

Timing of breeding

At most localities where information on breeding phenology is available, it appears that the smaller rockhopper penguins breed two to three weeks later than the larger species (Table 7.1). This corresponds to the duration of the brood-guard period (Brown 1987a; Hull 1997) and staggers peak energy demands of rockhopper penguins to minimise competitive overlap, similar to the allochrony observed in sympatric Adélie and chinstrap penguins (Trivelpiece et al. 1987). Interestingly, Warham (1972) noted a correlation between the date at which rockhopper penguins started breeding and the local sea temperature at each locality (Fig. 7.4). The two outliers of this relationship are Marion and the Falkland Islands. At Marion Island, rockhopper penguins breeding later than predicted by this relationship, possibly due to competition with the more abundant macaroni penguins (Brown 1987a). At the Falkland Islands, rockhopper penguins breed earlier than predicted by this relationship, possibly due to the absence of a larger eudyptid species.

Diving behaviour

At all localities where the diving behaviour of sympatric eudyptids has been studied, the larger species dives deeper on average (Table 7.1). This is because the larger species performs a greater proportion of deeper dives but there is generally still considerable overlap in vertical habitat use. Deeper dives are likely linked to the pursuit of deeper-dwelling myctophid fish.

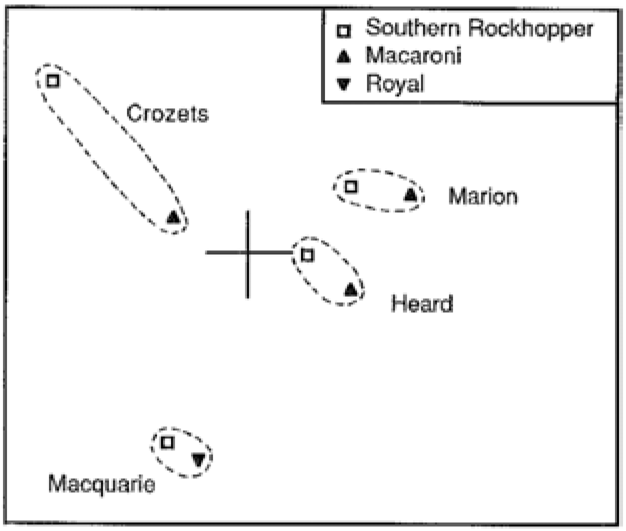


Figure 7.3. Correspondence analysis plot comparing the diets (presence/absence of prey taxa only) of sympatric crested penguins at studied breeding localities. Increasing distance reflects increasing differences in the diet composition (reproduced directly from Cooper et al. 1990).

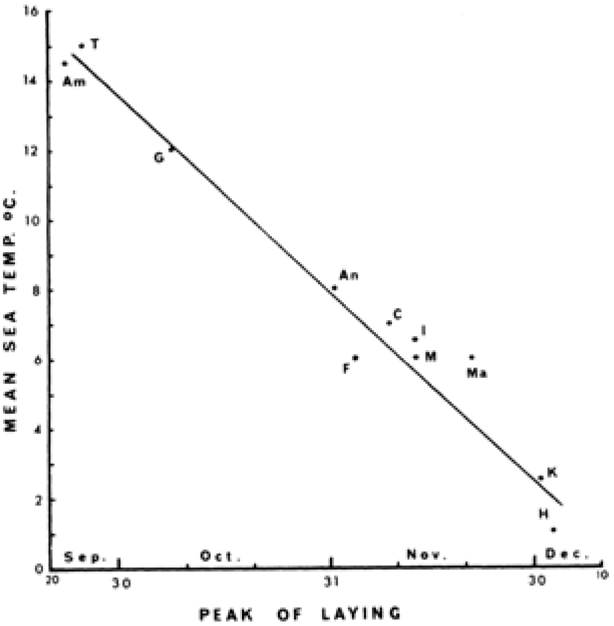


Figure 7.4. The relationship between the date of peak egg laying by rockhopper penguins sensu lato and mean annual sea temperature. Am, Amsterdam Island; An, Antipodes Island; C, Campbell Island; F, Falklands Islands; G, Gough Islands; H, Heard Island; I, Ildenfonso Island; K, Kerguelen; M, Macquarie Island; Ma, Marion Island; T, Tristan da Cunha (Warham 1972)

Habitat preferences

During the pre-moult period, macaroni penguins at Marion, Crozet and Kerguelen Islands forage in cooler waters 3 – 4 °C (Chapter 4). At Marion Island, macaroni and rockhopper penguins have similar habitat preferences, however, this is the only locality where pre-moult comparisons have been made. Further studies are required to confirm whether rockhopper penguins at other localities have similar habitat preferences to macaroni penguins during this stage, or whether this scenario is unique to crested penguins at the Prince Edward Islands owing to the elevated mesoscale activity and productivity in the lee of the South-West Indian Ridge (Chapter 4).

Winter tracking of macaroni and rockhopper penguins at the Crozet, Kerguelen and Prince Edward Islands suggest they have inherently different SST preferences (Thiebot et al. 2011, 2012, 2013; Chapter 6). However, although macaroni penguins at South Georgia segregate completely from rockhopper penguins from a colony in the north Falklands, they share winter foraging areas with southern rockhopper penguins from a colony in the south Falklands (Ratcliffe et al. 2014). The latter scenario suggests that spatial constraints linked to colony location play a greater role here than competition in deciding the best areas in which to forage. The fact that rockhopper penguins generally breed at localities closer to the SAF relative to macaroni penguins that occupy more southerly localities, further suggests that there are inherently different SST preferences between species. This may be driven by thermoregulatory processes, as maintaining body temperature in cooler waters may be too costly metabolically for the smaller-bodied rockhopper penguins.

During the breeding season, the larger *Eudyptes* species generally tends to have a larger foraging range, suggesting a preference for more distant/pelagic waters (Table 7.1). This may also be related to larger colony sizes of macaroni/royal penguins that deplete nearby resources, enhancing potential intraspecific competition and forcing penguins to travel farther to find profitable prey patches. Looking at the distribution of macaroni penguins in relation to local bathymetry, it appears that they depend on access to pelagic waters beyond the shelf break. For instance, there are few macaroni penguins that breed at the inter-island shelf at Marion Island and none at Prince Edward Island (Fig. 2.5). Additionally, the macaroni penguin colonies at the Kerguelen Islands are all located along the open coast, with most on capes at the four corners of the archipelago (Fig. 7.5; Weimerskirch et al. 1988). Furthermore, distance to the shelf edge was the single most important factor explaining the foraging distribution of macaroni penguins at the Kerguelen Islands (Thiebot et al. 2011). Contrastingly, rockhopper penguins feed in a wider variety of habitats, including pelagic and neritic zones (Weimerskirch et al. 1988; Tremblay and Cherel 2003; Chapter 3). At Kerguelen Island, most rockhopper penguin colonies are located in bays and fjords (Weimerskirch et al. 1988), where they feed primarily on *E. vallentini* (which is also the main prey item of macaroni penguins; Tremblay and Cherel 2003). So why don't macaroni penguins also breed in the bays and fjords? Perhaps the prey concentrations in shelf waters are insufficient to sustain the larger energy requirements of macaroni penguins, and therefore it is the lower energy requirements of rockhopper penguins that allow them to exploit such habitats during the breeding season.

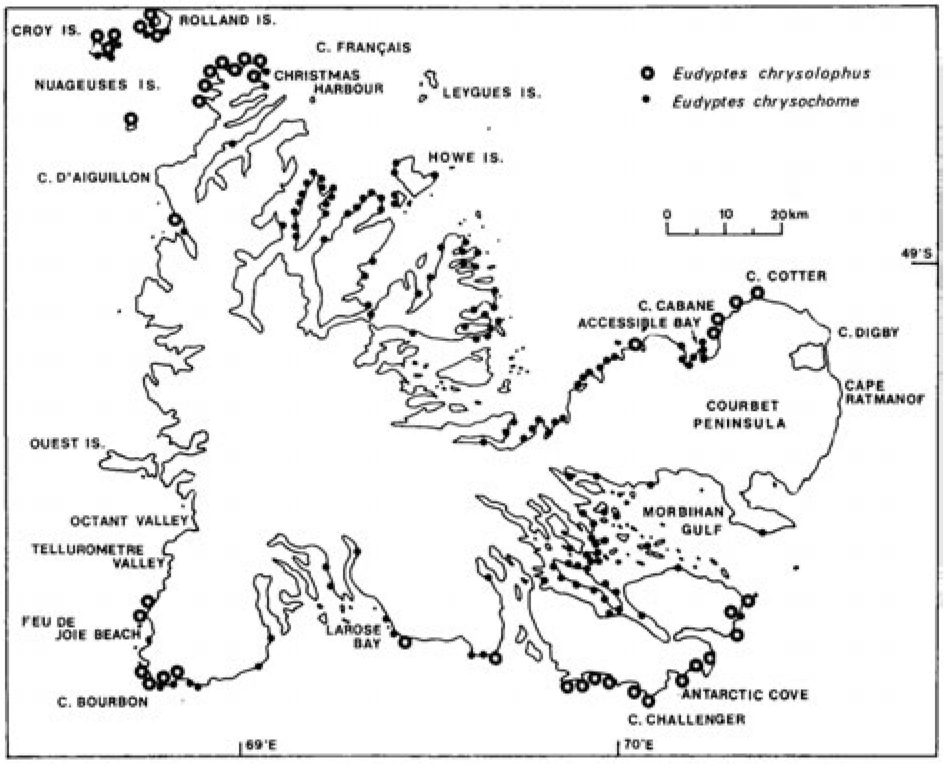


Figure 7.5. Distribution of penguins and albatrosses at the Kerguelen Islands (Weimerskirsch et al. 1988). Note the different breeding sites of macaroni and rockhopper penguins

Overall, it seems that the larger species travels farther, dives deeper and feeds on more fish. The higher energetic requirements of the larger species likely limit breeding sites to stretches of coast in close proximity to shelf breaks, beyond which resource availability and renewal is generally higher. Conversely, the lower energy requirements of rockhopper penguins allows them to exploit a wider range of environments, including neritic and pelagic zones. These behavioural differences, combined with partial allochrony, appear to be sufficient to reduce competitive overlap to the extent that reproductive performance is sufficient to maintain stable populations of both species. Environmental and human-induced pressures on resource availability may, however, have shifted the ecological balance between species.

Population drivers of crested penguins

Top-down processes

Predators may impact penguin populations through predation of adults, chicks and/or eggs. At the Prince Edward Islands, predators of crested penguins include brown skuas *Stercorarius antarcticus*, southern/northern giant petrels *Macronectes* spp., killer whales *Orcinus orca*, and Antarctic *Arctocephalus gazella* and sub-Antarctic *A. tropicalis* fur seals. The extent to which killer whales predate on crested penguins is unknown but the affect at the population level is likely negligible (Reisinger 2015). Fur seals have been observed predating on penguins in shallow waters when penguins arrive back from foraging trips during the summer, but they seldom actually eat the penguins (pers. obs.). Sub-Antarctic fur seals are the main cause of adult mortality at several rockhopper penguin colonies at Campbell Island (Morrison 2015). The diet of giant petrels at Marion Island is dominated by crested penguins during the breeding season (Hunter and Brooke 1992) but the extent to which this impacts crested penguin populations at the island has not been assessed. At South Georgia, recent population increases of giant petrels are correlated with decreases in the survival of juvenile and adult macaroni penguins (Horswill et al. 2015). At Marion Island, the diet of brown skuas consists primarily (68-75 %) of penguin eggs and chicks, whereas at Prince Edward Island > 96 % of the diet consists of burrowing petrels (Ryan et al. 2009; Cerfonteyn and Ryan 2016). The differences are attributed to contrasting burrowing petrel densities, as the introduction of feral cats in the 1950s led to the decimation of the burrowing petrel population at Marion Island (Schramm 1986; Dilley et al. 2016). At Macaroni Bay on Marion Island, a recent increase in skua predation has reduced the breeding success of the small macaroni penguin colony to zero (pers. obs; DEA, unpubl. data), indicating that skuas can have a large influence on breeding success at least at a local scale. At Macquarie Island, reproductive failure of rockhopper penguins occurs primarily during incubation, with most eggs lost to brown skuas (Hull 2004). Fledging success is also correlated with the position of the nest in the colony, with penguins more likely to successfully raise offspring from centrally-located nests (Hull 2004). It is possible that at Marion Island, the dietary shift of skuas from burrowing petrels to crested penguins may have contributed to poor reproductive success and observed population declines. It is also important to note that macaroni and rockhopper penguins may experience contrasting predation pressures. Macaroni penguins are larger and nest in large, dense colonies, so may be better able to fend off predators. However, their colonies are more exposed than most rockhopper penguin colonies, which often nest in rockier areas that might offer greater protection from skuas. The contrasting nesting preferences may influence the ability of skuas and/or giant petrels to prey on eggs, chicks and/or adults. Future studies should investigate the impact of land-based predators on macaroni and rockhopper penguins at Marion Island.

Bottom-up processes

In the coming decades, rising temperatures, retreating sea ice and ocean acidification are expected to considerably alter Antarctic and sub-Antarctic marine ecosystems (Harley et al. 2006). Such changes will influence currents and primary productivity, with important knockon effects for higher trophic level organisms. Understanding how these changes influence populations of marine top predators is critical to the development of efficient conservation measures (Lewison et al. 2012).

Sea surface temperatures at the Prince Edward Islands increased by 1.4 °C from 1950 to 2000 (Fig. 7.6; Melice et al. 2003). The average position of the SAF has shifted farther south and intrusions of warmer waters have become more common (Hunt et al. 2001; Pakhomov et al. 2004). As a consequence, primary productivity over the inter-island shelf has decreased (Allan et al. 2013). This has led to changes in the diet of the decapod shrimp *Nauticaris marionis* (Allan et al. 2013) that has in turn become less prominent in the diet of inshore-feeding gentoo penguins and Crozet shags *Leucocarbo melanogenis* (Crawford et al. 2014; Carpenter-Kling 2015). In the offshore zooplankton community, sub-tropical and sub-Antarctic species have become more common, linked to increased intrusions of warmer waters (Pakhomov et al. 2000). This includes the euphausiid *E. vallentini* (Hunt and Pakhomov 2003), a main prey species of macaroni and rockhopper penguins (Brown and Klages 1987).

Recent declines of macaroni and rockhopper penguins at the Prince Edward Islands suggest that foraging conditions have deteriorated but the environmental drivers and the mechanistic links involved are not well understood. Here I briefly discuss some of the insights I have gained into the potential drivers of population dynamics and foraging behaviour of crested penguins at the Prince Edward Islands.

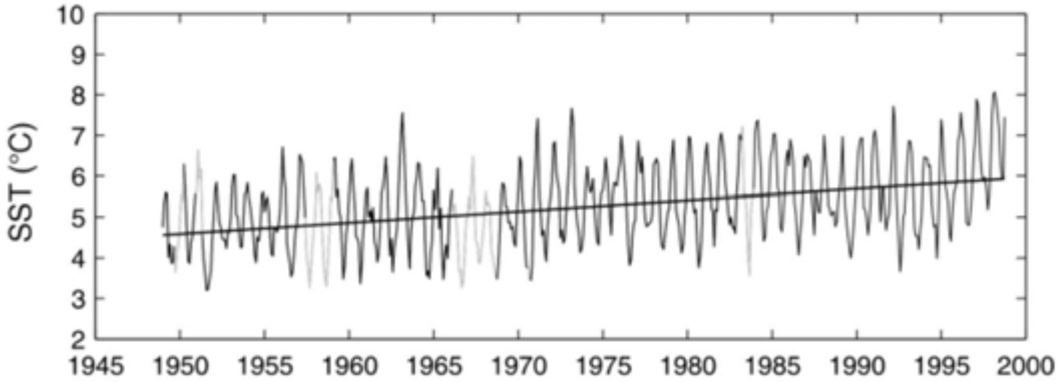


Figure 7.6. Monthly sea surface temperatures at Marion Island. The breaks in the record, which have been re-constructed, are plotted in grey (Mélice et al. 2003)

The most dramatic declines in populations of macaroni and rockhopper penguins at the Prince Edward Islands occurred in the 1990s and early 2000s (Fig. 7.7), similar to gentoo penguin and Crozet shag populations (Fig. 7.8). From the mid-2000s, population trends of all four species have been relatively stable (Figs. 7.7 and 7.8). In contrast to the inshore- and mixed-feeding seabirds, populations of offshore-feeding and far-ranging king penguins, albatrosses and petrels have remained stable or increased (Allan et al. 2013). This suggests that drivers of crested penguin declines at the Prince Edward Islands are local and likely relate to fluctuations in the positions of the SAF and APF, which drive macro- and mesoscale processes in the vicinity of the Prince Edward Islands (Ansorge et al. 2009).

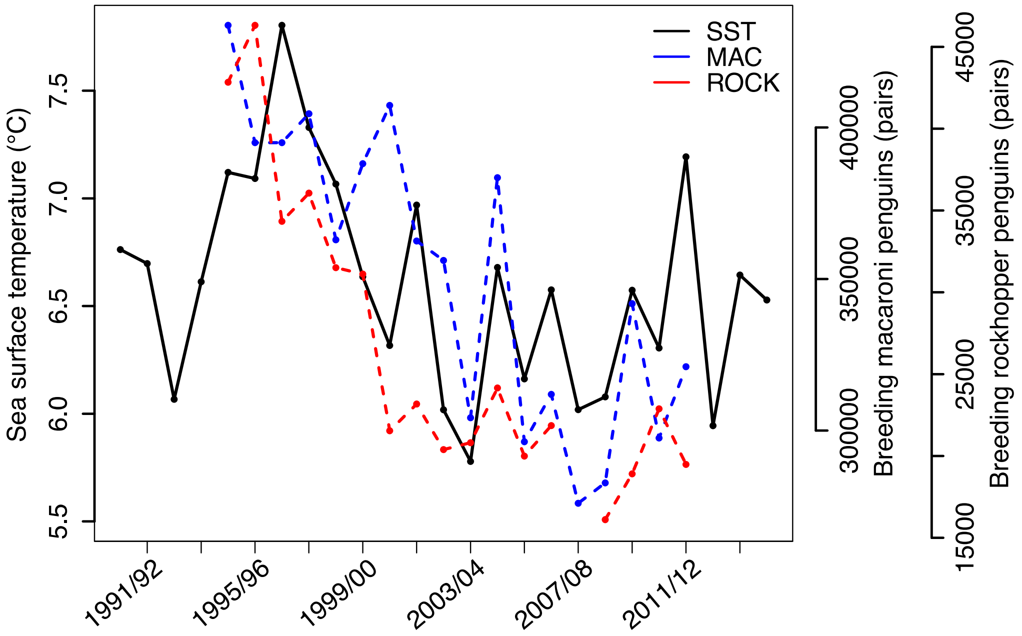


Figure 7.7. Mean sea surface temperatures (SST; Reynold's weekly) during December and January and numbers of macaroni (MAC) and rockhopper (ROCK) penguins that initiated breeding. Only rockhopper penguins in regularly counted management zones are considered (DEA, unpubl. data)

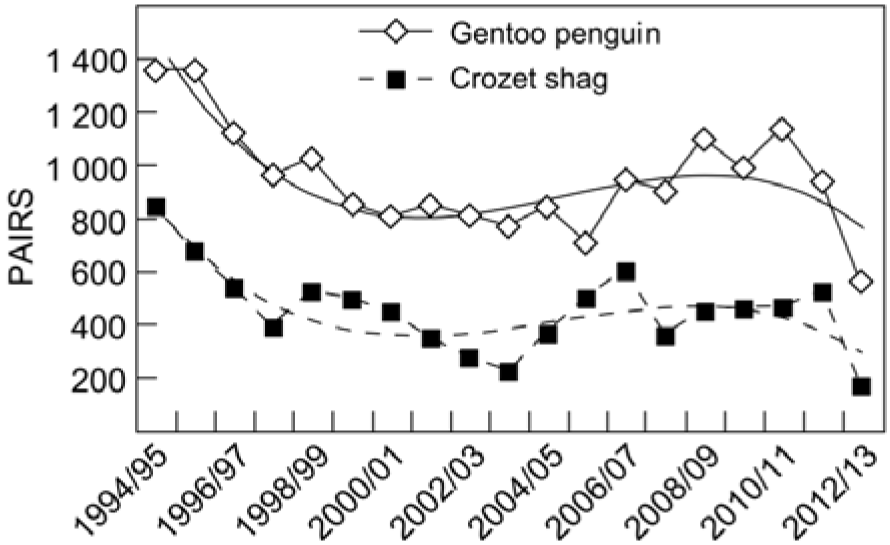


Figure 7.8. Trends in numbers of gentoo penguins and Crozet shags breeding at Marion Island, 1994/1995–2012/2013. The best-fitting third-order polynomial regressions are shown (Crawford et al. 2014)

During late winter (pre-breeding period), crested penguins must accumulate sufficient resources to endure the incubation fast and, for females, invest energy into egg production. Previous studies have identified the link between mass of rockhopper penguins on arrival and the number of birds that initiate breeding and breeding success (Crawford et al. 2006, 2008). No such trends have been observed for macaroni penguins. This suggests that environmental conditions at foraging areas prior to the arrival of rockhopper penguins influences their population dynamics. It also suggests that macaroni and rockhopper penguins either forage in different areas during late winter or that environmental conditions impact each species differently. Given that stable isotope analyses revealed that both species foraged in PFZ waters during late winter (Chapter 6), the latter scenario is more plausible. Rockhopper penguins, however, exhibited high individual variability in foraging strategies during late winter (Fig. 6.3). Those that foraged in cooler waters farther south were heavier on arrival, suggesting that foraging conditions were better in such waters. It is unknown whether this is natural variation or whether it is a recent response of some individuals to deteriorating foraging conditions in warmer waters. Continued monitoring of winter foraging is necessary to determine how penguins respond to a wider range of environmental conditions during late winter.

The fact that the reproductive success of macaroni and rockhopper penguins has been below a threshold required to maintain a stable population (Crawford et al. 2003a, b) suggests that, together with poor foraging conditions during late winter, resource availability during the chick-rearing period has been poor. Deployments of GPS-TDR units were only carried out over three breeding seasons, and mainly during short periods in the guard stage, but environmental conditions were sufficiently variable to investigate drivers of variation in diving behaviour. During the two years when warmer conditions associated with the close proximity of the SAF persisted, both species dived more efficiently and fed primarily on euphausiids compared to the other year (Chapter 3). This suggests that such conditions benefit penguins, possibly due to an increased advection of *E. vallentini* to the islands (Hunt and Pakhomov 2003). This may, however, be related to the increased geostrophic flow that coincided with such conditions. Ultimately, these processes are intertwined and it is difficult to tease apart single drivers. Further studies are required to determine whether warm conditions will continue to benefit crested penguins, as this is contrary to what is expected. Warmer waters are often associated with lower primary productivity and have been suggested as the main driver of population declines of rockhopper penguins throughout their range (Cunningham and Moors 1994; Hilton et al. 2006). However, at South Georgia, recent local warming has had a positive effect on the survival of adult macaroni penguins (Horswill et al. 2014).

Beyond the breeding season, macaroni and rockhopper penguins exhibited contrasting responses to changes in primary productivity during the pre-moult period. Macaroni penguins travelled farther and spent more time at sea during less productive years, whereas rockhopper penguins spent more time at sea but only travelled farther in one of three less productive years (Chapters 4 and 5). This has consequences for adult survival, as penguins must return to shore before they start moulting. When they spend more time at sea during years of reduced productivity they risk having to return to shore without sufficient energy reserves to survive the moult. Indeed, the annual survival of adult rockhopper penguins at the Falklands is linked to sea temperatures during the pre-moult period (Dehnhard et al. 2013).

Future changes in the carrying capacity at pre-moult foraging areas may have implications for adult survival of crested penguins at the Prince Edward Islands. Given the predicted southward shift in the position of the APF (Hunt et al. 2001; Downes et al. 2011) and the strong SST preferences of both species during the pre-moult period (Chapter 4), penguins will have to travel farther south to locate preferred foraging areas. This is predicted for king penguins that depend on myctophids near the APF to provision offspring (Le Bohec et al. 2008; Peron et al. 2012; Bost et al. 2015).

One of the novel findings in this thesis was the association of macaroni and rockhopper penguins with mesoscale and submesoscale features. These play an important role in structuring prey in the pelagic marine environment and likely serve as predictable foraging areas for penguins. It is unknown how such features will be influenced by the predicted changes in the Southern Ocean, but it seems likely that any changes will affect crested penguins.

Implications for conservation management

With the continued exploitation of krill and fish stocks in the Southern Ocean, it is vital that fishing activity in ecologically important areas is well managed to help ensure the preservation of sufficient resources to sustain marine predator populations. The only active fishery within the Prince Edward Island's Exclusive Economic Zone in recent decades is the demersal longline fishing for Patagonian toothfish *Dissostichus eleginoides*. Extensive illegal fishing took place until 1996, when sanctions were put in place to try curb and monitor catches (Ryan et al. 1999). Although this fishery negatively affected many albatrosses and petrels via bycatch, there were few penguin mortalities (Ryan et al. 1999; Nel et al. 2002). Until recently, there was no formal protection of the waters around the Prince Edward Islands, but in 2013, the Prince Edward Islands Marine Protected Area (MPA) was established, making it South Africa's first offshore MPA. The MPA management plan includes a 40-km radius Strict Nature Reserve (IUCN Category Ia) around the islands (Fig. 7.9; Lombard et al. 2007), which encompasses the mean foraging ranges of both macaroni and rockhopper penguins during the chick-rearing period, but many penguins still forage outside of this area. Ideally, the existing 40 km radius should be extended to at least 60 km during the core summer months (December to February) to help conserve resources for penguins near the islands. However, such a measure does not consider that planktonic prey is advected from upstream of the islands via currents and eddies (Ansorge et al. 2009). Most of these eddies travel to the islands from the southwest (Durgadoo et al. 2010), an area that falls under the Abyss Strict Nature Reserve and Conservation Zone set out in the Prince Edward Islands MPA plan (Fig. 7.9), therefore providing adequate preservation of such resources. The pre-moult foraging areas identified in this thesis do not fall within the MPA, but they do fall within the jurisdiction of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and as such are reasonably well managed. This helps ensure that fisheries do not impact on the penguins' ability to accumulate sufficient resources for a successful moult and survival into the winter period. Foraging areas during winter are spread out over a vast area but the most critical stages are immediately following the moult and prior to arrival back at the islands. Following the moult, both species utilise similar foraging areas to pre-moult. Prior to arrival, both species forage in PFZ waters, presumably near or to the north of the islands, which falls within the broader MPA. Overall, crested penguins at the Prince Edward Islands do not face any immediate pressures from fisheries but rather face global threats such as climate change, which are hard to address at a local level.

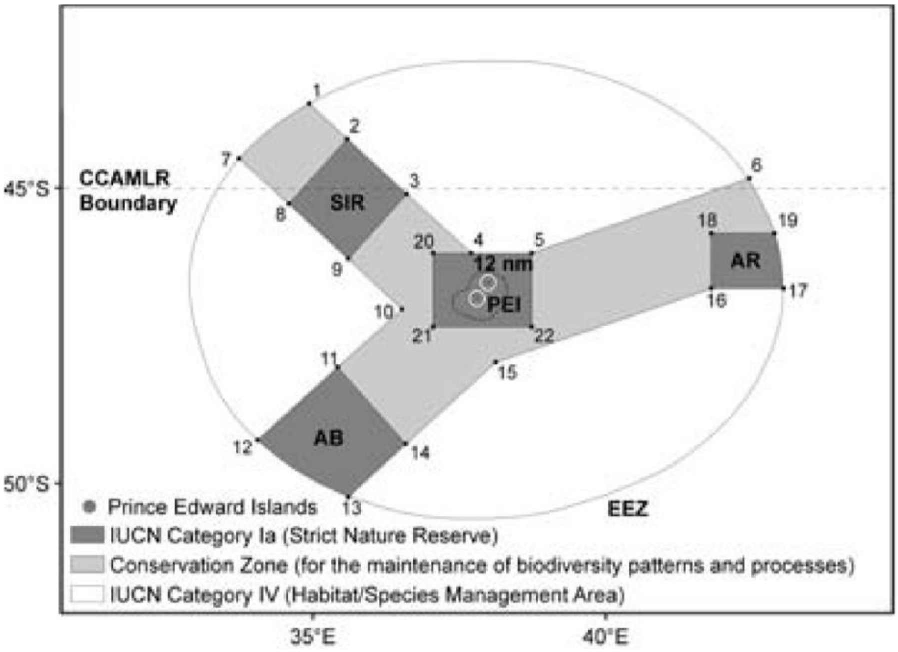


Figure 7.9. Prince Edward Islands (PEI) Marine Protected Area management plan (Lombard et al. 2007). SIR = South-West Indian Ridge, AB = Abyss, AR = Africana II Rise

Future research

The opportunity to intimately explore the at-sea lives of crested penguins at the Prince Edward Islands has revealed a complexity far beyond what I could have imagined. There are so many unknowns and so much exciting research to be done, especially given that technology is evolving so rapidly and opening up the doors to address questions that, in the past, were the stuff of dreams.

Is there fine-scale spatial segregation during January?

One of the drawbacks of this study was the poor temporal resolution of GPS data recorded during the chick-rearing period, which precluded investigations of fine-scale habitat preferences and the quantification of spatiotemporal overlap during January; the period of highest potential overlap between species. Simultaneous deployments on macaroni and rockhopper penguins are needed to investigate the potential for fine-scale spatiotemporal segregation during this period, when macaroni penguins provision large chicks (crèche) and rockhopper penguins provision small chicks (brood-guard). Such a study may reveal inshore foraging strategies of rockhopper penguins. To acquire data with a sufficiently high temporal resolution, rapid acquisition devices that use Fastloc technology (Sirtrack and Wildlife Computers) could be used, but this comes at a substantial financial cost.

Density-dependent competition and spatial variation

The role of competition in structuring the life history characteristics of animals is an important field of research in ecology. Evidence of interspecific competition is hard to come by. One way to identify competition is to ask: how does behaviour change when competitors occur at different densities or when they are entirely absent? Case studies on Galapagos finches (Grant and Grant 2006) and coal tits *Parus ater* in Sweden (Norberg and Norberg 2015) indicated that after congeneric species were removed, remaining congeners increased in population size and expanded their niche to use resources previously usurped by the other species. To some degree, I investigated differences in the behaviour of rockhopper penguins in relation to contrasting densities of macaroni penguins (Funk Bay, very high; Swartkops, medium; Ship's Cove, low) but different marine environments at each site prevented the attribution of behavioural differences to varying degrees of competition. Given the uneven distribution of crested penguins around Marion Island (Figs. 2.5, 2.9), it appears that, together with the coastal geology influencing suitable landing sites and breeding areas, the interactions of currents with local bathymetry must aggregate prey at different concentrations, leading to variable carrying capacities between colonies. For instance, the concentration of euphausiids at the inter-island shelf is considerably lower than near the shelf break or in deeper waters offshore (Hunt et al. 2001). This may explain the relatively small numbers of penguins that breed near the inter-island shelf. In contrast, the waters beyond the shelf break south of the island must have relatively high prey concentrations as this stretch of coast supports > 85 % of macaroni and > 30 % of rockhopper penguins breeding at Marion Island. In addition to contrasting prey availability and environmental conditions, different stretches of coast probably have varying degrees of inter- and intraspecific competition. For instance, rockhopper penguins breeding on the southeast coast should theoretically be more affected by competitive interactions with macaroni penguins than those on the west coast where numbers of each species are similar. To date, there have been no studies on the breeding chronology and success of penguins on the west coast. This information is vital to gauge the influence of competitive interactions on the life history traits of rockhopper penguins at the island. For instance, do rockhopper penguins on the west coast breed earlier than those on the east coast due to reduced competition with macaroni penguins during the guard stage? Is the breeding success of rockhopper penguins better on the west coast? Census data do not reveal any obvious differences in population trends between west and east coasts (DEA, unpubl. data) but these questions need to be explored. Interestingly, the number of rockhopper penguin pairs breeding in regularly counted areas adjacent to the inter-island shelf declined by 71 % between 1994/95 and 2012/13, whereas those located opposite open ocean coasts declined by only 30 % (DEA, unpubl. data). However, when total counts of the island population are considered, shelf and open ocean colonies declined at similar rates (66 % and 61 %, respectively; DEA, unpubl. data). Altogether, a better understanding of island-wide breeding success and chronology is needed. During the course of this thesis I initiated a study to investigate differences in breeding chronology and success between the west and east coast using remote timelapse cameras, which will hopefully continue well into the future. This technique is being used to study the breeding chronology and success of pygoscelid in Antarctica (Southwell and Emmerson 2015) and there are sites that have been set-up throughout the sub-Antarctic and Antarctic (penguinlifelines.org, Tom Hart, Oxford University, UK). Maintenance of time-lapse cameras is only needed every few months (sometimes up to a year) and data can be efficiently analysed using citizen science and machine learning.

Animal-borne cameras

The recent miniaturization of animal-borne cameras has provided researchers with a new tool with which to study the foraging behaviour of marine animals. The increased sensitivity of camera sensors has also improved low-light performance, allowing still imagery and videos to be captured at deeper depths. In seabirds, animal-borne cameras have been used to study interactions with prey (Takahashi et al. 2008; Thiebot et al. 2016), individuals of the same species (Takahashi et al. 2004; Handley et al. 2016), individuals from different species (Sakamoto et al. 2009) and fisheries (Votier et al. 2008). To expand on questions in this thesis, animal-borne cameras attached to macaroni and rockhopper penguins may reveal unique insights into foraging behaviours and intra- and interspecific interactions at sea (Fig. 7.10). For instance, do macaroni and rockhopper penguins encounter each other at sea? Do they feed on the same prey patches? Do they have contrasting preferences for krill swarm densities? Deploying animal-borne camera loggers on macaroni and rockhopper penguins at the Prince Edward Islands would most certainly yield some interesting results. Furthermore, at-sea footage could be combined with land-based video to provide informative science communication videos about the at-sea lives of these fascinating creatures.

Figure 7.10. Selected camera images from Takahashi et al. (2008) obtained from gentoo penguins foraging at King George Island showing encounters with benthic krill swarms (a), other individuals (b-g) and pelagic krill (h-i)

Final comments

In summary, it appears that subtle differences exist to minimise competitive overlap between macaroni and rockhopper penguins. A three-week difference in the onset of breeding staggers the peak energy demands of rockhopper penguins and minimises competitive overlap with macaroni penguins during late winter, incubation, brood-guard/crèche, pre-moult and post-moult stages. Macaroni penguins generally breed at more southerly localities and forage in cooler waters during winter compared to rockhopper penguins. Macaroni penguin breeding colonies are typically located near shelf breaks with close access to oceanic waters whereas rockhopper penguins also forage in shallow shelf waters. The larger-bodied macaroni penguins are capable of diving deeper, for longer and more efficiently than rockhopper penguins, which increases their behavioural flexibility and fitness by minimising stresses associated with reduced krill availability. These differences in diving behaviour and contrasting responses to environmental variation may explain the different rates of population decline at the Prince Edward Islands, and suggests that rockhopper penguins may continue to decline at a faster rate than macaroni penguins if ongoing climate change continues to reduce prey availability around the Prince Edward Islands.

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